The Genetics of Growth and Wood Density in Sitka Spruce

Estimated Using Mixed Model Analysis Techniques

by

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DECLARATION

This thesis has been carried out by myself and has not been submitted for any previous application for a degree. All information and assistance obtained from any other sources has been acknowledged in the appropriate places.

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ABSTRACT

This study estimated the variance and covariance components for growth (height and diameter) and wood density within a randomly selected population of Sitka spruce (*Picea sitchensis*, (Bong.) Carr.) trees known to derive from a single origin. Open-pollinated progeny from the original ortets had previously been planted in a replicated trial and assessed periodically for height, diameter and wood density (indirectly using the Pilodyn) from 1 to 19-years old; 23-year diameter was collected during the study period. Increment cores were also collected from a representative sub-sample of trees identified using a genotypic selection ellipse. Ring-by-ring wood density analysis was carried out using X-ray densitometry.

Variance and covariance components for all height, diameter and wood density assessments were estimated using Restricted Maximum Likelihood (REML).

Family heritability for growth traits varied little over a 23-year period (1-year height = 0.61; 23-year diameter = 0.57). Individual tree heritability was more variable reaching a peak at 7-year height (0.38) and then falling with age to 17-year diameter (0.12). Optimum family and individual tree selection ages for growth were found to be 5-year and 9-year height (breeding goal of 23-year diameter), and 3-year and 7-year height (breeding goal of 40-year diameter) from planting respectively; the latter were estimated with the use of a Lambeth regression equation.

Wood density was found to be more heritable than growth at equivalent ages, although estimates decreased with increasing age (individual tree heritability of the outer 4 rings at 9 and 22-years old of 0.85 and 0.34 respectively). Precision and accuracy of estimated variance components and heritabilities were unacceptable unless the traits used to calibrate the selection ellipse were included as covariates. Genetic correlations between all juvenile ring-groupings and the selection goal (outer 4-rings at 22-years from planting) were near unity. The optimum family and individual tree selection age for wood density was found to be the outer 4-rings at 9-years from planting.

REML was used to investigate the genetic correlation between genotypic values for wood density and growth traits measured on the original ortets and grafted-ramets

in a clone-bank, with breeding values of the same traits measured in progeny tests. Analysis was initially at a pilot study level, and subsequently for the randomly selected population. The investigation of the randomly selected population found ortet height (adjusted for height above sea level) to be strongly correlated with progeny breeding values for 23-year diameter and 9-year height ($r_{g,\ BV}$ = 0.95 and 0.93 respectively) and grafted-ramet wood density to be well correlated with progeny breeding values for juvenile wood density (0.58) and 23-year diameter (-0.45). The study indicates the potential of combining progeny test data with certain alternative data sources in order to increase the precision of estimated variance components and breeding values for growth and wood density.

The genetic correlation of wood density (assessed using the Pilodyn or X-ray densitometry) with 23-year diameter is strongly negative ($r_{g,\ BV}$ = -0.81 and -0.80 respectively). A 5% selection differential for 9-year height causes the outer 4-rings at ages 9 and 22-years to fall by 2.5% and 1.1% respectively, demonstrating the problems of attempting concurrent improvement of growth and wood density.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

LIST OF COMMONLY USED ABBREVIATIONS

ASReml	A Spacial Restricted Maximum Likelihood
AiReml	Average Information Restricted Maximum Likelihood
BLP	Best Linear Prediction
BLUP	Best Linear Unbiased Prediction
BS	British Standard (eg BS4978)
BV	Breeding Value
cm	Centimetre
cm^3	Cubic centimetres
DM	Diameter in centimetres (cm)
DM__	Diameter in centimetres (cm) at a specific age from planting e.g. DM10 = diameter (cm) 10-years from planting, DM23 = diameter (cm) 23-years from planting
DN	Density in kg m^{-3}
DN17	Density in millimetres assessed indirectly at 17-years from planting using the Pilodyn gun
FIC	Forestry Industry Council
g	Grams
GBP	General Breeding Population
GxE	Genotype x environment interaction
ha	Hectares
HT	Height in centimetres (cm)
HT__	Height in centimetres (cm) at a specific age from planting e.g. HT01 = height (cm) at age 1-year from planting, HT09 = height (cm) 9-years from planting
ID	Identification number. Unique number to identify each tree during analysis with ASReml
JDF	Job Description File
kg	Kilogram
km	Kilometre
m	Metre
m^3	Cubic metres
mm	Millimetre
MM	Mixed Model
MMA	Mixed Model Analysis
NC	North Carolina
NRS	Northern Research Station, Forest Research, Forestry Commission
PROC GLM	Procedure General Linear Model (within SAS)

PROC MEANS	Procedure Means (within SAS)
PROC REG	Procedure Regression (within SAS)
OFI	Oxford Forestry Institute
QCI	Queen Charlotte Islands
REML	Restricted Maximum Likelihood
RG	Ring-groupings (in years since planting)
RG__	Ring-grouping over a specific range of years e.g. RG19-22 = ring-grouping of years 19-22 from planting
SC	Strength Class; goes from SC1 to SC5, SC5 = strongest
SD	Standard Deviation
SE	Standard Error
SLM	Standard Linear Model
SPP	Single Plant Plot
TIB	Tree Improvement Branch
UK	United Kingdom
USA	United States of America
yr	Year

LIST OF COMMONLY USED SYMBOLS

b_{YX}	Correlated response in Trait Y following selection for Trait X
CG_m	Correlated gain for mature trait
$COV_{A_1A_2}$	Covariance of Trait A_1 and Trait A_2
d	Delay between selection and production of sufficient propagules to allow establishment of new genetic tests
G_m	Genetic gain of the mature trait
h	Square root of the heritability
h_f^2	Family-mean heritability
h_i^2	Single tree heritability
h_j^2	Single tree heritability of the juvenile trait
h_m^2	Single tree heritability of mature trait
I	Index value
i_j	Selection intensity of the juvenile trait
i_m	Selection intensity of the mature trait
k	Intrinsic maximum growth rate
l	Mean growth loss due to extraneous factors
$\log_e$	Natural logarithm
n	Number of trees per family
N	Number of familes
Q_{gen}	Generation efficiency relative to direct selection for the breeding goal
Q_{year}	Efficiency of correlated response relative to direct selection expressed in terms of gain per year
r	Correlated coefficient
r_A	Additive genetic correlation
$r_{g,\ BV}$	Genetic correlation between genotypic values and breeding values
r_P	Phenotypic correlation
T_j	Selection age (of juvenile trait)
$(T_j + d)$	Generation interval
Trait X	Trait subject to direct selection
Trait Y	Trait subject to indirect selection
σ^2_A	Additive genetic variation
$\sigma^2_{A_j}$	Additive genetic variance of the juvenile trait
$\sigma^2_{A_m}$	Additive genetic variance of mature trait
σ^2_e	Environmental variation

σ_f^2	Variation between family means
σ_{fr}^2	Family by replication interaction
σ_{fs}^2	Family by site interaction
σ_G^2	Genetic variation
σ_{NA}^2	Non-additive genetic variance
σ_P^2	Phenotypic variance
σ_{P_m}	Phenotypic standard deviation (of mature trait)
$\sigma^2_{P_m}$	Phenotypic variance (of mature trait)
σ_w^2	Independent random environmental effect
$>$	Greater than
$<$	Less than
$\leq$	Equal to or less than
$\not>$	Must not be greater than

CHAPTER 1

Introduction, Literature Review and Objectives

1.1 GENERAL INTRODUCTION

The within-provenance genetic improvement of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Britain commenced in 1963 with the selection of good quality phenotypes known as plus-trees (Fletcher and Faulkner, 1972). Planting of field-based half-sibling (half-sib) progeny tests to determine the breeding value (BV) of selected plus-trees commenced in 1967 and continued through to 1993 (Lee, 1993). The main objective of the Sitka spruce breeding programme remains to develop populations well adapted to a range of site-types, with improved stem-form and growth potential and wood qualities satisfactory for the sawn-timber market (Lee, 1993).

The initial selection intensity for plus-trees was very high at one tree every 15-20 ha; (Lee, 1993). Selection was for vigorous, straight, disease free individuals (Fletcher and Faulkner, 1972). Identification of progeny with above average growth rate (height or diameter), stem-straightness and wood density has been followed by re-selection amongst the original parent plus-trees (backward selection) for inclusion in either the (i) General, (ii) High Straightness, (iii) High Vigour or (v) High Density breeding populations (Lee, 1995). Estimates of BVs for the original plus-trees are based on the mean performance of the progeny across a number of forest sites. Mean progeny performance is always compared to that of a standard unimproved Queen Charlotte Islands (QCI) direct import stock, the most commonly planted origin of Sitka spruce (see 1.2.1 below) which is planted as a control in every test. In this way BVs are expressed relative to the QCI control.

The general purpose General Breeding Population (GBP) is the most advanced of the above breeding populations in terms of selection of tested genotypes. The maximum economic gain from first generation production populations of the GBP is predicted at 24.7% for end-of-rotation volume, 16.3% for stem-straightness and -0.5% for wood density (Lee, 1995).

Work carried out by Gill (1987) and Wood (1986) suggests that the best indicator traits and earliest selection ages for mid-rotation volume and whole-tree wood density are 6-year height and the weighted density of rings 11-15 (from the pith) at breast height respectively. Wood (*op. cit.*) also found the density of rings 11-15 to be well correlated with the pin penetration of a Pilodyn gun fired into 15-year-old trees at breast height. The Pilodyn is effectively a gun which fires a blunt pin into the tree with a fixed force. The penetration of the pin is measured in millimetres. The Pilodyn can be used as a fast, non-destructive, indirect assessment of wood density since the further the pin penetrates the wood, the less dense is the timber. Following the work of Wood (*op. cit.*), Pilodyn assessment in progeny tests at 15-years from planting became the routine method of indirectly assessing wood density in the Sitka spruce breeding programme (Lee, 1992).

Whilst the genetic and phenotypic correlations (r_A and r_P respectively) of wood density and vigour with stem-straightness are close to zero (Lee, 1993 and 1995), there is a strong negative correlation between whole tree density and diameter for a given age (r_P = −0.34 to −0.69, Wood 1986; r_A = −0.66, Lee 1995). Concurrent improvement of diameter and wood density through selection and breeding is therefore very difficult.

A further frustration for the tree breeder is the 9-year delay between indirect selection of the best families for mid-rotation volume (6-year height) and wood density (15-year Pilodyn). The rate of generation turn-over would be substantially improved if suitability for timber quality could be reliably assessed at an age closer to 6-years rather than 15-years from planting.

1.2 LITERATURE REVIEW

1.2.1 Sitka spruce and its uses

The principle forestry species in Britain is Sitka spruce (Forestry Industry Council, 1995; Forest Enterprise, 1996). The species is native to the Pacific North West of Canada and USA where it extends over a narrow coastal strip from Kodiak Island, Alaska to Mendocino Country, California; a range of nearly 3,000 km (Lines, 1987). Extensive origin trials within Britain have demonstrated that seed collected from the mid-range QCI (British Columbia, Canada) is the best adapted over most of upland Britain. Faster rates of growth can be obtained from planting more southern origins on sites where there are no problems with autumn frost (Lines, 1964; Fletcher, 1992).

Sitka spruce thrives better than any other common conifer on the majority of moist, exposed sites available for afforestation in upland Britain where yields range from 6-24 m^3 ha^{-1} yr^{-1} (Crowther *et al.*, 1991), leading to optimum economic rotation lengths of 35-70 years (Hamilton and Christie, 1971). The species produces a clear white wood which, due to its long fibres (Rydholm, 1965) and low resin content and other extractives, makes it a preferred wood for high quality mechanical pulp used in newsprint and other paper products (Harding, 1988). However, it is intended that the largest potential market for the sawlog-dimension Sitka spruce timber coming from British forests will be the construction market (Forest Industry Council, 1995). In order to be acceptable for this market, Sitka spruce must satisfy certain strength grading rules as determined using calibrated Machine Strength Graders (BS4978, 1988). BS5268: Part 2 (1987) defines a series of 5 strength classes (SC) for softwoods; SC1 through to SC5 with SC5 being the most demanding. Most commercial grades of structural softwoods including Sitka spruce fall into SC3 and SC4 (general carcassing and trussed rafters respectively). There is little possibility of Sitka spruce ever satisfying SC5 (Thompson, 1992), but since there is little market demand for SC2, the strength of Sitka

spruce should not be allowed to drop below SC3. The emphasis should be on growing Sitka spruce with strength properties similar to imported whitewood (Harding, 1988).

1.2.2 Wood density of Sitka spruce

Wood density is an indication of the amount of wood substance contained in a dry piece of wood and as such it is a good indicator of the over-all strength of a piece of timber (Elliott, 1970; Zobel and Talbert, 1984). It is calculated as the ratio of oven-dry weight to green volume and is therefore measured in kg m^{-3} or g cm^{-3} (Zobel and Jett, 1995). The higher the value of wood density the less 'void' or air there is within the wood.

Wood density is not a simple characteristic but is a complex of the effect of several growth and physiological variables compounded into one index (Elliott, 1970). Variations in cell wall thickness and cell diameter in particular determine the value of wood density.

The wood density of Sitka spruce was found by Brazier *et al.* (1976) to be around 340 kg m^{-3}. This is considered low compared to UK grown conifers such as Scots pine (*Pinus sylvestris*; 420 kg m^{-3}), Douglas fir (*Pseudotsuga menziesii*; 410 kg m^{-3}) and European larch (*Larix decidua*; 450 kg m^{-3}) (data from Lavers, 1983). Further, wood density is not a fixed value within a tree; it varies considerably from year to year and also within the material laid down in each year.

1.2.2.1 Juvenile and mature wood

The first 12 to 15 annual rings laid down from the pith in any position in a Sitka spruce tree are collectively referred to as juvenile wood (Brazier, 1972). Larson (1969), preferred the term crown-formed wood to juvenile wood in recognition of the close proximity of the wood to the foliage or crown of the tree. Juvenile wood is continuously produced by the tree, and the rings near the pith show similar characteristics up the entire

tree. For this reason, some authors prefer the term core wood as better reflecting the more or less cylindrical core of juvenile wood in the tree (Zobel, *et al.*, 1959).

Regardless of the terminology, it is clear that the characteristics of the juvenile wood are different and inferior to the mature wood which subsequently forms; mean density is lower, fibre length is shorter and grain inclination is greater (Brazier, 1972; Zobel, *et al.*, 1972; Pearson and Gilmore, 1980). These are all features which reduce the final strength of a piece of timber (Thompson, 1992).

Several studies have observed the same general trend for within-tree variation of Sitka spruce wood density from the pith to the cambium e.g. Bryan and Pearson (1955), Brazier (1967) and Wood (1986). In each case the density is actually at its highest for the first 5 years or so, then falls quickly to a minimum between 10 and 15 years. Density starts to rise again and becomes stable between 12 to 15 years. At this point the period of juvenile wood is thought to have ended and growth has entered the mature phase. A similar trend in variation of density from pith to bark was found in white spruce (*Picea glauca* (Moench) Voss) by Talyor, *et al.* (1982). Bryan and Pearson (1955) found that, although strength was proportional to wood density, there was a superimposed trend of increasing strength with distance from the pith, i.e. the high density of the early rings did not have corresponding high strength.

Variation in wood density can be high during the juvenile wood stage. Using figures presented by Brazier (1967) and assuming a 'mean' mature wood density of 340 kg m^{-3} as found by Brazier *et al.* (1976), annual ring density can vary from > 400 kg m^{-3} at about 3-years-old to nearly 300 kg m^{-3} at 10-years-old before climbing to 340 kg m^{-3} about 15-years-old after which there is little change in density from ring to ring.

1.2.2.2 **Within ring variation**

The generally low density of juvenile wood is associated with a period of rapid growth of the tree. Growth rate also varies within the growing season which has an effect on the density of the wood laid down. Cells with large lumens and thin walls, referred to as earlywood (or springwood), predominate during the vigorous growth early in the growing season. The proportion of small lumen, thick walled cells referred to as latewood (or summerwood) is small by comparison although it does increase with age, thereby increasing the overall ring density as it enters the mature wood phase (Brazier, 1977).

Authors have often had problems in deciding when earlywood ends, and latewood begins. The most universally accepted definition of latewood was made by Mork (1928). He stated that cells are latewood when twice the cell-wall thickness is greater than the lumen size. Many people ignore this definition or find it unworkable. Brazier (1970) found that if he adopted the Mork definition for young, vigorous-growth Sitka spruce a large number of rings would have no latewood at all. He needed some distinction between first and later-formed wood in the growth ring and arbitrarily selected a rise to a density of 400 kg m^{-3} as a boundary figure. Brazier (1977) stated that as more Sitka spruce trees are planted per hectare, the competition between trees increases. This has the effect of reducing the proportion of earlywood, increasing the proportion of latewood and advancing the age when mature wood density is reached. Brazier (1970) found the effect of increased vigour on wood density to be the same with both juvenile and mature wood; in each case there was an increase in the width of the earlywood without a corresponding increase in the amount of latewood, resulting in a fall of overall ring density.

Brazier (1967) studied samples of rings 21-25 from the pith, taken from plantation grown trees which would be considered as mature wood at conventional spacings. He found that within a given annual ring, density can vary over a wide range from a

minimum of 140 to 220 kg m^{-3} in the earlywood zone to a maximum 540 to 750 kg m^{-3} in the latewood.

1.2.2.3 Desirable wood density features within a tree

Since the wood density of Sitka spruce is already relatively low, it follows that silviculture and tree breeding should prevent it falling further if the final product is to meet construction grade timber quality. In practical terms, Thompson (1992) proposed that it is more important to increase wood density in the juvenile phase only. This is because modern sawing patterns often lead to construction sawnwood being taken from the centre of sawlogs, making it impossible to avoid juvenile wood. A greater proportion of the final-crop tree will consist of juvenile wood as either rotation lengths are reduced following improved silviculture and tree breeding techniques (Hibberd, 1991) or crops are switched to no-thin regimes (Brazier and Mobbs, 1993). This problem is not unique to Sitka spruce, but is common to plantation grown softwoods such as loblolly pine in south-eastern USA (*Pinus taeda*; Loo, *et al.*, 1985; Williams and Megraw, 1994) and Douglas fir in Canada (King, *et al.*, 1988; Loo-Dinkins and Gonzalez, 1991). In this regard tree breeders can help by selecting for trees that have higher density during the juvenile wood stage and trees that make the transition to mature wood at an earlier age (Loo, *et al.*, 1985).

Brazier (1967) suggested that breeding and selection may have a role to play in trying to reduce the large variation in density between earlywood and latewood. An improvement of earlywood density would do much to upgrade quality by producing timbers of more uniform texture. Brazier (*op. cit.*) also suggested that trees with higher densities seem to have smaller proportions of earlywood and more latewood. Vargas-Hernandez (1990) similarly found that families of Douglas fir with higher wood density normally had an earlier date of transition to latewood, increasing the period of latewood production at the expense of earlywood formation.

1.2.3 Genetic characteristics of vigour and wood density

Tree breeders are usually interested in end-of-rotation gains as the breeding goal. This in turn is often an amalgam of a number of different traits, each contributing to total economic value. The economic traits subject to selection and breeding in the Sitka spruce breeding programme are vigour, wood density and stem-form (Lee, 1993).

When any trait is subject to selection, breeders need to know the gain relative to the existing population as a result of selecting a favoured proportion of the population. Gain resulting from direct selection on the mature trait can be expressed as:

$$G_m = i_m h_m^2 \sigma_{P_m} \qquad (1.1) \qquad \text{(Falconer, 1981)}$$

where: 'm' refers to parameters at maturity and

G_m = Genetic gain

i_m = selection intensity

σ_{P_m} = phenotypic standard deviation

h_m^2 = heritability = $\dfrac{\sigma_{A_m}^2}{\sigma_{P_m}^2}$

and $\sigma_{P_m}^2$ = phenotypic variance

$\sigma_{A_m}^2$ = additive genetic variance

One of the main differences in determining genetic gain for growth rate and wood density is the much higher single tree heritability associated with wood density at comparable ages.

A representative list from the literature comparing single tree heritabilities for stem diameter and wood density for Sitka spruce and other species is given in Table 1.1. Although the absolute values may vary, the relative superiority of heritability for wood density is common. This means that for a common value of variability (σ_{P_m}) and selection intensity (i_m), genetic gain will always be greater for wood density.

Table 1.1: Examples from the literature of single tree heritabilities (h_i^2) for wood density and vigour traits

Species	Wood Density	Vigour	Traits
[1]Sitka spruce	0.73	0.08	15-year diameter and density
[2]Sitka spruce	0.41	0.12	19-year diameter, 15-year density (Pilodyn)
[3]Douglas fir	0.9	0.23	12-year diameter and density
[4]Jack pine	0.4	0.14	10-year diameter and density
[5]Radiata pine	0.64	0.36	10-year height, 9-year density
[6]Loblolly pine	0.42	0.25	12-year height and density
[7]Loblolly pine	>1.00-0.77	-	Rings 16-22. Similar for all ages from 2-22 years.
[8]Caribbean pine	0.62	0.43	11-year diameter and density
Loblolly pine (Heritability study)	[9]0.45	[10]>0.05-0.25	[9]20-year density (same value for juvenile and mature wood portions), [10]height over a period from age 5-20 years
[11]Interior spruce	0.47	0.11	15-year old density and diameter

1 = Wood (1986)
2 = Lee (1993)
3 = King *et al.* (1988)
4 = Park *et al.* (1989)
5 = Dean (1990)
6 = Williams and Megraw (1994)
7 = Loo *et al.* (1984)
8 = Allen (1992)
9 = Talbert *et al.* (1983)
10 = Balocchi *et al.* (1993)
11 = Yanchuk and Kiss (1993)

1.2.4 Genetic relationship between vigour and wood density

The correlation between vigour and wood density is often negative. A summary from the literature is given in Table 1.2.

Table 1.2: Examples from the literature of correlations between wood density and vigour-related traits

Species	Genetic Correlation	Correlated Traits
[1]Sitka spruce	r_P = -0.34 to -0.69	15-year diameter and whole-tree density
[2]Sitka spruce	r_A = -0.66	15-year diameter and Pilodyn pin penetration
[3]Douglas fir	r_A = -0.53	12-year wood density and diameter
[4]Jack pine	r_A = -0.68	10-year old wood density and diameter
[5]Radiata pine	r_A = -0.34	Increase in surface area between years 3 and 7; density at 9 years
	r_A = +0.08	10-year height, 9 year density
[6]Loblolly pine	r_A = -0.39	25-year density and diameter
[7]Caribbean pine	r_A = -0.72	11-year diameter breast height and 11 year density
	r_A = +0.02	11-year height and 11 year density
[8] Interior spruce	r_A = -0.46	15-year diameter and density

Note: r_A = genetic correlation; r_P = phenotypic correlation

1 = Wood (1986)
2 = Lee (1995)
3 = King *et al.* (1988)
4 = Park *et al.* (1989)
5 = Dean (1990)
6 = Loo *et al.* (1984)
7 = Allen (1992)
8 = Yanchuk and Kiss (1993)

The strength of the relationship amongst diameter-traits varies from r_A = -0.72 in Caribbean pine (*Pinus caribaea* var. *hondurensis* Barr. and Golf.) to r_A = -0.34 in radiata pine (*Pinus radiata* D. Don.). Sitka spruce has a strong negative correlation between 15-year diameter and wood density (Wood, 1986; Lee, 1995). It is interesting to note that the correlation between wood density and height can be close to zero or positive for the same species in which it is strongly negative between density and diameter eg radiata pine (Dean, 1990) and Caribbean pine (Allen, 1992).

1.2.5 Principles of early selection

A major goal of tree breeders is to select the best individuals for a particular trait well before the final rotation age (mature trait). Gain in the mature trait based on selection for a juvenile indicator trait is indirect selection. Equation (1.1) above becomes modified as:

$$CG_m = i_j h_m h_j r_{A_{jm}} \sigma_{P_m} \qquad (1.2) \qquad \text{(Falconer, 1981)}$$

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

CG_m = correlated gain for mature trait

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

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

$$= \frac{Cov_{A_j, A_m}}{\sqrt{\sigma^2_{A_j} \sigma^2_{A_m}}}$$

and Cov_{A_j, A_m} = additive covariance of the juvenile and mature traits.

The generation efficiency 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:

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

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

This simplifies to:

$$Q_{gen} = r_{A_{jm}} \frac{i_j h_j}{i_m h_m} \qquad (1.3) \qquad \text{(Falconer, 1981)}$$

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. Gain per year can be expressed in either absolute terms eg King and Burdon (1991) or an absolute gain discounted back to a standard age (such as when breeding commenced) eg McKeand (1988) and White and Hodge (1992).

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

$$= \frac{CG_m}{(T_j+d)} \qquad (1.4) \quad \text{(Lambeth, 1980)}$$

where: (T_j+d) = Generation interval

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.

Similarly, the efficiency of correlated response relative to direct gain can be expressed in terms of gain per year:

$$Q_{year} = r_{A_{jm}} \frac{(i_j h_j h_m \sigma_{P_m})\ (T_m + d)}{(i_m h_m^2 \sigma_{P_m})\ (T_j + d)} \qquad (1.5) \quad \text{(Lambeth, 1980)}$$

It follows from equations (1.3) and (1.5) 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 $(r_{A_{jm}}\ i_j\ h_j) > (i_m\ h_m)$. Lambeth *et al.* (1983) stated that there was no real trend in how heritability estimates varied with age, and that on average they remained constant. If it is assumed that juvenile and mature heritabilities are similar and selection intensities have little scope to vary, the success of indirect selection is then very

dependent on the magnitude of the genetic correlation between the juvenile and mature trait and equation (1.5) reduces to:

$$Q_{year} = r_{A_{jm}} \frac{(T_m + d)}{(T_j + d)} \qquad (1.6) \qquad \text{(Lambeth, 1980)}$$

1.2.5.1 Models to assist early selection

The main restriction in calculating the ratio of gain from juvenile and mature selection ages has often been the lack of age:age (juvenile:mature) correlation coefficients. Very few progeny tests have been measured at regular intervals until end-of-rotation age.

Lambeth (1980) proposed a predictive model to assist tree breeders in calculating age:age correlation coefficients and, by substitution in Equation 1.6, optimum selection ages. Using matrices of age:age phenotypic correlations $r_{P_{jm}}$ and vectors from 5 published studies, each concerning a different species, he derived a generalised regression model for $r_{P_{jm}}$ concerning tree height in *Pinaceae*:

$$r_{P_{jm}} = 1.02 + 0.308 \log_e (T_j/T_m) \qquad (1.7) \qquad \text{(Lambeth, 1980)}$$

Lambeth (1980) concluded that for species of 30- and 40-year economic rotations, early selection for growth is most efficient around years 6 and 8, regardless of species providing trees exceed 2 m height.

It is interesting to note that the Lambeth model makes use of r_{P_m}. This was a result of the very restricted data available from the literature at that time involving $r_{A_{jm}}$ compared to the more generally available data involving $r_{P_{jm}}$. Lambeth (*op. cit.*) acknowledges that equations of correlated gain (1.2) and efficiency (1.5 and 1.6) require estimates of $r_{A_{jm}}$ but due to restrictions of data he makes the assumption that $r_{A_{jm}} = r_{P_{jm}}$. He did recognise

however that if $r_{A_{jm}} > r_{P_{jm}}$ the optimum selection age calculated using $r_{P_{jm}}$ would be over-estimated whilst it would be inappropriate to use r_P if $r_P > r_A$. Magnussen (1988) also preferred the use of $r_{P_{jm}}$ rather than $r_{A_{jm}}$, considering the former to provide a form of 'safety margin'. He argued that due to the numerous errors associated with the estimation of genetic correlations, it is better to estimate phenotypic correlations accurately, rather than values of r_A which resulted in potentially lower selection ages, but with large standard errors.

Magnussen and Yeatman (1987) considered the Lambeth equation as a useful first approximation of age:age correlations but list 3 main concerns:

i. it predicts equal correlations for similar age:age ratios with a markedly different biological basis (for example, $r_{10, 50} = r_{4, 20}$);

ii. its predictive power decreases with younger ages (which are often the ages of interest);

iii. the logarithmic model concept is more appropriate in the exponential growth-phase of younger plantations (T_j) than in older plantations (T_m) in which growth rate is declining.

Magnussen (1988), also developed a method for estimating $r_{P_{jm}}$. It was based on the concept that since growth rates, experimental design, spacing and competition can all affect the variances used in the calculation of correlation co-efficients, time itself is a poor scale for comparing and predicting correlations. Correlations are expressed in terms of a fixed intrinsic maximum growth rate (which is assumed constant for a given population) and a random component which is assigned to individual trees to express the amount of growth lost to extraneous growth factors (eg poor fertility, drainage, frost and other aspects of climate, pest attack etc). Thus:

$$r_{P_{jm}} = \frac{(1 + k.t).\sigma_{P_j}}{\sigma_{P_m}} \quad (1.8)$$

where: k = intrinsic maximum growth rate

t = the mean growth loss due to extraneous factors

σ_{P_j} and σ_{P_m} = phenotypic standard deviations of the juvenile and mature traits respectively

The model is much more complex than that of Lambeth and involves a number of assumptions; consequently it has been largely ignored in the literature whilst the Lambeth model has been used in radiata pine (King and Burdon, 1991), jack pine (*Pinus banksiana* Lamb.; Riemenscheider, 1988), loblolly pine (Mckeand, 1988) and in a limited population of Sitka spruce in Denmark (Jensen *et al.*, 1996). Genetic correlations were used in preference to phenotypic correlations in each of the above (more recent) studies so correctly recognising that it is genetic correlations that determine expected correlated response.

Franklin (1979), divided the development of a crop into three phases: juvenile, mature/genotypic and codominance/suppression. He investigated four different conifer species and found roughly similar trends in that heritability started high and then fell in the first phase, rose to a maximum in the second phase and then generally fell off in the third. He concluded that although correlation within a phase could be high, changes between phases were so marked that selection (at conventional spacing) should be deferred to at least half-rotation.

1.2.5.2 **Early selection for vigour traits**

Table 1.3 is a summary from the literature of optimum selection ages for vigour related traits. There has been a tendency to ignore the advice of Franklin (1979) and merely compare trees at earlier and later ages, investigate the genetic correlation and draw a conclusion accordingly. It is quite probable that since the 'mature' trait is often taken to

be around 15-years from planting, which is far from the rotation age for temperate coniferous species, this is still within the 'juvenile' stage described by Franklin (1979).

Table 1.3: Examples from the literature of optimum selection ages for vigour traits

Species	Optimum Age	Genetic/Phenotypic Correlations
[1]Sitka spruce	6 year height m = 15 year diameter	$r_{A_{6,\ 15}} = 0.78$
[2]Radiata pine	7-8 year diameter (using Lambeth formula) m = 17 year diameter	$r_{A_{5,\ 17}} = 0.64$
[3]Radiata pine	6½ year height m = 16 year volume	$r_{A_{6½,\ 16}} = 0.81$
[4]Slash pine	10 year height or diameter (exercise in discounted selection efficiency) m = 15 year volume	$r_{A_{10,\ 15}} = 0.96$ $r_{A_{5,\ 15}} = 0.67$
[5]Loblolly pine	Between 6 and 8 years height (Optimum genetic gain/year) m = 16 year height	$r_{P_{4,\ 12}} = 0.74$ $r_{P_{4,\ 6}} = 0.61$
[6]Loblolly pine	Height between 3-5 years m = 15 year volume	$r_{A_{3,\ 15}} = 0.67$
[7]Douglas fir	8-year height and diameter m = 15 year volume	$r_{A_{8,\ 15}} = 0.81$ $r_{A_{2,\ 15}} = 0.78$

Note: m = mature trait against which earlier traits are correlated.

1 = Gill (1987)
2 = King and Burdon (1991)
3 = Cotterill and Dean (1988)
4 = White and Hodge (1992)
5 = McKeand (1988)
6 = Foster (1986)
7 = Bastien and Roman-Amat (1990)

As Lambeth (1980) predicted, between 6 and 8 year height is a common indirect selection age for mid- to final-rotation volume. The optimum selection age for vigour of Sitka spruce in Britain was found to be 6-years from planting (Gill, 1987), assuming 15-year diameter represented the breeding goal.

1.2.5.3 **Early selection for wood density**

Table 1.4 presents a summary from the literature of the success of early selection for wood density. Generally, juvenile:mature correlations for wood density are high suggesting that regardless of species, there is a good correlation between juvenile and mature wood which would allow selections to be made based on juvenile wood density values. Loo *et al* (1984) and Williams and Megraw (1994) both suggest that the selection age can be as early as just 2 or 3 years from planting for loblolly pine. Maddern-Harris (1965) also found high (phenotypic) correlations in radiata pine in which the mean density of ring 3 from the pith correlated well with the density of ring 15 and older, from the pith.

The published work into early selection for wood density in Sitka spruce is far from exhaustive. Brazier (1970) based his findings on cores taken from superior, plantation grown phenotypes; not trees from a replicated progeny test. Wood (1986) investigated age:age correlations at an individual tree level for one open-pollinated family of Washington origin (USA) and compared this with the QCI control. A good correlation was found between whole-tree density at age 30 and density of rings 11 to 15 from the pith for both treatments but the correlation between rings 1-15 and whole tree density was rather erratic. This was a very small sample size, but based on these findings, the decision was made by Sitka spruce breeders in Britain to delay the assessment of wood density in progeny tests until 15-years from planting.

Table 1.4. Examples from the literature of juvenile:mature correlations for wood density.

Species	Comments on Correlation Coefficients
[1]Sitka spruce	Of 15 trees with above average juvenile wood density; 11 had above average mature wood density. Suggested a relationship exists.
[2]Sitka spruce	Individual tree $r_{P_{11\text{-}15,\ 30}}$ = 0.9 between 30 year whole tree density and rings 11-15 from pith for two treatments of different origins. $r_{P_{1\text{-}15,\ 30}}$ = 0.45 and 0.96 for the same two treatments.
[3]Loblolly pine	$r_{A_{2,\ 25}}$ = 0.96. Wood density at 2-years well correlated with density at 25-years. $r_{P_{11\text{-}15,\ 30}}$ = 0.9
[4]Douglas fir	$r_{P_{1\text{-}10,\ \text{outer 10 rings}}}$ = 0.74-0.95. 64-year old progenies.
[5]Douglas fir	25-year old progenies.
[6]Loblolly pine	Juvenile wood density at 2 or 3 years old correlated well with 'mature' wood density at 12 years.
[7]Radiata pine	Ring 3 from the pith correlated with outer wood (more than 15 growth layers from the pith).
[8]Loblolly pine	Rings 1 to 10 represent juvenile wood whilst rings 11-20 represent mature wood.
[9]White spruce	Genetic correlation of relative density.
[10]Douglas fir	

1 = Brazier (1970)
2 = Wood (1986)
3 = Loo *et al.* (1984)
4 = McKimmy and Campbell (1982)
5 = Abdel-Gadir *et al.* (1993)
6 = Williams and Megraw (1994)
7 = Maddern-Harris (1965)
8 = Talbert *et al.* (1983)
9 = Corriveau *et al.* (1991)
10 = Adams *et al.* (1990)

1.2.6 Assessment of wood density

Gravimetric techniques are commonly used to assess the density of samples of wood. The water displacement technique is used to estimate the mean wood density of larger pieces such as 3-5 ring sections (eg Petty *et al*, 1990; Brazier, 1967) whilst the

maximum moisture technique (Smith, 1954) is often used for small samples of 1-ring width or less. The maximum moisture technique can therefore provide data for investigation of ring-by-ring development of wood density but is highly time consuming since each bark-to-pith sample must be cut into individual rings, which are then subjected to separate gravimetric assessment.

X-ray densitometry is an alternative wood density assessment technique. It too can provide results at the ring-by-ring level, but without the time consuming element of having to section the sample into individual rings for separate assessment. The saving in time and manpower for detailed investigation of large sample sizes is considerable (Harris and Polge, 1967). This was the technique used by Wood (1986) and Brazier (1970) in their limited investigation into the variation of wood density with age of Sitka spruce trees in a progeny test and standing in a plantation respectively.

The X-ray densitometry process was developed and improved by Polge (1962, 1965 and 1978). Its application in wood density assessment was thoroughly reviewed by Kanowski (1985). The technique involves taking an X-ray image of a transverse cross-section of wood samples. The X-ray film is then scanned by an optical densitometer that converts the film density of the wood image to plotted and digital form. By comparing the recorded optical densities to densities of plastic standards, X-ray densities are calculated. The X-ray densities are then converted to gravimetric densities using a transformation formula obtained by measuring a sample of cores by X-ray densitometry and gravimetric means.

Two methods of radiation densitometry exist. The method outlined above is indirect in that an X-ray is first taken of the wood samples and wood density is calculated using a conversion from optical density to wood density. Direct methods involve recording the amount of radiation that pass through the wood sample. Both methods are in current use and are accepted as accurate means of wood density assessment. Equipment for the direct technique is cheaper than the indirect, but the indirect technique is faster (Harris

and Polge, 1967 and Polge, 1978). Harris and Polge (1967) found excellent agreement between the two techniques.

Few studies appear to have been carried out to compare gravimetric with densitometric techniques. Phillips (1960) compared the densities of very small samples (about 0.03 cm^3) of Douglas fir determined by the direct beta-ray method with gravimetrically determined densities and found on average, a 2.5% difference in calculated density. Heger *et al.* (1974) also found very similar results for small samples measured by X-ray densitometry and gravimetric methods although the X-ray values appeared to be slightly lower within the 0.95 to 1.05 g cm^{-3} range. Moura *et al.* (1987) found significant but low and rather erratic correlations between X-ray densitometry and gravimetric techniques for individual trees of *Eucalyptus camaldulensis* Dehnh. and other *Eucalyptus* species in Brazil (r = 0.47 to 0.59) although it was rather higher at the species and provenance means level (r = 0.63 to 0.90). Hughes and Sardinha (1975) in their description of the procedure employed at the Oxford Forestry Institute (OFI) report that in a series of separate analyses to compare indirect X-ray wood density and gravimetric wood density, linear regressions of were obtained for all species tested.

The strength of X-ray densitometry is not necessarily in its ability to determine the mean density of a large number of timber samples; that can be achieved quicker and more cheaply using simple gravimetric techniques, but rather in the very high detail with which wood samples are investigated. The technique calculates not only the total density of a piece of wood, but also individual ring-by-ring density allowing investigations of how density varies with age from the pith to the bark. Transition from earlywood to latewood and the nature of that transition can also be investigated.

1.2.7 Prediction of breeding values and estimation of variance components:

Successful tree breeding involves predicting breeding values (BVs) and the estimation of variance components. Following this, the best genotypes can be selected for use as future parents in the production of improved planting stock, and informed decisions can be made regarding the optimum breeding strategy to achieve the selection goal. The degree to which the appearance (phenotype) of a standing tree gives reliable information on the genetic quality (genotype) of that tree is dependent on the influence of the environment. A trait which is strongly influenced by the effect of the environment is said to have a low heritability (< 0.5) whilst one which is little effected by the environment is said to have a high heritability (> 0.5).

In simple terms: phenotype = genotype + environment

or $P = G + E$ (Falconer, 1981)

and phenotypic variation = genetic variation + environmental variation

or $$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 \qquad (1.9)$$ (Zobel and Talbert, 1984)

Prediction of the breeding value of a selected tree is more accurately carried out by comparing the performance of offspring (progeny) collected from the selected tree against the offspring of other similar selected trees in an experiment (progeny test) replicated across a number of representative, uniform environments (Zobel and Talbert, 1984). The breeder then ranks parents according to the predicted BVs calculated from progeny-mean performance across the representative sites.

The Standard Linear Model (SLM) for data collected from an open-pollinated progeny test with a randomised complete block design, replicated across a number of test sites is represented as:

$$y_{ijkl} = \mu + E_i + B_{ij} + f_k + fe_{ik} + p_{ijk} + W_{ijkl} \quad (1.10) \quad \text{(White and Hodge, 1989)}$$

where:
- μ = a fixed general mean;
- E_i = fixed effect of test environment i;
- B_{ij} = fixed effect of block j in test i;
- f_k = random effect of family k;
- fe_{ik} = random effect of family k in test i;
- p_{ijk} = random plot error of family k in block j in test i;
- W_{ijkl} = random tree error of tree l in plot ijk.

The effect of Equation 1.10 is to divide the progeny test into each of its constituent elements thereby giving a more precise estimation of variance components and mean tree values. The SLM above is considered a Mixed Model (MM) since it incorporates both fixed and random effects.

The success of the breeder in predicting true breeding value and estimates of variance components depends on how accurately the above elements are predicted, and, in particular, how accurately the fixed effects (test site, block) are estimated. This would be relatively straight-forward in a fully-balanced series of progeny tests where all progenies ever to be tested were present at all sites and represented by an equal number of trees. But this is rarely true.

In practise, the progeny of selected trees are established in tests over a large number of years and locations (Lee, 1993; White and Hodge, 1988) each with differing survival, growth rates, and family representation. In addition the design of progeny tests may vary across time. The precision of data collected from each test will also vary due to differences in experimental error (site heterogeneity). It is common in forestry to calculate the progeny-mean of all offspring for a particular parent by averaging site-

specific family-means across all tests in which the parent is represented. But some families may be present in more tests than others and so introduce possible variation in precision of BV prediction between families within years even before attempts are made to combine years and sites. Also, some parents may have been represented in full-sib tests or clonal tests as well as the more routine half-sib tests. If extra data are available from a related source it would seem sensible to include these in BV prediction if it would have the effect of reducing errors.

The breeder clearly has a problem when ranking original selections based on test-mean performance if there are year, design and genetic test effects, as well as site and block effects. Each one of these effects however, may be considered a fixed effect and, if accurately estimated, BV predictions can be weighted accordingly.

1.2.7.1 Use of Mixed Model Analysis

It is possible to bring together all these data from different sites and years using Mixed Model Analysis (MMA) techniques and matrix algebra to more accurately predict the true (but always unknown) breeding values and variance components. Techniques referred to as Best Linear Prediction (BLP) and Best Linear Unbiased Prediction (BLUP) were developed by Henderson (1949, 1973, and 1977) to estimate breeding values once variance and covariance components are known, whilst Restricted Maximum Likelihood (REML) was developed by Patterson and Thompson (1971) to estimate more accurately the required variance and covariance components. The objective of these respective MMA techniques is to more accurately predict true BVs and estimates of variance components by incorporating all available related data (across sites, years, test designs etc) than would be possible by a system of unweighted grouping together of data.

REML is an iterative procedure in which equations of estimation are solved by successive approximations. A key feature of the procedure is to separate out those contrasts (and associated degrees of freedom) which are estimators of the fixed effects

and the remaining orthogonal contrasts (and associated degrees of freedom) which represent error terms. As the acronym implies REML estimates the components of variances by maximising the likelihood of all contrasts with zero expectation.

In the case of BLP and BLUP a function of the observed (*n x 1*), data vector **y** is used to predict, both accurately and precisely, **g** a (*q x 1*) non-observable random vector of genetic values (White and Hodge, 1989).

The mixed linear model used in BLP and BLUP is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e} \qquad (1.11)$$ (Henderson, 1973 and 1977)

where:

- **y** = *n x 1* vector of observations; *n* = number of observations;
- **b** = *p x 1* vector of fixed effects; *p* = number of levels for fixed effects (eg sites, years etc);
- **g** = *q x 1* vector of random tree effects; *q* = number of levels for random effects (eg family or individual tree);
- **e** = *n x 1* vector of random residual effects;
- **X** = design matrix of order *n x p*, which relates records to fixed effects;
- **Z** = design matrix of order *n x q*, which relates records to random tree effects.

A matrix of additive relationships must be added to the above equation in order to specify the genetic relationship between all the trees in the analysis. A separate equation is then generated for each tree or parent whose breeding value is to be estimated.

1.2.7.2 Comparison of BLP and BLUP

The major difference between BLP and BLUP is the treatment of fixed effects. In BLP the fixed effects are assumed known without error and are estimated by arithmetic or least squared means of complete or sample data. In BLUP the fixed effects are assumed not to be known and are estimated using Generalised Least Squares as part of the computational process. It follows that BLUP is computationally more complex than BLP, but is particularly valuable when it is difficult to estimate precisely the fixed effects without bias.

Henderson (1963, 1973, 1977 and 1984) developed the principles of BLUP which are now widely used in animal breeding specifically to deal with the horribly unbalanced data in breeding of dairy cattle. BLUP now has worldwide usage in genetic evaluation of domestic animals such as sheep and cattle (Mrode, 1996).

Once the matrices have been constructed in BLP and BLUP, prediction of the BVs can follow, the only difference being the simultaneous estimation of fixed effects in BLUP against pre-estimated values of fixed effects in BLP. It can be shown (Henderson, 1963, 1984) that estimation of true breeding values, **g**, is as follows:

i. BLUP

$$\hat{g} = \mathbf{c}' \mathbf{v}^{-1} (y - X) \qquad (1.12)$$

where

$= (\mathbf{X}' \mathbf{v}^{-1} \mathbf{X}) - (\mathbf{X}' \mathbf{v}^{-1} \mathbf{y})$

= estimation of fixed effects.

ii. BLP

$$\hat{g} = \mathbf{c}' \mathbf{v}^{-1} (\mathbf{y} - \propto) \qquad (1.13)$$

where $\propto$ = calculated fixed effects.

c = an (n x q) matrix of covariances between the observations and the genetic values being predicted;

v = (n x n) matrix of variances and covariances of the observations;

X = (n x p) design matrix that relates fixed effects to observations.

Since BLP does not require the estimation of **b**, it is computationally less intensive than BLUP.

In each case the model takes account of factors such as differing replicate or site qualities and varying number of progeny representing different parent trees. As White and Hodge (1989) point out, it is this last point that makes BLUP attractive as tree breeding enters advanced generations and material from differing generations is tested on different sites. BLUP will make use of the links between trees in different environments and generations to improve the prediction of the adjustment factors for the different classes of fixed effects and the expected breeding values of different trees. This will allow an unbiased comparison of trees across generations (Borralho, 1995).

Tree breeders have traditionally made predictions of BVs and estimates of variance components based on analysis of trees in a single generation. In practice, data are often available from a number of genetic sources in tree breeding, but rarely have they been used together. Possible sources include phenotypic value of the original selected tree (ortet), measurement of grafts in clone banks and occasional representation of trees in advance generation (full-sib) progeny tests, as well as first generation half-sib progeny tests. There is no reason why the principles of REML and BLUP can not be employed with trees as they have with animals since most of the benefits which are derived from the better use of covariance relationships between relatives are not peculiar to animals (Borralho, 1995).

1.2.7.3 **Fixed or random effects?**

Since MMA involves estimation of fixed as well as random effects, it is necessary to decide which elements are fixed and which are random. Calculated variance components will vary depending on whether effects are considered fixed or random.

Williams and Matheson (1994) stated that it is usual for seedlots to be specified as fixed effects. The source of this common view is often attributed in animal breeding to the argument put forward by Henderson (1973), who showed that predictors of BVs, derived ignoring selection, can be biased if there is an association between BVs and random herd-year sub-class. This bias disappears if random herd-years are treated as fixed. The equivalent in tree breeding would be a bias due to site or planting-year sub-class if a progeny test was to investigate the BV of trees selected from across a number of different stands.

Estany and Sorensen (1995) question Henderson (1973) and take a more pragmatic approach when investigating the genetic parameters of litter size for pigs in which they saw their objective as reducing the errors associated with predictive ability. They found models in which herd-year effects were treated as random to be marginally more effective than when they were considered fixed.

White and Hodge (1989) suggest that deciding whether a set of effects is to be considered fixed or random depends on the inference to be drawn from the experiment and hence the sampling process. If calculation of variance components is the main objective and conclusions are to apply to a broader population of which the treatment levels of a certain factor in the experiments are a sample, then the factor is random. Williams and Matheson (1994) agree that seedlots can be considered as random when they form a sample from a very large population and when the objective of the experiment becomes an estimation of variance components, rather than BVs.

White and Hodge (1989) explain that variance components associated with blocks, sites and years are commonly considered as 'nuisance' factors in MMA. Treating these factors as random effects implies their estimated variance components will apply to a larger population of blocks, sites and year. However, nuisance factors are omitted from the phenotypic variance in heritability calculations.

The general tendency is to regard block and site effects as fixed (Becker, 1984; White and Hodge, 1989) since often the observed phenotypic mean will be adjusted for the specific set of fixed effects prior to ranking genotypes. This point is also implicit in implementing the MMA principles outlined above.

1.3 VARIANCE COMPONENTS IN AN UNSELECTED POPULATION

A soundly-based breeding strategy depends on reliable information on the underlying variation and pattern of inheritance of the characters for which selection will be made. When accurate estimates of genetic variances are available, it is possible to make realistic predictions of genetic gains as well as estimates of times and costs likely to be incurred under different breeding schemes and selection intensities (Samuel and Johnstone, 1979). Estimates of genetic variances obtained from a population for which there has already been an element of selection are liable to be biased relative to the true variances that exist in an unselected population (Bulmer, 1976). This restriction will apply to the variance components operating in Sitka spruce and reported by Gill (1987) and Wood (1986) by an unknown quantity.

The effect of selection, either natural or artificial (i.e. induced by man) on a hitherto unselected population is to increase the frequency of genotypes which contain the favoured genes. The degree of success depends on the intensity of selection and the initial gene frequency (Falconer, 1981). The result should be a change in the population mean and the variance of the character subject to selection (Bulmer, 1976).

If breeders want to know true inherent variation and to derive heritabilities of traits for which there may be selection at some future date, analysis should initially be based on data collected from a representative, randomly selected population. In practice, this is rarely the case. Breeders are usually under pressure to select trees, establish progeny tests and compose breeding and production populations following either forward or backward selection. It would be unacceptable to most organisations to delay selection and progeny testing until end-of-rotation estimates of genetic variances had been obtained from a randomly selected population.

It would be of value to carry out an investigation into genetic variances and derived heritability of economic traits of interest from a randomly selected population in parallel to the mainline selection and testing programme. Important guidelines for future developments may result especially in the comparison of genetic gains from alternative breeding strategies (Samuel and Johnstone, 1979).

If variance components are known for all traits of interest from a randomly selected population, it becomes possible to estimate the effects of selection for each of those traits including their mutual interaction (e.g. gain for Trait Y as a result of selecting for Trait X). Investigation of a randomly selected population allows complete analysis of traits with and without selection pressures being applied. This may be of particular value when investigating wood quality traits. Since single tree heritability of wood density is often high (Table 1.1), yet has a negative genetic correlation with diameter (Table 1.2), variance components for wood density estimated within a population selected primarily for vigour could be different from those estimated within a randomly selected population.

The breeding of Sitka spruce in Britain has included the establishment of a large progeny test replicated across sites, involving open-pollinated families collected from randomly selected parents trees across the spectrum of dominance classes. Parent trees were destructively measured for various vigour traits soon after cone collection. Scion material from all parent trees was grafted into juvenile root-stocks and planted in a

clone-bank. Variance components and single tree heritability for glasshouse, nursery and the first six-years of height growth in the progeny tests were reported by Samuel and Johnstone (1979). This investigation into variance components in an unselected Sitka spruce population has become known as the 'Population Study'.

A similar investigation into inheritance patterns from a randomly selected population of loblolly pine trees was established in Georgia, USA in 1961-62. Variance components and heritability for early height growth, straightness, wood density and resistance to the fusiform rust (*Cronartium quercuum* [Berk.] Miyabe ex Shirai f.sp. *fusiforme*) were reported by Stonecypher *et al.* (1973). Subsequent reports by Talbert *et al* (1983) and Balocchi *et al* (1993) have presented estimates of variance components and heritabilities for wood density and tree height calculated over a 20-year and 26-year period respectively.

1.4. OBJECTIVES OF THE SITKA SPRUCE POPULATION STUDY

The following were listed by Samuel and Johnstone (1979) as the original objectives of the Sitka spruce 'Population Study':

1. To estimate additive genetic variances operating within a population of Sitka spruce which was representative of the material (species and origin) most commonly planted in Britain and which forms the basis of the main breeding programme, to derived estimates of heritability, and predictions of genetic gains from alternative breeding strategies.

2. To allow long-term assessments of vigour. In this way it would be possible to study family rank changes with age, enabling the assessment and selection criteria used in a breeding programme to be refined.

3. To investigate the relationship between measurements collected on parent trees and the performance of their progeny.

4. Using grafted parent material, to carry out controlled crossing to a pedigree design allowing estimates of non-additive genetic variances.

To date, these objectives have been only partly achieved:

1. The additive genetic variances and heritabilities of 1 to 6-year height were reported by Samuel and Johnstone (1979) but variances and heritabilities for later vigour traits (height or diameter) and wood density (at any age) have not been reported.

2. Although family-rank changes over a 6-year period were presented by Samuel and Johnstone (1979) they did not extend beyond 6-year height.

3. No investigations have been carried out into the relationships between ortets and progeny for related data.

4. Only a limited controlled crossing programme has been carried out to date.

The field-based open-pollinated progeny tests are now over 20-years-old. It would now be possible to investigate variances, covariances and heritabilities for vigour and other traits such as wood density at a mid-rotation age. Analysis of such data would more fully address Objectives 1 and 2 (above) whilst incorporation of data from the ortets and/or grafted-ramets, would address Objective 3.

1.4.2 Sources of data for this study

A thorough investigation into the genetic variances, covariances and heritabilities of vigour and wood density, and how they each vary with age across an unselected population of Sitka spruce would be possible if data could be collected and analysed from the following sources:

i. Open-pollinated progeny from planting to present day;

ii. Original parent trees at felling;

iii. Grafted-ramets from the clone bank.

There would be the potential for use of the MMA techniques to see if the accuracy of variance components could be increased as more data are introduced from genetically related sources.

1.5 OBJECTIVES OF THE STUDY

Published estimates of variance components from a randomly selected Sitka spruce population relate to between 1 and 6 year heights (Samuel and Johnstone, 1979). Estimates of variance components and heritabilities beyond 6 years have been made based on data collected from selected populations (Gill, 1987; Wood, 1986; Lee, 1995). All reported estimates of variance components (randomly selected or selected) have involved analysis of data collected at just one genetic level; open-pollinated progeny. No studies have included data from several genetic sources (parental, grafted-ramet, half-sib progeny) to investigate the genetic correlation between sources.

The only published report of estimated variance components for direct assessment of wood density in Sitka spruce was Wood (1986) who also reported phenotypic

correlations between wood density and mid-rotation diameter and age:age correlations for wood density in a selected Sitka spruce population. Among the conclusions of Wood (*op. cit*) was that the earliest selection age for wood density should be 15 years from planting. This was based on a small sample size. The literature for other species suggests selection ages lower than 15 years are common amongst coniferous species (Table 1.4). There is the need for a more detailed investigation into age:age correlations for wood density in Sitka spruce and from a randomly selected population if possible.

The objectives of this study were therefore:

i. Investigate variance components for height, diameter and wood density in a randomly selected Sitka spruce population;

ii. Determine age:age correlations and optimum selection ages for vigour traits and wood density;

iii. Investigate the genetic correlations for vigour and wood density traits across different genetic populations and make recommendations as to which could be included along with progeny test data in the future evaluation of breeding values and variance components;

iv. Make recommendations regarding the use of MMA techniques in the multi-trait selection and breeding of Sitka spruce in Britain.

CHAPTER 2

MAIN STUDY: Height, diameter and indirect assessment of wood density

2.1 INTRODUCTION AND OBJECTIVES

The data for this study were collected in an experiment known as Garcrogo 3 which is an open-pollinated (half-sib) progeny test growing within the Glaisters block of the Castle Douglas District, south-west Scotland (55° 6' N, 3° 54' W), operated by the Forest Enterprise (the commercial agency of the British Forestry Commission). The primary objective of this progeny test was to investigate the genetic variances and covariances of a number of economically important traits operating within an unselected population of Sitka spruce parent trees known as the 'Population Study' (see Chapter 1.3).

Progeny from 125 of the original 150 randomly selected parents were planted in Garcrogo 3. The experiment represents the most complete source of genetic information relating to this unique unselected population and is referred to as the "Main Study".

The objectives of the work reported in this Chapter were to analyse the half-sib progeny data collected from this population of randomly selected Sitka spruce parent trees over the first half of its rotation in order to determine:

i. the genetic variance components and heritabilities for a large number of vigour traits and one indirect assessment of wood density;

ii. how genetic variance components associated with the vigour traits vary with age;

iii. the genetic and phenotypic correlations between vigour traits with time, and between vigour traits and the indirect assessment of wood density;

iv. optimum selection ages for vigour in terms of Generation Efficiency (Q_{gen}) and relative Gain Per Year (Q_{year}).

2.2 MATERIAL AND METHODS

2.2.1 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. Altitude across the site varied from 30 to 130 m with an average rainfall of 1780 mm. The soil was mainly brown earth with some surface water gley. The site had a south-westerly aspect and uneven topography with shallow gullies. Full site details are given in Appendix 2.1. 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. During an initial survey of the stand, 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 144 trees took place. The selection was essentially random and aimed to reflect the distribution of dominance classes already noted in the stand as a whole. Six 'plus-trees' (selected according to Fletcher and Faulkner, 1972) identified previously were also included. The final composition of the sample was:

Table 2.1: Composition of selected trees in the 'Population Study'

	Number	Percent
Plus trees	6	4
Dominants	48	32
Co-dominants	61	41
Sub-dominants	35	23
Total	**150**	**100**

Note: Co-dominant and sub-dominant trees are 84-95% and 74-84% of the height of dominant trees (Assman, 1970). Plus trees are outstanding phenotypes for height, diameter and certain quality traits.

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. Similarly, flowering-times across the stand were sufficiently matched for mating within the stand to be considered as random, with the pollen contribution to any given female flower having derived from a large number of unrelated trees.

In 1969, approximately 100 wind-pollinated cones were collected from each selected tree. Extracted seed were raised in the nursery for two years prior to planting out to three forest sites in 1972. The sites chosen were typical of those commonly planted with Sitka spruce in Britain. Following losses at germination and in the nursery a maximum of 134 families were planted at one site, with different sets of 125 families planted at the other two sites; 116 families were common to all three sites.

The selected parent trees were destructively assessed for a number of traits including height, diameter and stem straightness. Wood density assessment was not carried out. Scion material was taken from all 150 trees, grafted onto root-stocks and planted in the main Sitka spruce clonebank in 1975 (details given in Chapter 5).

2.2.2 **Details of the "Main Study" and site:**

Garcrogo 3 was one of the three forest sites planted in 1972 with open-pollinated progeny collected from the randomly-selected parent trees. The other forest sites were Wark, Northumberland, north-east England (55° 6' N, 2° 8' W) and Tywi, central Wales (52° 10' N, 3° 50' W). Resources for this study would only allow the detailed examination of data from one of the three sites. Garcrogo was selected as the most suitable since growth rates were favourable and the site had proved to be relatively homogenous. Further, Wark was rejected on ground of extensive areas of windblow,

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and Tywi was rejected due to poorer growth rates and more heterogenous site based on analysis of 1-6 year height (Lee, unpublished[#]).

The Garcrogo progeny test site is located at an elevation of 230-240 m. The soil type is hill peat, generally 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 tree plots. There are 125 families in each of the three randomised complete blocks making this a large experiment extending over 9.5 hectares. Standard silvicultural management of the site was practised. Typically for Sitka spruce plantations in this part of Scotland, phosphate fertilizer was applied at planting with a phosphate/potassium mix applied in 1979. Full site and experimental details are given in Appendix 2.2.

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 which had been retained in the nursery. A list of families represented in this "Main Study" is given in Appendix 2.3.

Although plot size was 49 trees in a 7 x 7 configuration, only the central 5 x 5 trees were measured to ensure all trees within a family had similar inter-genotypic competitive effects. 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 injected 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). All live trees representing all 125 families across all 3 replicates were measured. 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. There was one indirect assessment of wood density (DN) using the

Pilodyn which was carried out at 17-years from planting (DN17). This differed from other assessments in that measurement was restricted to all live trees greater than 7 cm diameter at breast height. A complete list of the assessments carried out is given in Table 2.2.

All the above assessments apart from DM23 had been carried out prior to commencing this study and raw data were stored in a database. All surviving trees were assessed for DM23 in April 1994.

Table 2.2: Assessments carried out over a 23-year period in the Main Study (Garcrogo 3).

Height:	Diameter:	Density:
HT01	DM10	DN17
HT02	DM12	(indirect using
HT03	DM14	the Pilodyn)
HT04	DM16	
HT05	DM17	
HT06	DM19	
HT07	DM23	
HT09		
HT10		
HT11		

Note: HT = height, DM = diameter, DN = density. 01, 02 etc indicates year of assessment from planting e.g. DM23 = diameter 23-years from planting.

2.3 STATISTICAL METHODS

Routine analysis of the data was carried out using the Statistical Analysis System (SAS) package (SAS, 1982). Standard deviations and mean values for all traits were calculated using PROC MEANS within SAS.

The mixed, standard linear model employed to estimate trait specific variance components and fixed effects was:

$$Y_{ijk} = \mu + R_i + F_j + f_{ij} + e_{ijk} \qquad (2.1)$$

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, Var $(F_j) = \sigma_f^2$;

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

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

and Var = σ^2 = Variance.

All variance components, heritabilities and associated standard errors (SE) were estimated using **ASReml** (**A** Spacial **R**estricted **m**aximum likelihood), 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), which in turn calls upon the original concepts of REML (Patterson and Thompson, 1971). The introduction of an average information matrix increases computational efficiency considerably relative to the derivative free (DFREML) models used by Meyer (1989) in her suite of programs.

ASReml fits a general mixed model which is a modification of Equation 1.11 as follows:

$$y = Xb + Z_1 a_1 + Z_2 a_2 + e \qquad (2.2) \qquad \text{(Gilmour, 1996)}$$

where:

y = (n x 1) vector of observations (i.e. measurements such as Y_{ijk} in Equation (2.1) above);

X = (n x p) design matrix which relates each observation to the fixed effects b (replicates in Equation (2.1) above);

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_f^2 in Equation (2.1) above);

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_{fr}^2 in Equation (2.1) above);

e = (n x 1) vector of independent random residual effects (σ_e^2 in Equation (2.1) above).

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. The only fixed effects to be generated were those for 'replicate'.

As the model indicates, analysis was carried out at the individual tree level. Each tree was given a unique number (ID) . Information regarding tree ID, plot, replicate, female and male ancestry (when known) was attached to each individual tree measurement. ASReml used this information to construct the model given in Equation 2.2.

In order to achieve the objectives reported in this Chapter it was necessary to carry out both univariate and bivariate analysis using ASReml. Univariate analysis of each trait was required to estimate trait specific variance components and heritabilities, while

bivariate analysis of selected traits was required to estimate covariances and phenotypic and genetic correlations between traits. Although estimates of variance components and ultimately heritabilities would be obtained from the bivariate analysis, it was computationally faster to perform the procedure in two stages.

The ASReml procedure involved a series of input, output and instruction files in order to generate the required variance and covariance components, heritabilities, and phenotypic and genotypic correlations. Appendix 2.4 is a flow chart outlining the sequence of data analysis required, which is briefly described as follows:

i. the parameter file (extension *.as*) contains instructions regarding which effects are to be estimated and whether they are fixed or random; likely starting values of the effects to be estimated; which file contains the data; and (if applicable) which file contains pedigree (ancestral) information;

ii. an output file (extension *.asr*) to the parameter file which contains estimates (complete with SE) of all variance components and fixed effects specified in the parameter file;

iii. an instruction file (extension *.pin*) which contains information required to calculate meaningful functions of the variance components (heritability, phenotypic and genetic correlations etc) generated in the *.asr* file;

iv. an output file (extension *.pvs*) to the instruction file which contains the calculated functions of the variance components complete with SE.

2.3.1 **Univariate analysis:**

All traits were subject to univariate analysis. The parameter (*.as*) file was constructed to generate variance components and estimates of fixed effects according to

Equation (2.1). Examples of parameter input and output files are given in Appendix 2.5 and 2.6. It was necessary to enter starting values in the parameter file of likely final variance components. The program then makes iterations from these starting values until convergence is achieved. If convergence can not be achieved over 19 iterations, it may be necessary to alter the starting values and re-run the program.

The output (*.asr*) file included estimates of the fixed and random effects specified by the model:

i. σ_f^2 which is the variance between family means equivalent to ¼ of the additive genetic variance (¼ σ_A^2, Falconer 1981) and referred to as 'dam' in the output file;

ii. σ_{fr}^2 which is the variance of family by replicate interaction referred to as 'plot' in the output file;

iii. σ_e^2 which is the residual variance made up of the sum of the balance of the additive genetic variance (¾ σ_A^2) and all the non-additive genetic variance (σ_{NA}^2) and all the remaining independent random environmental effects (σ_w^2), referred to as 'variance' in the output file;

iv. estimates of replicate mean.

The variance components were used to estimate narrow sense single-tree (h_i^2) and family-mean (h_f^2) heritabilities and associated SEs. These were calculated within ASReml by constructing the instruction (*.pin*) file according to the following formulae:

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_e^2 + \sigma_{fr}^2 + \sigma_f^2} \qquad (2.3) \quad \text{(Wright, 1976)}$$

$$h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_e^2}{nr} + \frac{\sigma_{fr}^2}{r} + \sigma_f^2} \qquad (2.4) \quad \text{(Wright, 1976)}$$

where: n = number of trees per plot

r = number of replicates.

Examples of univariate instruction (*.pin*) and output (*.pvs*) files are given in Appendix 2.7

2.3.2 **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:

i. reducing computation loading by ensuring an assumption of homogeneous variances would be met;

ii. providing a more stable means of estimating initial variance components since all variances (σ_f^2, σ_{fr}^2 and σ_e^2) within bivariate runs sum to 1.00 in the *.as* file.

Not all traits were compared in a complete bivariate analysis since this would have required a matrix of 171 (19 x 18/2) separate comparisons. Analysis was 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. For example, all traits were involved in analysis with DM23 whilst only a few were involved with HT01 after a preliminary investigation.

DN17 was analysed with vigour traits representing approximately every other growing season from HT01 to DM23. HT06 and ages close to this were analysed with more mature ages since Gill (1987) had found HT06 to be a suitable early selection age. Height and diameter of similar ages were compared to investigate their correlation.

Examples of the parameter (*.as*) file and the resulting output (*.asr*) file are given in Appendix 2.8 and 2.9. Phenotypic (r_P) and genetic (r_A) correlations between two traits were calculated by constructing the instruction file (*.pin*) according to the following formulae:

i. Phenotypic correlation:

$$r_{P_{1,2}} = \frac{COV_{P_1 P_2}}{\sigma_{P_1} \sigma_{P_2}} \qquad (2.4) \quad \text{(Falconer, 1981)}$$

ii. Genetic correlation:

$$r_{A_{1,2}} = \frac{COV_{A_1 A_2}}{\sigma_{A_1} \sigma_{A_2}} \qquad (2.5) \quad \text{(Falconer, 1981)}$$

where: COV = covariance;

σ_{P_1}, σ_{P_2} = phenotypic variance of trait 1 and trait 2;

σ_{A_1}, σ_{A_2} = additive variance of trait 1 and trait 2.

Sample bivariate *.pin* and *.pvs* files are given in Appendix 2.10.

2.3.3 **Optimum selection age for vigour:**

The objective of determining optimum selection ages for vigour was investigated for single tree and family selection. Family selection is important in 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.

Two different breeding goals were investigated as follows:

i. Selection goal of 23-year diameter:

Twenty-three year diameter was the most mature vigour related trait assessed. This mid-rotation assessment of diameter was taken as the breeding goal and analysis was carried out to determine the most efficient selection trait and age for this breeding goal. Analysis was restricted to the 11 height and 7 diameter traits assessed.

ii. Selection goal of 40-year height or diameter:

Phenotypic and genetic correlations estimated from the bivariate analysis were used to calculate respective Lambeth (1980) regressions as outlined in Chapter 1.2.5.1. Using the desired regression equations, it was possible to estimate the phenotypic and genetic correlation for any combination of juvenile and mature ages. In this way juvenile:mature correlations can be extrapolated beyond the age of the most mature vigour trait assessed. The selection goal was now extended to 40-year height (or diameter). Juvenile:mature phenotypic or genetic correlations were calculated according to the calculated Lambeth regression assuming a mature age of

40 years and a variety of juvenile ages. The calculated correlation coefficients could then be used in a similar manner to (i) above to estimate optimum selection ages for 40-year height or diameter.

2.3.3.1 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 according to equations (1.3) and (1.5) in Chapter 1.2.5.

Estimation of Q_{year} involved calculating the generation interval ($T_j + d$) where T_j is the age when the tree is selected and (d) is the delay before sufficient propagules are obtained to allow establishment of genetic tests for the next generation. In a breeding programme involving mainly recurrent selections, this delay is primarily the time taken to bring the trees to a state of readiness for flowering followed by time required to carry out the pollination programme. In the case of family selection, the parents are already physiologically mature and have demonstrated their ability to flower. The delay (d) can be considered to be exclusively associated with technical ability. Forward selection of individual trees which have not previously flowered is more complicated since (d) is dependent on an unknown combination of technical ability and physiological maturity of the tree. The delay due to technical ability will decrease with increasing physiological age.

Sitka spruce is a late flowering species (Gordon and Faulkner, 1992) and it would be unrealistic to assume (d) was exclusively due to technical ability prior to $T_j = 15$ years. In order to calculate Q_{year} it was necessary to make assumptions of how (d) might vary when $T_j < 15$ years. Table 2.3 presents the most likely delay currently achievable in practice (J J Philipson[#], *pers. comm.*). It makes the assumption that $d = 10$ years for

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very early selections, until $T_j = 7$ after which due to slight physiological maturation, $d = 9$ years. Delay (d) then continues to fall by one year for each 2 year increase in selection age, to a minimum of $d = 5$ years when $T_j = 15$ years from planting. This model is referred to as d = variable.

Table 2.3: Variation in delay (d) with early selection age (T_j), as used in the model (d = variable). All figures are in years.

Selection Age (T_j)	Delay (d)	($T_j + d$)
1	10	11
2	10	12
3	10	13
4	10	14
5	10	15
6	10	16
7	9	16
8	9	17
9	8	17
10	8	18
11	7	18
12	7	19
13	6	19
14	6	20
15	5	20
16	5	21
17	5	22
18	5	23
19	5	24
20	5	25
40	5	45

Note: When $T_j > 15$, $d = 5$. When $T_j < 15$, d varies between $d = 10$ and $d = 6$.

Three different models of (d) were used to investigate their impact on Q_{year}:

i. Model 1, d = variable (see Table 2.3);

ii. Model 2, $d = 5$ years;

iii. Model 3, $d = 3$ years.

It is implicit that Model 1 refers to forward selection of individual trees, whilst Model 2 and Model 3 refer to family selection and forward selection if technical ability and manipulation of physiological maturity develop sufficiently.

2.3.3.2 **Selection goal of 40-year height or diameter:**

Phenotypic and genetic correlations (r_P and r_A respectively) estimated from the data using bivariate analysis were regressed against the natural logarithm of the ratio of the younger to the older age (LAR) as described by Lambeth (1980) and outlined in Chapter 1.2.5.1. Correlations involving DN17 were not included.

Parameters of the model:

$$r = b + m\,(LAR) \qquad (2.6)$$

where: r = phenotypic or genetic correlation;
m = slope of regression line;
b = intercept on the X-axis;
LAR = $\log_e (T_j/T_m)$;

and: T_j = younger age of trait 1;
T_m = older age of trait 2.

were estimated by simple linear regression using PROC REG within SAS (1982). Correlations involving HT01 were omitted as being unreliable (Lambeth, 1980).

The original Lambeth equation involved age:age correlation of total height only. Regressions restricted here to height only would reduce the age-range from a possible 2-23 years to just 2-11 years. It was decided to generate three predictive equations for both the phenotypic and genetic correlations (i.e. 3 x 2 = 6 equations in total) generated in this study according to the relationship of the traits involved in the bivariate analysis as follows:

i. $diameter_j$:$diameter_m$ correlation coefficients only ($r_{A_{DD}}$ and $r_{P_{DD}}$);

ii. $height_j$:$height_m$ correlation coefficients only ($r_{A_{HH}}$ and $r_{P_{HH}}$);

iii. $height_j$:$diameter_m$ correlation coefficients only ($r_{A_{HD}}$ and $r_{P_{HD}}$).

In this way it would be possible to compare predictive equations across traits as well as comparing the effectiveness of predictive equations generated using phenotypic and the more appropriate genetic correlations.

By assuming a selection goal of 40-year height or diameter (T_m), the efficiency of indirect selection (Q_{year}) based on a juvenile trait when T_j = 2 years through to T_j = 15 years was investigated for each of the above regressions (i. to iii). Substitution of the respective LAR, b and m values in equation (2.6) allowed calculation of the corresponding $r_{A_{j,\ 40}}$ or $r_{P_{j,\ 40}}$ which was in turn substituted in equation (1.6) to give an estimated Q_{year}.

It was not possible to estimate the heritabilities of height or diameter traits for any ages other than those calculated as part of the univariate analysis. No assumptions could be made regarding trends of heritability of height and diameter beyond 11-years and 23-years from planting respectively, or diameter between years 1 and 10. The calculation of Q_{gen} and Q_{year} would involve estimates of heritabilities for both the juvenile and mature traits. The heritability for 40-year height or diameter was unknown, as was the

heritability of many, but not all, of the juvenile traits. The same problem was encountered by Lambeth (1980), King and Burdon (1991) and Riemenschneider (1988). Lambeth (*op. cit.*) decided to assume equal (height) heritabilities with age. King and Burden (*op. cit.*) estimated (diameter) heritabilities of younger ages by interpolating from point estimates, and assumed a constant heritability for all ages beyond the last assessment (17 year diameter to 25 and 30 year diameter). Reimenschneider (1988) also assumed a constant heritability beyond the last height assessment (7 years to 30 years).

Since in this study both height and diameter were assessed, but at different ages and in each case only for a small but different proportion of the rotation, it was decided that the approaches of interpolation (for younger ages) and constant heritabilities (for older ages) contained too many assumptions. It was therefore decided to assume equal heritabilities between juvenile and mature ages.

For this reason there was no need to calculate Q_{gen} since (from equation 1.3) if $h_j^2 = h_m^2$ and assuming $i_j = i_m$, then Q_{gen} would equal $r_{A_{jm}}$ calculated from the model. Q_{year} was calculated and as in 2.3.3.1, (*d*) varied according to the 3 different models; *d* = variable, *d* = 5 years and *d* = 3 years.

2.4 RESULTS

2.4.1 Univariate analysis:

i. *Basic trait statistics*:

Trait specific details of the numbers of trees analysed, mean, maximum and minimum values, and standard deviation are given in Table 2.4. The number of trees increased slightly after HT01 as trees which had died during the first growing season were replaced with trees retained in the nursery. Over 9,200 trees were consistently measured until the 50% chemical thinning reduced the number of trees to around 4,500 for the subsequent traits of DM19 and DM23. The number of trees assessed for DN17 was

slightly lower than the equivalent aged diameter assessment (DM17) as a result of the standard instruction to assessors not to use the Pilodyn on trees below 7 cm DBH. Any bias due to this effective selection should be slight since only 4% of the live trees were rejected on this basis.

Table 2.4: Total number of trees and trees per plot, mean value, standard deviation and maximum and minimum values by trait.

Variable	No of Trees		Mean	Std Dev	Minimum	Maximum
	Total	Per Plot				
Height (cm)						
HT01	8948	23.86	27.63	7.2708	1.00	59.00
HT02	9275	24.73	46.60	13.7892	11.00	95.00
HT03	9242	24.65	69.49	20.6637	7.00	141.00
HT04	9240	24.64	100.46	30.2997	4.00	197.00
HT05	9238	24.63	149.93	39.2107	15.00	295.00
HT06	9239	24.64	189.65	48.1869	23.00	357.00
HT07	9240	24.64	255.42	63.8969	30.00	460.00
HT08	9240	24.64	324.20	73.5832	30.00	530.00
HT09	9227	24.60	359.64	75.1060	30.00	590.00
HT10	9227	24.60	436.56	84.8558	60.00	690.00
HT11	9227	24.60	511.78	93.6187	70.00	780.00
Diameter (cm)						
DM10	9205	24.55	7.41	1.7408	1.00	14.00
DM12	9207	24.55	8.76	1.9278	1.40	16.20
DM14	9207	24.55	9.78	2.1206	2.40	18.10
DM16	9206	24.55	11.15	2.4397	2.70	20.10
DM17	9164	24.43	11.92	2.6608	2.70	21.80
DM19	4542	12.11	12.66	2.7647	2.70	23.40
DM23	4438	11.84	15.08	3.4022	3.40	28.70
Density (mm)						
DN17	8766	23.38	13.06	2.0122	7.00	21.00

Note 1: HT = height, DM = diameter, DN = density, 01 = 1 year from planting etc. Total number of families (f) = 125.

Note 2: Minimum tree size varies greatly and even decreases between HT01 and HT04. Assessors were told to measure all live trees although this interpretation may vary between assessors across years for trees close to death.

ii. *Variance components*

Details of estimated variance components and their proportion of the total phenotypic variance are presented by trait in Table 2.5. The residual error variance (σ_e^2) contained the greatest proportion of the total phenotypic variance although it did seem to fall from HT02 to HT11 (89.1% to 71.9%) with a corresponding increase in σ_f^2 (3.8% to 9.2%) and particularly σ_{fr}^2 (7.2% to 20.36%). As diameter was assessed and the age of the experiment increased (DM10 to DM23), the importance of σ_e^2 increased again (71.9% to 95.9%), and that of σ_f^2 and σ_{fr}^2 decreased (7.7% to 3.7% and 1.6% to 0.4% respectively). Although it was difficult to differentiate between changes in variance components associated with trait and those associated with time, similar aged assessments (HT10 and DM10) suggest a decrease of σ_f^2 (8.8% and 7.7%) and particularly σ_{fr}^2 (20.6% and 1.56%) for diameter traits relative to height traits.

DN17 went against the trend for diameter traits around the same age. There was a greater proportion of variance between family (σ_f^2) for this trait (10.8%) than any other trait analysed and while σ_{fr}^2 was larger than any diameter trait it was lower than most of the height traits.

iii. *Heritabilities*

Total phenotypic (σ_P^2) and additive (σ_A^2) variance components, and single tree (h_i^2) and family mean (h_f^2) heritabilities are presented in Table 2.6. The variation with trait of h_i^2 and h_f^2 is given in Figure 2.1. Single tree heritability reflects the relative importance of σ_f^2 in Table 2.5 in that it tended to rise with age of HT assessment and fall with age of DM assessment. A slight reversal of this trend has occurred following thinning. The values of σ_f^2, σ_A^2 and h_i^2 all increased slightly for DM19 and DM23 relative to DM17. The h_i^2 for DN17 was very high. The values of h_f^2 remained fairly constant with age and trait (HT02 = 0.52, DM23 = 0.57); only DN17 had an appreciably higher h_f^2 (0.71).

Table 2.5: Univariate Analysis: Estimated variance components and standard errors

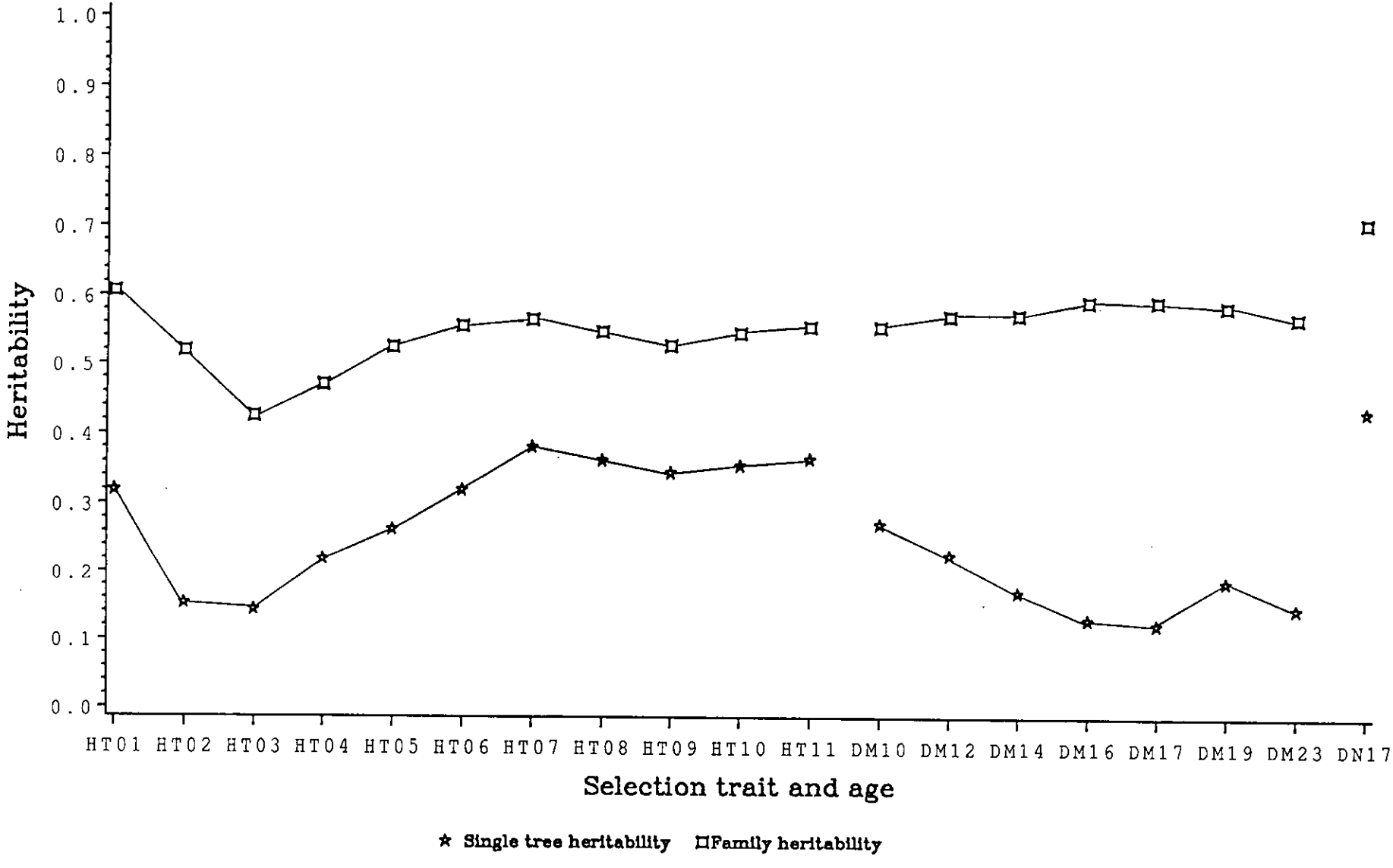
	σ_f^2	SE	σ_f^2/σ_p^2 x 10^2	σ_{fr}^2	SE	σ_{fr}^2/σ_p^2 x 10^2	σ_e^2	SE	σ_e^2/σ_p^2 x 10^2
HT01	4.2256	0.9203	7.98%	6.4650	0.7437	13.03%	42.2289	0.6450	79.80%
HT02	7.0509	1.8213	3.83%	12.9222	1.7612	7.23%	163.979	2.4580	89.14%
HT03	14.5290	4.6880	3.60%	44.9151	5.2986	11.40%	344.506	5.1743	85.28%
HT04	47.6876	13.7353	5.51%	132.887	14.4445	15.98%	684.785	10.2859	79.13%
HT05	95.0619	24.2200	6.60%	211.085	23.1115	15.42%	1133.23	17.0236	78.73%
HT06	175.228	41.8560	8.02%	350.316	37.5375	17.08%	1658.55	24.9136	75.94%
HT07	368.670	86.3050	9.57%	731.852	75.7902	20.50%	2752.32	41.3409	71.44%
HT08	470.626	114.117	9.12%	1007.41	103.924	20.98%	3680.62	55.2840	71.35%
HT09	467.114	118.081	8.69%	1090.18	111.869	21.69%	3816.82	57.3718	71.02%
HT10	619.232	150.676	8.93%	1329.83	137.673	20.56%	4987.83	74.9734	71.90%
HT11	779.747	186.108	9.18%	1608.38	166.766	20.36%	6104.35	91.7561	71.88%
DM10	0.2000	0.0477	7.74%	0.0381	0.0428	1.56%	2.3464	0.0353	90.79%
DM12	0.2055	0.0475	5.71%	0.3317	0.0411	9.63%	3.0643	0.0461	85.08%
DM14	0.1893	0.0436	4.30%	0.2561	0.0376	6.01%	3.9604	0.0596	89.89%
DM16	0.1944	0.0431	3.30%	0.1699	0.0357	2.96%	5.5232	0.0831	93.81%
DM17	0.2188	0.0485	3.11%	0.1730	0.0402	2.52%	6.6330	0.1001	94.42%
DM19	0.3573	0.0801	4.71%	0.1624	0.0682	2.22%	7.0699	0.1545	93.15%
DM23	0.4282	0.1005	3.70%	0.0406	0.0894	0.36%	11.0900	0.2459	95.94%
DN17	0.4349	0.0791	10.97%	0.3908	0.0472	10.83%	3.1383	0.0485	79.17%

Note: 1. Total phenotypic variation, $\sigma_p^2 = \sigma_f^2 + \sigma_{fr}^2 + \sigma_e^2 = 100\%$; 2. $\sigma_e^2 = \frac{3}{4}\sigma_A^2 + \sigma_{NA}^2 + \sigma_W^2$; 3. σ_W^2 = random environmental error.

Table 2.6: Univariate Analysis: Estimates of total phenotypic and additive variance, together with single tree and family heritabilities

	σ_P^2	SE	σ_A^2	SE	h_i^2	SE	h_f^2	SE
HT01	52.9195	1.1887	16.9024	3.6815	0.3194	0.0655	0.6062	0.0614
HT02	183.952	3.1508	28.2036	7.2951	0.1533	0.0386	0.5194	0.0748
HT03	403.950	7.5021	58.1160	18.7923	0.1440	0.0455	0.4256	0.0894
HT04	865.360	18.8730	190.750	54.9848	0.2204	0.0614	0.4710	0.0823
HT05	1439.38	32.1697	380.248	97.1536	0.2642	0.0644	0.5259	0.0738
HT06	2184.09	52.8014	700.912	167.2146	0.3209	0.0724	0.5573	0.0689
HT07	3852.84	104.5949	1474.68	345.1849	0.3828	0.0836	0.5673	0.0673
HT08	5158.66	139.5216	1882.50	456.4898	0.3649	0.0830	0.5497	0.0700
HT09	5374.11	145.5198	1868.46	472.8942	0.3477	0.0829	0.5295	0.0732
HT10	6936.89	184.8443	2476.93	602.0937	0.3571	0.0816	0.5480	0.0703
HT11	8492.48	225.4183	3118.99	735.3257	0.3673	0.0821	0.5576	0.0688
DM10	2.5845	0.0633	0.8000	0.1904	0.2734	0.0622	0.5576	0.0688
DM12	3.6015	0.3115	0.8220	0.2386	0.2283	0.0506	0.5746	0.0662
DM14	4.4058	0.0765	0.7572	0.1757	0.1719	0.0384	0.5764	0.0659
DM16	5.8875	0.0947	0.7776	0.1686	0.1321	0.0286	0.5962	0.0629
DM17	7.0248	0.1091	0.8752	0.1866	0.1246	0.0270	0.5969	0.0629
DM19	7.5896	0.1441	1.4292	0.2222	0.1883	0.0409	0.5896	0.0638
DM23	11.5588	0.1929	1.7128	0.2636	0.1482	0.0340	0.5733	0.0675
DN17	3.964	0.0958	1.7396	0.3127	0.4389	0.0725	0.7131	0.0447

Figure 2.1: Variation of single tree and family heritability with selection trait



2.4.2 Bivariate analysis:

A total of 86 separate bivariate analyses were carried out. A matrix of the estimated r_A and r_P values is given in Table 2.7. In general, r_A was always greater than r_P for two given traits. This was particularly the case for correlations between earlier height traits, and also DN17 with later diameter traits; exceptions involved bivariate analysis of most traits with some of the later diameter assessments (> DM16). Once the standard errors (SE) attached to r_A are taken into account they nearly always embraced the higher r_P. The standard errors associated with r_P were consistently lower than those associated with r_A reflecting the greater precision with which the former was calculated e.g. $r_{A_{6,23}} = 0.7611 \pm 0.0920$, $r_{P_{6,23}} = 0.6466 \pm 0.0093$.

Genetic correlations of early height traits with DM23 rose quickly to $r_{A_{j,DM23}} > 0.70$ at HT04 and then continued to rise more gradually with age thereafter. All diameter traits had $r_{A_{j,DM23}} > 0.90$. DM10 was better correlated with DM23 than HT10 ($r_{A_{j,DM23}} = 0.90$ and 0.81 respectively) and DM10 and HT10 were not perfectly correlated ($r_A = 0.90$).

Genetic correlations between DN17 and height and diameter traits were initially steady (around 0.50) but rose steeply with later diameter traits reaching $r_A = 0.81$ with DM23.

2.4.3 Optimum selection ages:

2.4.3.1 Selection goal of 23-year diameter:

i. *Generation Efficiency*

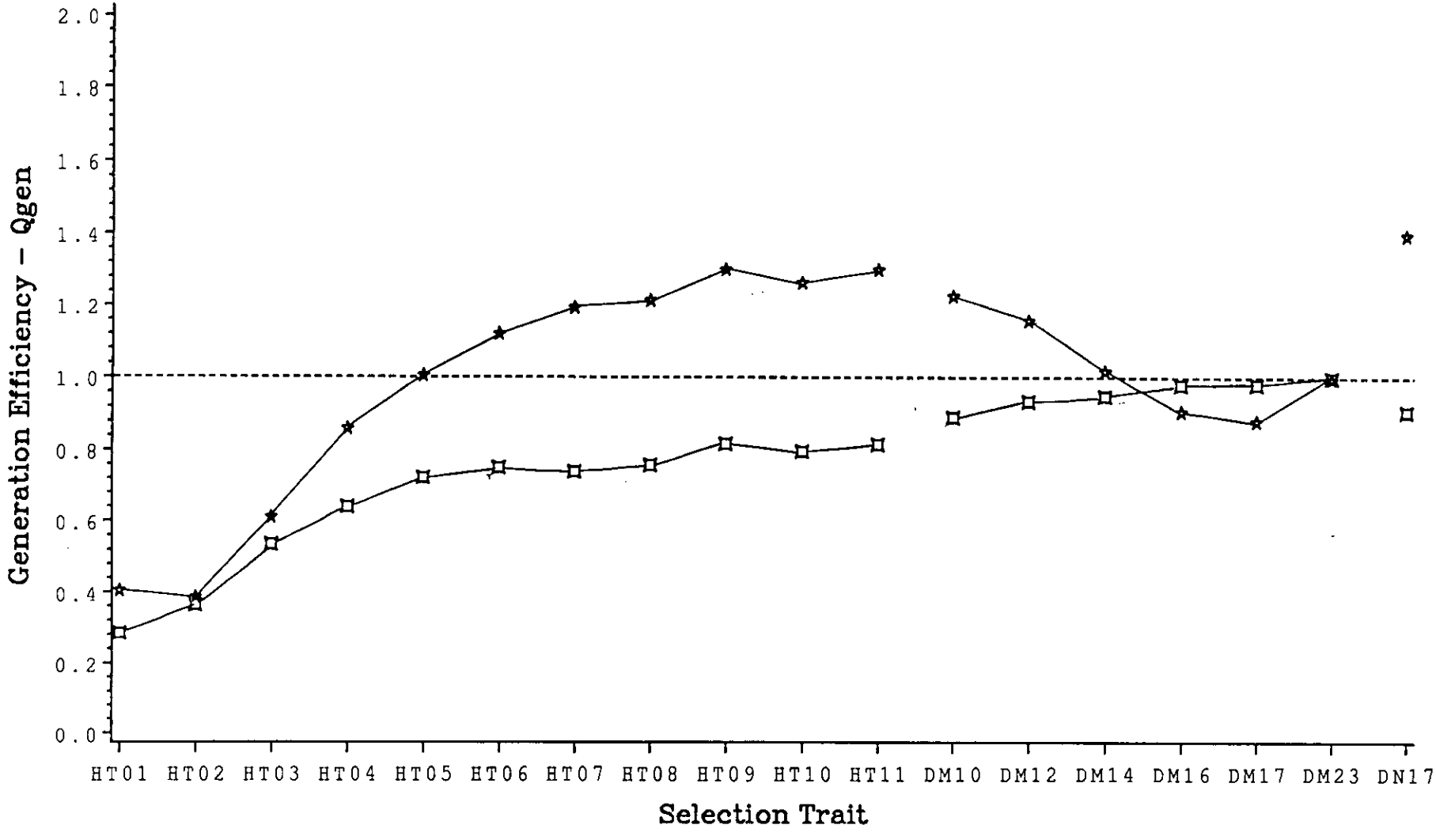
Figure 2.2 shows how Q_{gen} varied with age (data in Appendix 2.11). There was a clear distinction between Q_{gen} for the individual tree which rose to a peak of 1.30 between HT09 and HT11 before falling, and that for family selection which rose gradually between HT01 to DM23 years, but never exceeded 1.00. The maximum value of Q_{gen} was 1.40; this would be achieved by carrying out indirect, individual tree selection for DM23 based on DN17.

Table 2.7: Bivariate Analysis. Genetic (below diagonal) and phenotypic (above diagonal) correlations between selected traits.

	HT01	HT02	HT03	HT04	HT05	HT06	HT07	HT08	HT09	HT10	HT11	DM10	DM12	DM14	DM16	DM17	DM19	DM23	DN17
HT01	1	0.2243				0.1793				0.1206						0.0735		0.1382	
SE		±0.0130				±0.0160				±0.0170						±0.0165		±0.0155	
HT02	0.9003	1	0.7967	0.6869	0.6595	0.6197		0.4951		0.4410	0.4236		0.5277	0.5024	0.4858	0.4700		0.4264	0.2114
SE	±0.1117		±0.0044	±0.0068	±0.0074	±0.0083		±0.0106		±0.0113	±0.0116		±0.0093	±0.0093	±0.0091	±0.0092		±0.0124	±0.0135
HT03		0.9343	1				0.6746				0.5421		0.6292		0.5687		0.5205	0.4927	
SE		±0.0474					±0.0076				±0.0101		±0.0079		±0.0081		±0.0113	±0.0013	
HT04		0.8544		1	0.8916	0.8329		0.6841			0.6127		0.6906	0.6502	0.6188			0.5402	0.2964
SE		±0.0718			±0.0028	±0.0043		±0.0081			±0.0097		±0.0071	±0.0075	±0.0076			±0.0107	±0.0147
HT05		0.8431		0.9754	1	0.9506		0.7620	0.7354		0.6977	0.7889	0.7624		0.6898		0.6535	0.6127	
SE		±0.0719		±0.0122		±0.0043		±0.0063	±0.0070		±0.0079	±0.0055	±0.0058		±0.0066		±0.0089	±0.0095	
HT06	0.5780	0.7890		0.9303	0.9731	1		0.8203		0.7725	0.7552		0.8011		0.7247	0.7084		0.6466	0.3959
SE	±0.1386	±0.0826		±0.0258	±0.0088			±0.0051		±0.0063	±0.0068		±0.0050		±0.0061	±0.0063		±0.0093	±0.0144
HT07			0.8179				1				0.8158			0.7708			0.6971	0.6465	
SE			±0.0685								±0.0055			±0.0054			±0.0082	±0.0093	
HT08		0.7048		0.8514	0.9157	0.9476		1			0.8632	0.8326	0.8101		0.7370			0.6518	0.4171
SE		±0.1085		±0.0540	±0.0323	±0.0195					±0.0041	±0.0044	±0.0046		±0.0061			±0.0092	±0.0148
HT09					0.8804				1				0.8497			0.7643		0.7004	
SE					±0.0423								±0.0040			±0.0061		±0.0084	
HT10	0.4129	0.6314				0.9114				1		0.8361		0.8000			0.7542	0.7139	0.4310
SE	±0.1519	±0.1199				±0.0312						±0.0044		±0.0048			±0.0072	±0.0082	±0.0144
HT11		0.6053	0.8694	0.7477	0.8408	0.8952	0.9343	0.9454			1		0.8151		0.7806			0.7223	
SE		±0.1223	±0.1067	±0.0792	±0.0526	±0.0360	±0.0239	±0.0184					±0.0046		±0.0052			±0.0080	
DM10					0.8307			0.9073		0.9037		1				0.9079	0.8896	0.8373	0.5133
SE					±0.0521			±0.0278		±0.0295						±0.0031	±0.0042	±0.0051	±0.0120
DM12		0.5802	0.8453	0.7481	0.8095	0.8450		0.8679	0.9249		0.8642		1		0.9642	0.9514	0.9377	0.8872	
SE		±0.1252	±0.1119	±0.0804	±0.0593	±0.0470		±0.0386	±0.0246		±0.0392				±0.0015	±0.0020	±0.0028	±0.0035	
DM14		0.5712		0.7241			0.7896			0.8032				1				0.9305	0.5727
SE		±0.1336		±0.0918			±0.0592			±0.0555								±0.0021	±0.0093
DM16		0.4852	0.5301	0.6301	0.6922	0.7167		0.7068			0.7477		0.9420		1			0.9629	0.5860
SE		±0.1416	±0.1374	±0.1103	±0.0891	±0.0785		±0.0791			±0.0574		±0.0222					±0.0011	±0.0084
DM17	0.3111	0.4506				0.6897			0.7171			0.8370	0.9146			1		0.9715	0.5808
SE	±0.1329	±0.1442				±0.0839			±0.0807			±0.0432	±0.0317					±0.0008	±0.0084
DM19			0.5309		0.6606		0.6400			0.7032		0.8398	0.8909				1		
SE			±0.1474		±0.1019		±0.0970			±0.0867		±0.0569	±0.0428						
DM23	0.2766	0.3810	0.6204	0.7048	0.7537	0.7611	0.7430	0.7737	0.8497	0.8142	0.8264	0.9033	0.9335	0.9460	0.9620	0.9630		1	0.5753
SE	±0.1455	±0.1455	±0.1382	±0.1175	±0.0981	±0.0920	±0.0932	±0.0915	±0.0807	±0.0811	±0.0788	±0.0536	±0.0402	±0.0288	±0.0172	±0.0140			±0.0105
DN17		0.3264		0.4453		0.5107		0.4843		0.4816		0.5488		0.6466	0.6915	0.7020		0.8142	1
SE		±0.1450		±0.1394		±0.1172		±0.1175		±0.1157		±0.1082		±0.0894	±0.0808	±0.0796		±0.0725	

Note: light shading in the body of the table signifies $r_P > r_A$.

Figure 2.2: Variation of individual tree and family Qgen with selection trait



Note (1) : ★ Individual tree ☐ Family (2): Reference line drawn at Qgen = 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 h_f^2 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 greatly with age. Calculated h_i^2 of younger indicator traits often exceeded the 0.15 calculated for DM23, and as $r_{A_{j,\,DM23}}$ increased with the age of the indicator trait, so Q_{gen} occasionally exceeded 1.00.

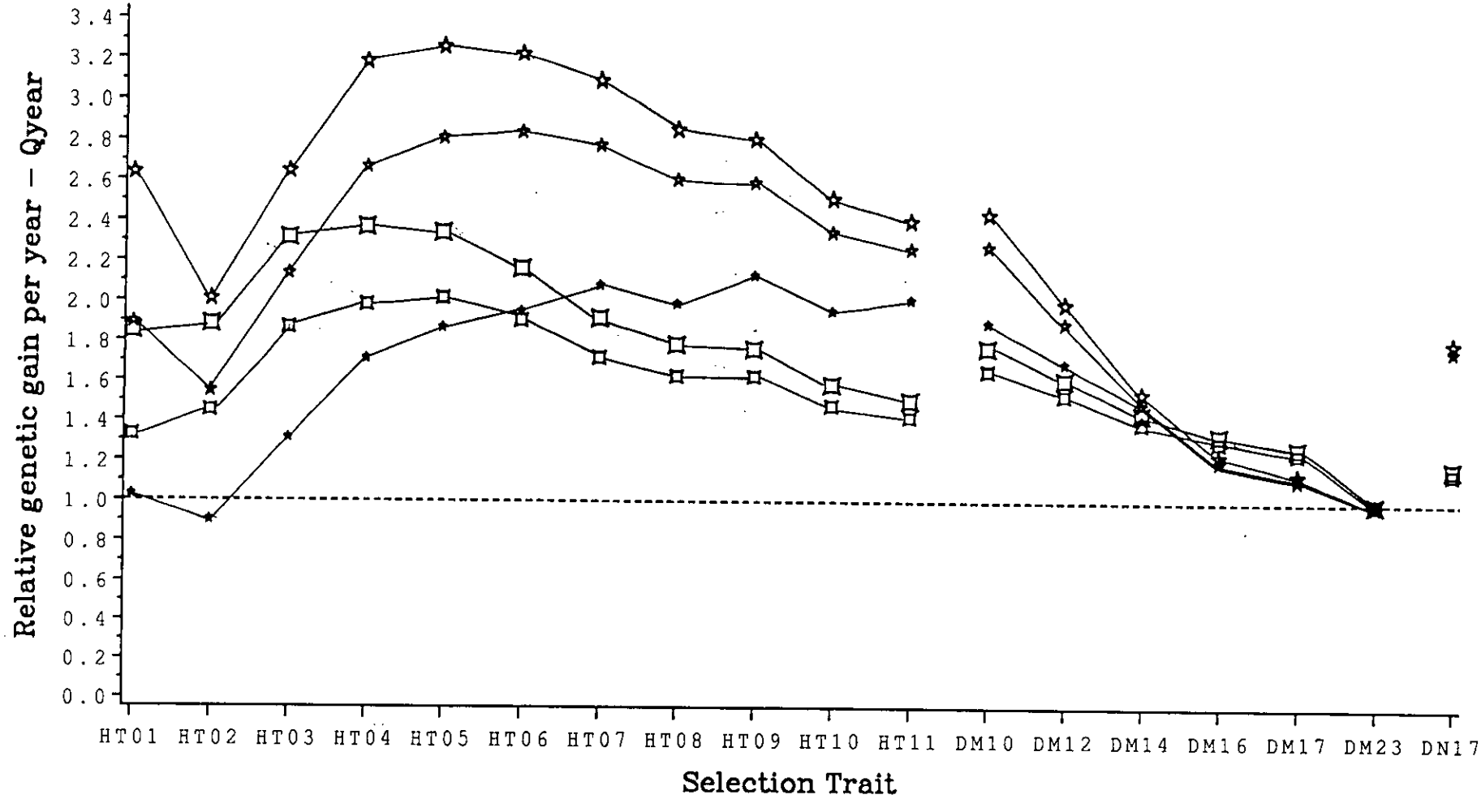
ii. *Relative genetic gain per year*

Figure 2.3 shows how Q_{year} varied with age for family and individual tree selection according to the 3 different Models of delay (*d*) in generation turn-over (data in Appendix 2.11). A summary of the optimum Q_{year} selection age is given in Table 2.8. 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 was reduced to HT04 and efficiency per year was further increased ($Q_{year} = 2.37$). When *d* was either 3 or 5 years, the value of Q_{year} for family selection varied only slightly between HT03 and HT06.

Table 2.8: **Selection goal of 23-year diameter: summary of optimum selection traits and ages in terms of genetic gain per year (Q_{year}). All figures are in years**

Delay (*d*)	Optimum Selection Age	
	Family	Individual Tree
variable	-	HT09
5 years	HT05	HT06
3 years	HT04	HT05

Figure 2.3: Variation of relative individual tree and family Qyear with selection trait



Note (1): ★ Indiv, d=variable ☆ Indiv, d = 5 years ☆ Indiv, d = 3 years
Note (2) □ Family, d = 5 years □ Family, d = 3 years
Note (3) : Reference line drawn at Qyear = 1.00

The selection trait which optimised Q_{year} for individual tree selection when d = variable was HT09 which was 4-5 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 and HT05 respectively.

2.4.3.2 **Selection goal of 40-year height or diameter**

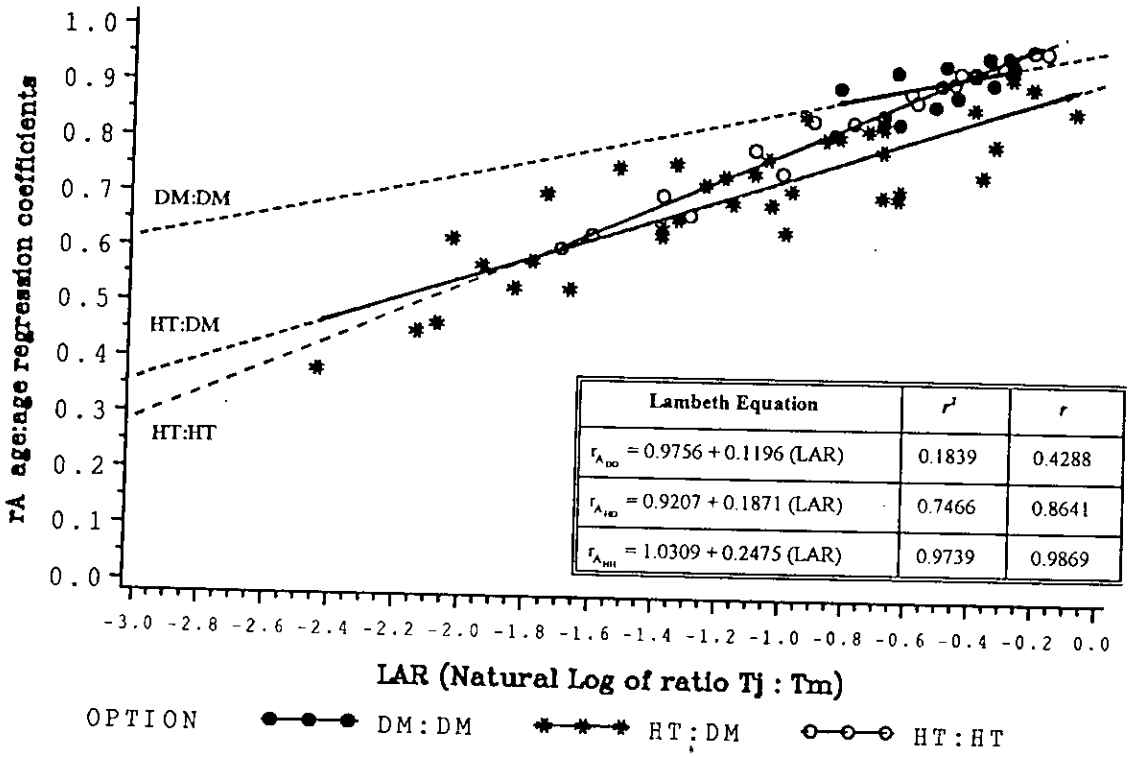
i. *Comparison of predictive equations*

Figures 2.4 and 2.5 show the linear relationship between LAR and (i) $r_{A_{DD}}$, $r_{A_{HH}}$, $r_{A_{HD}}$ and (ii) $r_{P_{DD}}$, $r_{P_{HH}}$ and $r_{P_{HD}}$ respectively together with the estimated Lambeth regression equation and correlation coefficients. The data used to plot Figures 2.4 and 2.5 are given in Appendix 2.12.

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

The regression equations for $r_{A_{DD}}$ and $r_{P_{DD}}$ were based on a narrow range of LAR (-0.30 to -0.83 DM10 to DM23). The range of LAR increased for $r_{A_{HH}}$, $r_{P_{HH}}$ (-0.40 to -1.17; HT02 to HT11) and $r_{A_{HD}}$, $r_{P_{HD}}$ (-0.09 to -2.44; HT02 to DM23), giving extrapolation of these latter regression lines a more reliable foundation.

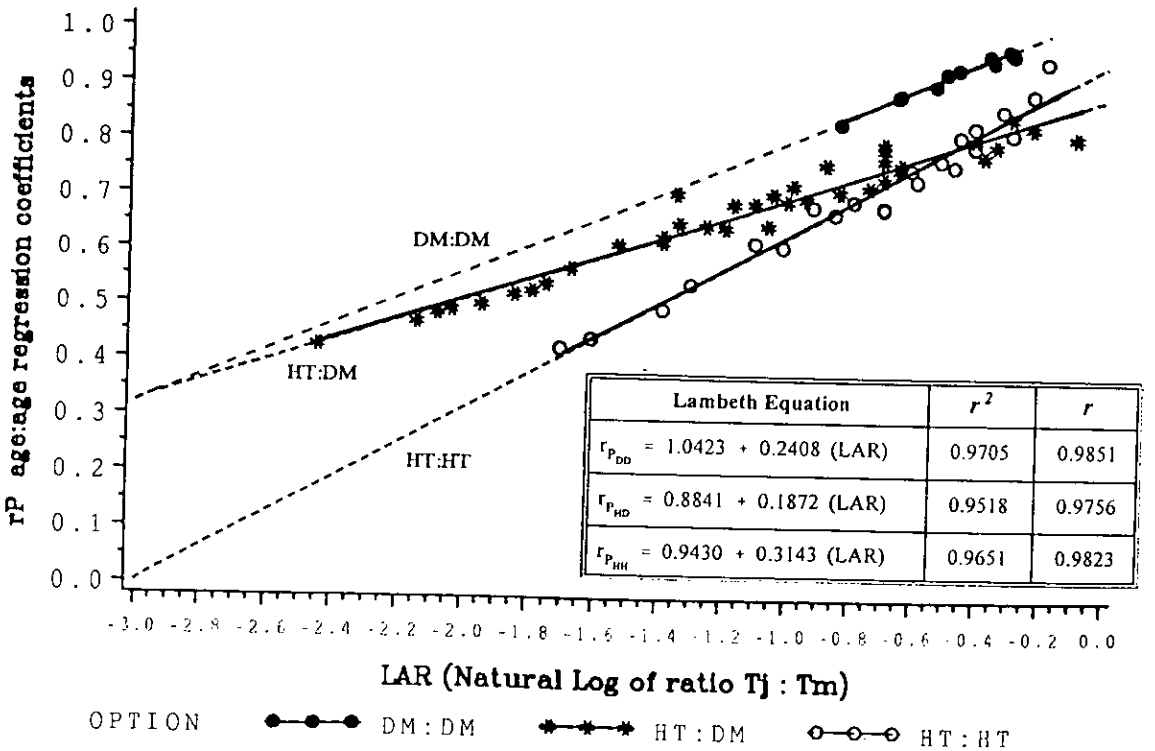
Figure 2.4: LAR against genetic correlations for
(i) diameter:diameter, (ii) height:diameter, (iii) height:height



Lambeth Equation	r^2	r
$r_{A_{DD}} = 0.9756 + 0.1196$ (LAR)	0.1839	0.4288
$r_{A_{HD}} = 0.9207 + 0.1871$ (LAR)	0.7466	0.8641
$r_{A_{HH}} = 1.0309 + 0.2475$ (LAR)	0.9739	0.9869

Note: dotted line indicates extrapolation of regression line

Figure 2.5: LAR against phenotypic correlations
(i) diameter:diameter, (ii) height:diameter, (iii) height:height



Lambeth Equation	r^2	r
$r_{P_{DD}} = 1.0423 + 0.2408$ (LAR)	0.9705	0.9851
$r_{P_{HD}} = 0.8841 + 0.1872$ (LAR)	0.9518	0.9756
$r_{P_{HH}} = 0.9430 + 0.3143$ (LAR)	0.9651	0.9823

Note: dotted line indicates extrapolation of regression line

ii. *Correlations with 40-year height or diameter*

Values of $r_{A_{j,40}}$ and $r_{P_{j,40}}$ 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 Figure 2.4 and 2.5. Data are presented in Appendix 2.13.

In all cases, since heritabilities were assumed fixed across age, $r_{j,40}$ increased with increasing value of T_j. Estimated values of $r_{A_{j,40}}$ were greater than $r_{P_{j,40}}$ on all occasions. Table 2.9 is a summary of the maximum genetic and phenotypic values estimated from all six equations; in all cases optimum T_j = 15 years.

Table 2.9: Maximum genetic and phenotypic correlations estimated by the three regression options of diameter:diameter, height:height and height:diameter

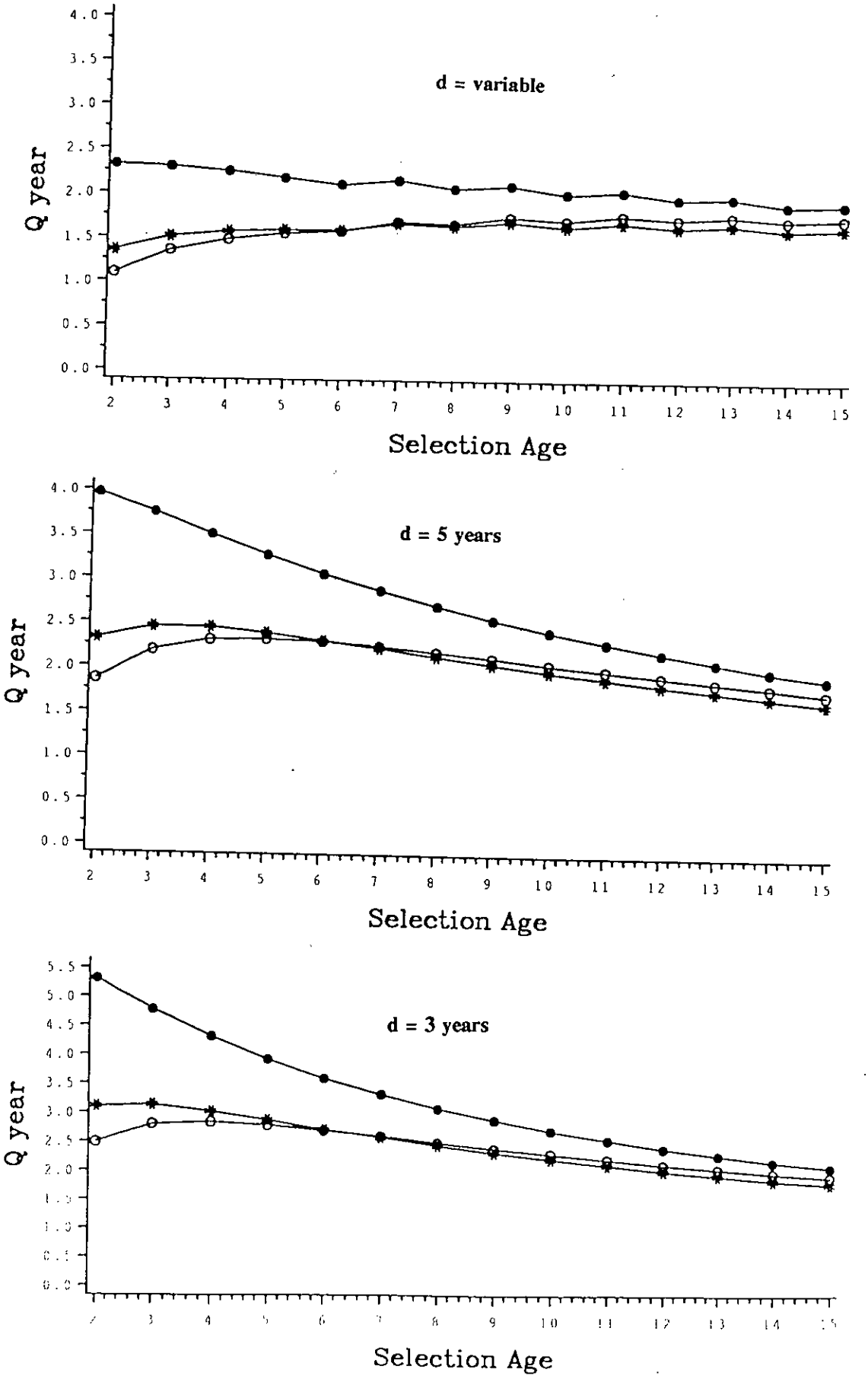
Regression Option	$r_{A_{15,40}}$	$r_{P_{15,40}}$
Diameter:diameter	0.8583	0.8062
Height:height	0.7882	0.6360
Height:diameter	0.7372	0.7005

Estimated $r_{A_{j,40}}$ and $r_{P_{j,40}}$ values were always higher for the diameter:diameter option and a given value of T_j compared to the other two regression options. Estimated $r_{A_{j,40}}$ values were higher for the height:height regression option compared to height:diameter although this was reversed for $r_{P_{j,40}}$ where the height:height regression option gave the lowest estimated values of $r_{j,40}$ for any value of T_j.

iii. *Relative genetic gain per year.*

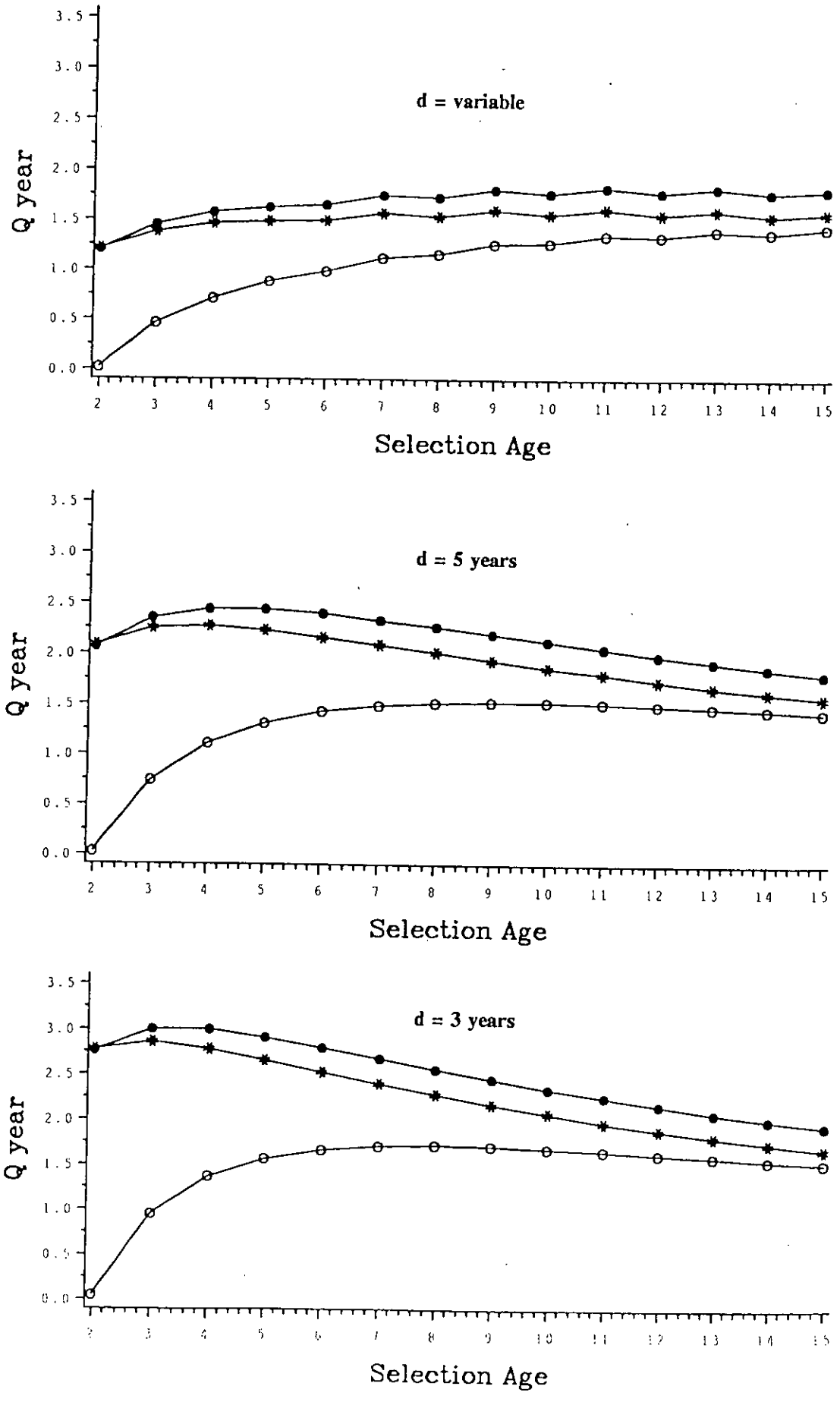
Figure 2.6 shows how Q_{year} varied with selection age when (i) d = variable, (ii) d = 5 years and (iii) d = 3 years for the genetic correlation options of diameter:diameter, height:height and height:diameter, following substitution of $r_{A_{j,40}}$ in equation 1.5. Figure 2.7 gives similar information for the phenotypic correlation options. Since

Figure 2.6: Genetic correlations – Qyear against selection age for regression options DM:DM, HT:DM and HT:HT



Note 1 : ● (i) diameter:diameter * (ii) height:diameter o (iii) height:height

Figure 2.7: Phenotypic correlations – Qyear against selection age for regression options DM:DM, HT:DM and HT:HT



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

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

heritabilities were assumed to be constant with age, the values of Q_{year} are applicable to both family and individual tree selection. (Data in Appendix 2.13.)

A summary of ages when Q_{year} is optimised using the Lambeth regression equations is given in Table 2.10. It is clear that optimum selection ages can be reduced, often by around 2-4 years, by building a model based on genetic rather than phenotypic correlations. Trends were similar to the selection goal of 23-year diameter in that the optimum age for individual tree selection (d = variable) was generally higher than family selection (d = 5 or 3 years). A common range of selection ages for both genotypic and phenotypic correlation when d = variable was 9-15 year height or diameter. This fell quickly to 7-11 year if just genetic correlation were considered and 4-6 years and 2-5 years when d = 5 and d = 3 respectively. Particularly low selection ages (DM02) were suggested by the $r_{A_{DD}}$ option regardless of the value of (d). This possibly illustrates the unreliability of extrapolating a narrow range of LAR to calculate $r_{A_{j.\,40}}$ using the Lambeth equation.

The lowest selection ages based on Q_{year} were generated by the $r_{A_{HD}}$ option; individual tree selection at 7-9 year height when d = variable falling to family selection based on 3-4 or 2-3 year height when d = 5 and 3 years respectively. 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.

Table 2.10: Selection goal of 40-year height or diameter: summary of optimum 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*)	$r_{A_{DD}}$	$r_{A_{HH}}$	$r_{A_{HD}}$
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*)	$r_{P_{DD}}$	$r_{P_{HH}}$	$r_{P_{HD}}$
variable	9-15	13-15	9
5 years	4-6	8-10	3-5
3 years	3-4	7-9	2-4

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

2.5 DISCUSSION

i. *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 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 calculated from combined analysis across sites for height and diameter over a limited number of ages between 1 and 15 years from planting when analysing variance components from a selected population. He generally found h_f^2 to be higher than the equivalent trait in this study (e.g. 0.83 and 0.82 for 3-year and 6-year height; 0.71 and 0.75 for 10-year and 15-year diameter).

A confounding element concerning comparisons with other studies involving Sitka spruce is that this study involved analysis at just one site, while Samuel and Johnstone (1979) and Gill (1987) investigated combined analysis across 3 and 8 sites respectively. It is possible that any family by site interaction (σ^2_{fs}) in this study will be included in σ^2_f, inflating estimated h_i^2. Samuel and Johnstone (*op. cit.*) actually found no significant σ^2_{fs} beyond 3-years old. Figures presented by Gill (*op. cit.*) however, suggest σ^2_f could be inflated by an average of 40% if it was inclusive of σ^2_{fs}. However Gill (*op. cit.*) was analysing progeny from (i) selected trees which were (ii) not all of the same 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. This illustrates the importance of knowing the origin and degree of selection operating in phenotypes when presenting variance components based on measurements of the genotypes.

The relatively high estimated h_i^2 for the indirect assessment of density using the Pilodyn (DN17) is similar to Lee (1993; $h_i^2 = 0.45$) who also measured density indirectly using the Pilodyn. Wood (1986) found an even higher value of h_i^2 (0.73) when assessing density directly using X-ray densitometry. As in Gill (1987), both Lee (*op. cit.*) and Wood (*op. cit.*) reported on selected trees which were not all from the same origin and some experiments were common to all three studies.

ii. *Genetic correlation*

Estimated genetic correlations tended to be lower than those found by Gill (1987) who found r_A between 6 and 10-year height, 6-year height and 10-year diameter and 6-year height and 15-year diameter to be 0.93, 0.90 and 0.78 respectively compared to 0.91, 0.84 (with DM12) and 0.72 (with DM16) in this study. The genetic correlations found here between DN17 and various vigour traits increased steadily to around $r_A = 0.50$ for HT06 through to DM12 before increasing again with age up to $r_A = 0.81$ with DM23. This latter value was higher than the previous correlations between wood density and

15-year diameter found by Wood (1986) and Lee (1995) (see Table 1.2). This is of some concern since Pilodyn reading is inversely correlated with density, suggesting a stronger negative genetic correlation between wood density and diameter than was previously considered.

In all cases, genetic correlations were assumed to be due to pleiotropy rather than linkage disequilibrium. Pleiotropy is simply the property of a gene whereby it affects two or more characters whereas linkage is more applicable to crosses between divergent strains (Falconer, 1981), which ought not to be applicable in this study.

iii. *Optimum selection ages for 23-year diameter*

The superiority of early height traits for h_i^2 relative to the selection goal of DM23 is important when calculating the selection age which optimises Q_{gen} for individual tree selection. Since h_f^2 does not vary much across ages, family selection Q_{gen} is more dependent on r_A which rises gradually but never exceeds 1.00 as indirect selection age approaches that of the direct selection age. The optimum selection age based on genetic gain per year (Q_{year}) for family selection falls dramatically from DM23 as predicted by Q_{gen} to HT05 or HT04. Optimum individual tree selection age based on Q_{year} when (*d*) is variable is similar to that predicted by Q_{gen} (HT09). This differential 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 that the optimum family selection ages from his selected Sitka spruce population were between 3 and 6-year height when the breeding goal was 15-year diameter. Variation in (*d*) or individual tree selection was not considered.

The accuracy of estimated Q_{year} when d = variable, is dependent on the probability that the values of (*d*) given in Table 2.3 are correct for a given selection age. Based on current knowledge, it is unlikely that the values of (*d*) are underestimated for

T_j < 15 years. If true values of (*d*) when T_j < 15-years are lower than those presented, the effect will be to lower the optimum selection age based on Q_{year} to less than HT09, but greater than HT06. Until such time that clear evidence can be presented regarding actual (*d*) when T_j < 15-years, it would be prudent to retain the optimum individual tree selection age based on Q_{year} as HT09.

iv. *Optimum selection ages for 40-years height or diameter*

The Lambeth regression equations were used to calculate optimum selection ages over a 40-year rotation and 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 4-5 years if the delay in generation turnover could be reduced by bringing trees to flower at an earlier age ($d = 5$ or $d = 3$ rather than $d = 8$ or 9 years);

iii. optimum individual tree and family mean selection ages were similar across the two breeding goals despite the 17-years 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. Previous studies involving the construction of a Lambeth regression equation had tended to involve either height (Lambeth, 1980, 1983; and Riemenschneider, 1988) or diameter (King and Burdon, 1991). However, a recent study with a highly selected population of Sitka spruce in Denmark (15 half-sib families) investigated use of the Lambeth regression when the

breeding goal was 21-year plot basal area and juvenile selection ages were height at 2-, 5-, 9- and 14-years (Jenson, *et al.*, 1996).

This is an important practical point since 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 (around 10-years from planting, equivalent to 4-5 m with Sitka spruce in Britain). Construction of a Lambeth equation based on the regression of LAR against $r_{A_{HD}}$ or $r_{P_{HD}}$ values from the data is conceptually acceptable provided it is restricted to those components and does not include $r_{A_{HH}}$ or $r_{A_{DD}}$ (or their phenotypic equivalents) in addition. 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 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 (i) there were differences between outcomes from using genetic rather than phenotypic correlations thus disproving Lambeth's (1980) basic assumption that $r_A = r_P$ and (ii) the benefits of breeding would be greater (shorter generation interval) as a result of using models based on genetic rather than phenotypic correlations. The $r_{A_{HD}}$ model gave the lowest optimum selection age of 7-9 year height for individual trees (d = variable) and 3-4 year height for family-mean selections (d = 5 years).

Jensen *et al.* (1996) concluded that the optimum family-mean selection age for their highly selected Sitka spruce families in Denmark was 9-year height based on correlated gain for 21-year plot basal area. They did not take generation turn-over delay into account. Obviously this is a much higher age than the 3-4 years found in this study and could reflect problems associated with a small sample size.

In practise, 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 7-9 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 these of Lambeth (1980) who concluded that 8-years height was the optimum selection age when rotation length is 40-years, however, this assumed $d = 5$ years and not $d = 9$ years as it would be in this study according to the model d = variable.

v. *Importance of the genetic structure of this study*

A major strength of the results reported here is that they represent vigour traits and one indirect assessment of wood density, over the first half of a rotation, from a large, randomly selected Sitka spruce population of known origin. These are the oldest assessments ever reported from a randomly selected (or indeed, selected) population of Sitka spruce growing in Britain. Comparison of variance components, heritabilities and genetic and phenotypic correlations with those found in previous studies carried out in Britain or elsewhere on selected populations is difficult since:

i. the effects of selection would have to be taken into account;

ii. the selected populations may not be of the same known origin;

iii. the selected populations may contain a low number of progenies.

The effect of selection would be to reduce σ_f^2 for a given age, which would in turn reduce estimates of h_i^2 and h_f^2. 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. The degree to which (i) and (ii) above have influenced the results of Gill (1987), Wood (1986) and Lee (1993) remains unknown.

The effect of (iii) above would be to increase the standard errors of any estimated variance component or heritability. This criticism is particularly applicable to the population of just 15 open-pollinated Sitka spruce families (Jensen *et al.*, 1996) all of which were *assumed* to be of Washington origin.

2.6 CONCLUSIONS

i. Individual tree heritabilities are higher for early height traits compared to later diameter traits. Family heritabilities are little changed across years regardless of whether the trait is height or diameter. Indirect assessment of wood density (DN17) is a highly heritable trait expressing the largest single tree and family heritabilities of all the traits measured.

ii. Genetic correlation tended to exceed phenotypic correlations. 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. The genetic correlation of DN17 with DM23 was very high (-0.81) suggesting a stronger negative correlation between wood density and diameter than had been previously considered.

iii. 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.

iv. Q_{year} for individual tree selection was also maximised by selecting for HT09 assuming a selection goal of DM23. 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.

v. Estimated Q_{year} based on various Lambeth regression equations and 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 ($r_{A_{HD}}$) against LAR. This model predicted an optimum individual tree selection age of 7-9 years height (when *d* = variable) and family-mean selection age of 3-4 year height (*d* = 5 years) for a selection goal of 40-year diameter. As in (iv) above optimum individual tree selection age is reduced (by 4-5 years) if (*d*) can be reduced to 5 years.

CHAPTER 3

MAIN STUDY: Collection and analysis of wood density data

3.1 INTRODUCTION

The only previous detailed study into the variation of wood density with age of Sitka spruce trees in a progeny test was carried out by Wood (1986) who investigated a selected population of trees, most of which were thought to be of QCI origin, but some of which were of unknown origin. The main findings of Wood (*op. cit.*) were:

i. a strong negative phenotypic correlation between whole-tree density and diameter breast height for trees aged 15-years from planting (r_p = -0.34 to -0.69);

ii. that the Pilodyn was a quick non-destructive tool for measuring wood density in a large number of trees and correlated well with density measured using X-ray densitometry (r_p = -0.69) in 15-year old trees;

iii. density was a highly heritable trait (h_i^2 = 0.73).

Genetic correlations between traits and methods of assessment of wood density were not investigated and, as outlined in Chapter 1, Section 2.5.3., age:age correlations for wood density were not investigated exhaustively by Wood (1986). However, it has since then been the practice of the Tree Improvement Branch of the British Forestry Commission to screen trees in progeny tests for wood density at about 15-years from planting (DN15), using the Pilodyn.

Under the current practice, the time delay between family-mean indirect selection for vigour (based on 6-year height) and wood density (based on 15-year pin penetration of the Pilodyn) is frustrating for tree breeders trying to progress through generations as quickly as possible. Final selection of genotypes for breeding and production populations has to be delayed until data are available for all traits 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 the work reported in this Chapter were to take increment cores from representative trees in the randomly selected Sitka spruce population of known origin growing in Garcrogo 3 (the "Main Study") and assess wood density using indirect X-ray densitometry techniques in order to obtain unbiased estimates of:

i. how variance and covariance components and heritabilities associated with wood density vary over a range of ages;

ii. the phenotypic and genetic correlations between mature wood density and density assessed at younger ages;

iii. the phenotypic and genetic correlation between wood density and vigour.

Additional objectives were to:

i. compare results with Wood (1986);

ii. recommend optimum early selection ages for wood density in progeny tests.

3.2 MATERIALS AND METHODS

3.2.1 Details of the main study and site:

Full details regarding the genetic structure of the families contained within Garcrogo 3 (the 'Main Study'), description of the site, experimental design, and silviculture practised since planting are given in Chapter 2 and Appendix 2.2.

3.2.2 Selection of Trees for X-Ray Densitometry Analysis:

The X-raying of the sample cores, passing the developed X-ray image through the densitometer and generation of the results files were all carried out under contract by Oxford Forestry Institute (OFI). An earlier estimate (supplied by OFI) of the unit cost of X-ray analysis meant that resources would allow a maximum of 700 trees to be analysed. It would therefore be necessary to select a sub-sample from the (approximately) 4400 live trees growing in the Main Study.

The total number of trees to be sampled is a function of the number of trees per family (n) and the number of families (N). In this case nN must not exceed 700 trees. It follows therefore that as n increases, N will decrease. The problem was to determine the correct balance of n and N to allow accurate, unbiased estimates of genetic variances and covariances; neither value could be ignored at the expense of the other. The number of trees per family (n) is important in influencing the errors attached to family-mean values and estimates of single-tree heritabilities, whilst the number of families (N) is important when investigating phenotypic and genetic correlations across sites and ages (Robertson, 1957). If all the families were to be assessed (N = 125) then n = (700/125) = 5.6 trees which is less than 2 trees per replicate. If all the trees representing a family were to be assessed, n would be (approximately) 12 trees/plot x 3 replicates = 36 and N would be (700/36) = 19. When N is maximised, n per replicate is too small and when n is maximised, N is too small.

Robertson (1959), found n to be optimised according to the formula:

$$n = \frac{1}{h_i^2} \times 4 \qquad (3.1)$$

Substituting previous estimates of h_i^2 for wood density from selected populations of Sitka spruce by Lee (1993; $h_i^2 = 0.41$) and Wood (1986; $h_i^2 = 0.73$) into Equation 3.1 gives values of $n = 10$ and 6 trees respectively (rounded up to nearest whole tree). These figures need to be treated with caution since (i) Lee (1993) estimated wood density indirectly by penetrating the outer 2-3 rings of 15-year-old trees using the Pilodyn and (ii) Wood (1986) restricted assessments to the outer 5 to 7 rings of similar aged trees. Nothing is known of heritability estimates of wood density for rings close to the pith or of trees from unselected populations. A large value of n would be necessary to reduce errors if $h_i^2 \leq 0.40$ for rings close to the pith.

Cotterill and James (1984) found a value of n of between 10 and 20 to be the optimum number of trees per family for most traits assessed in progeny tests assuming a Single Plant Plot (SPP) design. McCutchan *et al.* (1989) also recommended a SPP design and found $n = 5$, $n = 10$ and $n = 20$ to be the optimum number of trees when $h_i^2 = 1.0$, 0.33 and 0.18 respectively. Both studies found multiple plant plots to be less efficient (larger errors) in the estimation of h_i^2.

A restriction of the Main Study is the large plot size and relatively small number of replications. This is far removed from the optimum SPP design recommended by Cotterill and James (1984) and McCutchan *et al.* (1989). Any increase in n to compensate for restrictions of experimental design would cause a reduction in N. Also, any increase in n should ideally be in units of 3 to retain a balance of trees per family across replicates. As n is increased from 9 to 12, 15 or 18 trees, so N is reduced from 77 to 58, 46 or 39 families respectively.

It is rare amongst the literature to find N greater than 50 families. Only four of the studies previously listed in Table 1.1 (heritability of wood density) and two of the studies listed in Table 1.4 (age:age correlations of wood density) had values of N greater than 50 (Lee, 1993; Park, *et al.*, 1989; Dean, 1990 and Talbert, *et al.*, 1983; and Adams, *et al.*, 1990 and Talbert, *et al.*, 1983 respectively). One of the most comparable studies from Tables 1.1 and 1.4, is that by Talbert, *et al.* (1983) which reported heritabilities and age:age genetic correlations from an unselected population of loblolly pine progenies. The progeny test was replicated over two sites but the design at each site was just two replications of large multiple tree plots (originally $n = 25$). Investigations of density variance and covariance components used $n = 14$ (per site) and $N = 45$.

Values of $n = 15$ and $N = 46$, ($nN = 690$) were chosen for this study as the optimum combination of n and N likely to give the lowest errors attached to estimates of heritabilities and genetic correlations given the financial restriction of nN, and physical restrictions of experimental design.

3.2.2.1 **Selection of families to be sampled:**

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.

One option in selecting the sub-sample of families for wood density would have been to randomly select families from each dominance class in the same proportion as the complete population (see Table 2.1). Equations presented 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. This involves making estimates of variance

components based on the progeny of parents and selecting those individuals which expressed particularly high and low values for the trait of interest.

Whenever there is known to be a strong genetic correlation between a primary trait under selection (wood density) and a secondary trait (in this case stem-diameter; see Table 1.2 and Table 2.7), both traits need to be considered when selecting a sub-sample if bias, particularly in the relationship between those two traits, is to be avoided.

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 relationship regression of t_1 on t_2. Such a regression was referred to as a *phenotypic selection ellipse*. They suggested that parental data for t_1 and t_2 should be standardised before plotting t_1 on t_2. 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:

$$w = \frac{(t_1 + t_2)^2}{(1 + r_p)} + \frac{(t_1 - t_2)^2}{(1 - r_p)} \qquad (3.2)$$

where: w = index value calculated according to Equation 3.2 indicating distance from origin.

r_p = phenotypic correlation coefficient of t_1 on t_2.

and t_1, t_2 = standardised data for the two correlated traits of interest.

Although total tree height of the parental ortets was assessed at time of felling, wood density was not and therefore 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 DN17 and DM16 assessments carried out previously in the Main Study. 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.

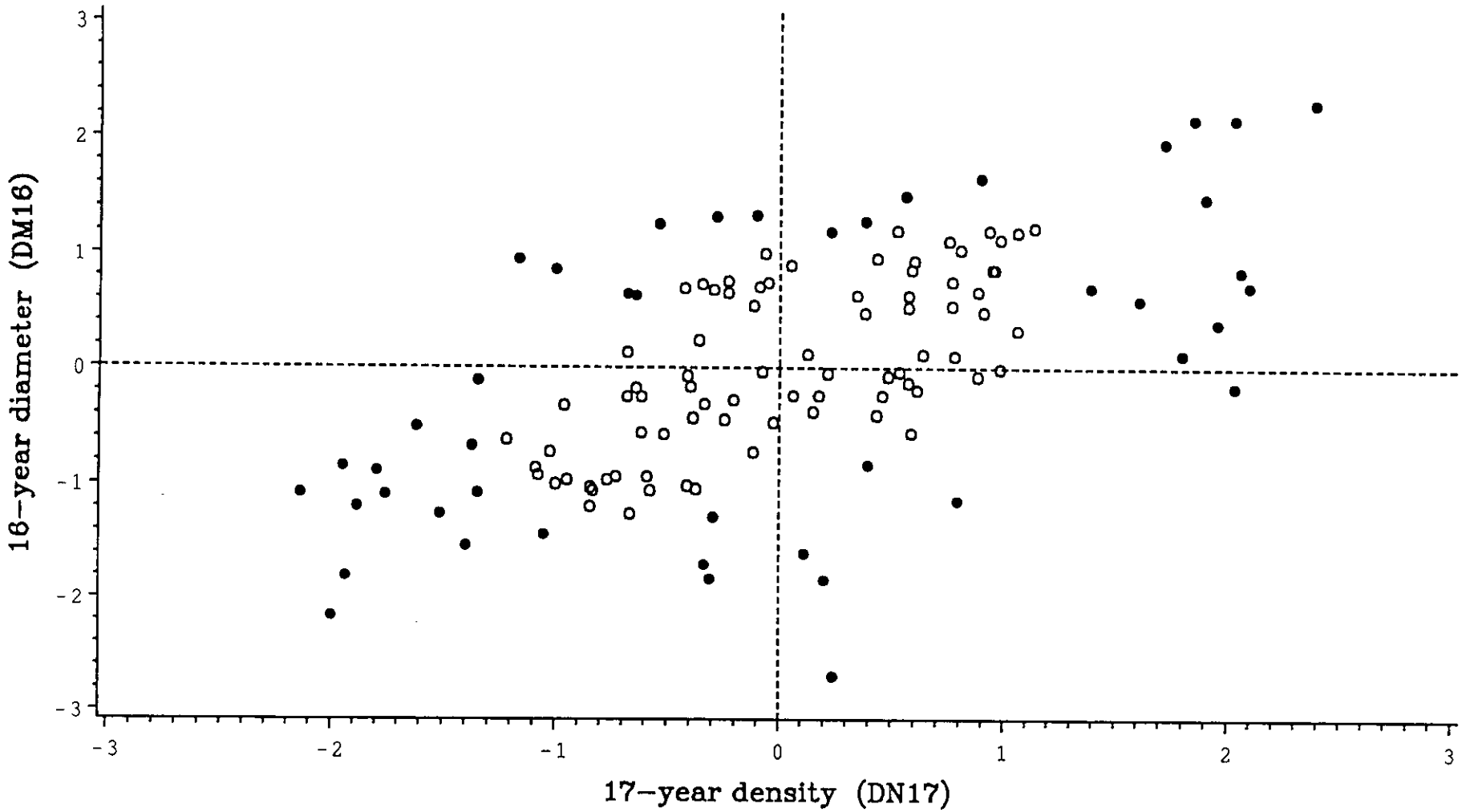
Figure 3.1 is a plot of standardised t_1 (DN17) and t_2 (DM16) taken from the Main Study. Standardised data were substituted in Equation 3.2 and the 46 families with the highest value of w were selected from the ellipse. The data used to plot Figure 3.1 are given (ranked by w) in Appendix 3.1.

Since an element of selection would be introduced in composing the sub-sample of families for the investigation of wood density, it would be necessary to always include DN17 and DM16 as covariates whenever analysis of data based on the sub-sample was carried out. The covariate data would include all 125 families present in the experiment and not just the 46 families at the extreme of the ellipse. Including the covariates would be necessary in order to link the density data with the unselected families via the design matrix in Equation 1.11, and remove bias in the estimation of variance components and fixed effects.

3.2.2.2 **Selection of individuals within families:**

Following the chemical thinning of July 1990, the maximum number of live trees per plot was either 12 or 13. Five trees were randomly selected from the 12 or 13 available

Figure 3.1 : Selection Elipse – Identification of the top 46 outlying families



Note: 1. Data have been standardised; units are standard deviations

Note: 2. ● = selected family ○ = family not selected

within each of three replicates for the 46 families identified from the ellipse using tables composed with the SAMPLE routine from the MINITAB statistical package (MINITAB, 1992). Conversion tables linked the tree number for core collection to the original tree number within the plot.

3.2.3 Collection of cores:

In April 1994, a visit was made to the Main Study to identify the 690 trees from which cores would be collected. If a randomly selected tree was found to be missing, dead, severely suppressed, blown, leaning or forked at 1 to 1.3 m above the ground, the next tree in an ascending numeric sequence was selected as a replacement. If, in turn, that tree had already been randomly selected or was in some way defective, the next available tree was selected which would involve going back to the start of the plot if the last tree was not suitable. Plots representing three families in replicate II were found to be unacceptably windblown. In order to keep the dataset balanced across families, these families were rejected from all three replicates and were substituted by the next three families from the list generated by Equation 3.2. (Appendix 3.1.)

Cores were collected during late May to early June 1994 as the trees were about to enter their 23rd growing season since planting in the spring of 1972. Eight millimetre diameter bark to bark cores were extracted along a north/south line as near to breast height (1.3 m) as possible. If it was not possible to extract cores at 1.3 m, the sampling point was moved down the tree to find a suitable site without reducing the potential number of rings within the core. The north side was identified on each complete core before storing in individually labelled polythene bags which had been perforated to allow desiccation. The cores were stored in their polythene bags at +2°C in the cold store of the Northern Research Station (NRS, Forestry Research, Forestry Commission, Roslin, Scotland).

3.2.4 Preparation of cores for sampling:

In July 1994, the cores were prepared for X-ray densitometry analysis at OFI following the method outlined by Hughes and Sardinha (1975). Each 8 mm core was reduced to a 5 mm square strip by passing the complete core through twin circular saws placed 5 mm apart, then turning the sample through 90° and repeating the process. In all cases, the north radius was the first to pass through twin circular saws. Occasionally one or two outer rings were lost from the south radius (the last radius to pass through the saws) during the sawing process. This would be recorded and used later in the construction of the Job Description File (see 3.2.5 below). Cores were relabelled on both the north and south side prior to conditioning to a standard moisture content of 12% after splitting at the pith into a north and south radius. In most cases the outer-most growth ring related to the 1993 growing season.

3.2.5 X-ray densitometry of cores:

Each X-ray plate held a maximum of 30 radii (3 plots x 5 trees x 2 radii). A total of 46 X-ray plates were scanned using the Joyce Lobel M4VI microdensitometer. The density of the timber sample image was calculated every 0.2 mm and stored in an X-ray plate-specific data file. The resulting data files were closely inspected at NRS together with a photograph (positive) of the X-ray plate and plot of density against distance from pith to generate a plate-specific Job Description File (JDF) i.e. 46 JDFs in total. This was a time consuming process which involved identifying the position of the start and end of each annual ring from the pith to the bark and details of the calendar year to be attached to the ring nearest to the pith, for all 30 radii on each plate. This process would have to be repeated for all 46 JDFs.

The calendar year to be attached to the ring nearest to the pith was calculated by assuming the outer-most ring related to growing season 1993, and then counting back in years towards the pith. If outer rings had been lost during the sawing process (see

3.2.4 above) it was important to know how many rings had gone missing in order to attach a new calendar year to the outer-most ring before counting back and attaching a calendar year to the ring nearest the pith.

Each JDF was then returned to OFI where the Fortran program XRAYDENS combined instruction from the JDF with the raw data file to generate various variables relating to ring density and width which were listed to the results (RES) file. Amongst the parameters calculated on an individual annual ring basis for each radius were (i) width and area; (ii) mean weighted (by ring area) and unweighed gravimetric density; (iii) maximum, minimum and range of density.

Each RES file was sent to NRS for analysis using SAS (1982 and 1992) and ASReml (Gilmour, 1996).

An outline of the general procedure used to arrive at ring-mean weighted density, together with an example of the data, photograph, plot of density against distance from the pith, JDF and RES file for just one of the 690 x 2 radii are given in Appendices 3.2 to 3.7.

The transition formula from Wood (1986) was used to convert optical density to physical wood density (Appendix 3.6). It was not necessary to extract resin prior to carrying out the X-ray densitometry procedure (Wood, *op. cit.*; Silva, *et al.*, 1994).

3.2.6 **Comparison of rings by cambial age or calendar year?:**

The mean weighted density of each annual ring within a tree could be described in terms of either of the following:

i. cambial age from the pith i.e. age since the tree reached breast height;

ii. calendar year and consequently the number of growing seasons since planting.

The standard method of analysis at OFI was by calendar year although it would be possible to convert to annual ring number from the pith if necessary.

Brazier (1970) concluded that it was necessary to compare timber laid down in the same calendar year due to the strong environmental climatic effects in any given year overriding any gradual developmental effects associated with age of ring from the pith. This same conclusion was drawn by Silva, *et al.* (1994) in their investigation of variation of wood density with age over a limited number (7) of selected Sitka spruce clones. Loo-Dinkins and Gonzalez (1991) made a detailed comparison of the two methods in their study of optimum sampling height for wood density in young Douglas fir trees and found much higher phenotypic correlations between sampling heights based on calendar year than cambial age. It was therefore decided to retain the standard OFI system of analysis by calendar year.

3.2.7 **Comparison of the north and south radii:**

The interpretation of the raw-data file and accompanying photograph and graphs to generate a JDF, was initially carried out on both the north and south radii of each tree. This was very time consuming (three hours per JDF) but could be halved if restricted to just one radius per tree. Such a decision may have consequences in terms of data interpretation since it was possible there could be:

i. significant position (north or south) by family interaction for density and ring width;

ii. significant density and ring width differences between the north and south sides;

iii. significant position by year interaction for density and ring width.

If there were no true differences for any of the above, then it would not matter which radius was analysed to represent a given tree; the ring-width and weighted density for that family and year would essentially be the same. Radii from each of the 690 trees could then be mixed from the north and south side if necessary. Significant interactions, however would suggest that it would not be possible to mix radii across trees if only one radius were to represent each tree. Consequently any conclusion would have to be restricted to that cardinal point - no general conclusion concerning the whole tree would be possible from a single core. An investigation was carried out to compare the north and south side according to (i)-(iii) above. The objective of the investigation was to investigate if interpretation of data would be restricted as a result of analysing just one radius.

3.2.7.1 **Methods:**

The comparison was carried out using data in the first 17 RES output files relating to the first 17 X-ray plates and JDFs returned from OFI. Output from all 17 RES files were combined into one large data file for analysis. The total data set was 255 trees from 44 families which were mainly restricted to replicate III although for 7 families (35 trees), the X-ray plates included additional trees from other replicates. For the purpose of this analysis, all trees were considered to be derived from the same replicate.

3.2.7.2 **Statistical analysis:**

A MMA approach was undertaken using the REML derivative (Patterson and Thompson, 1971) within the PROC MIXED procedure of SAS (1992). The two linear models used to investigate the variation of ring-width and density with position were explained by:

i. *Position by family interactions*:

$$Y_{ijkl} = \mu + P_i + C_j + F_k + N_{ik} + e_{ijkl} \qquad (3.3)$$

Where:

Y_{ijkl} = observed value of tree (l) in position (i) of year (j) and family (k);

μ = a fixed general mean;

P_i = the fixed effect of position i, i = north or south radii, Var $(P_i) = \sigma^2_P$;

C_j = the random effect of calendar year j, j = 1975, 1976, ..., 1993, Var $(Y_j) = \sigma^2_c$;

F_k = the random effect of family k, k = 1, 2, 3, ... 44, Var $(F_k) = \sigma^2_f$;

N_{ik} = the random effect of position i by family k interaction. Var $(N_{ik}) = \sigma^2_{fp}$;

e = residual error of tree l on position i of year j within family k.

ii. *Position by calendar year interaction:*

$$Y_{ijkl} = \mu + P_i + C_j + F_k + M_{ij} + e_{ijkl} \qquad (3.4)$$

Where:

M_{ij} = the random effect of position i by calendar year j interaction, Var $M_{ij} = \sigma^2_{pc}$;

and all other symbols are as in (3.3).

The effect of position was considered to be fixed whilst the effects of year, family, position x family and position x year were random. As shown by the models, analysis was carried out at the individual tree level. For each of the models the residual effect (e) contains the position x family x calendar year interaction.

3.2.7.3 **Results and discussion:**

Table 3.1 shows that there was no significant difference between the north and south radius for either ring-width or weighted-density, but there were significantly more rings within the north radius. Differences between the north and south radii for density and ring width at both the family-mean and calendar year level were very small and are given in Appendices 3.8 and 3.9.

Table 3.1: Combined and north and south side mean values for ring width, wood density and ring number

	Width (mm)	Wood Density (kg/m^3)	Number of Rings
Overall	4.180	0.5105	15.5529
North side	4.198	0.5106	16.0549
South side	4.162	0.5104	15.0510
SED	0.0446 NS	0.0014 NS	0.1116***

Note: *** = significant at p = 0.001, NS = not significant at p = 0.05, SED = Standard Error of the Difference

Table 3.2 shows that there were no significant interactions between position x family or position x year for either weighted-density or ring width. This lack of interaction means that the same values of ring-width and weighted-density would be expected for a given family and year regardless of whether the radius came from the north or south side of the tree, or a mixture of both across trees.

Table 3.2: Estimated variance components in the comparison of north and south radii

A. Density

Source of variation	df	Estimate	SE	Significance
σ_c^2	18	0.002820	0.000953	**
σ_f^2	43	0.000862	0.000194	***
σ_{pf}^2	43	0.000023	0.000015	NS
σ_{pc}^2	18	0.000000	--	NS
σ_e^2	7809	0.004051	0.0000065	--

B. Width

Source of variation	df	Estimate	SE	Significance
σ_c^2	18	2.648058	0.892311	**
σ_f^2	43	0.151874	0.036278	***
σ_{pf}^2	43	0.003508	0.007086	NS
σ_{pc}^2	18	0.008219	0.006941	NS
σ_e^2	7809	2.377280	0.038070	--

Note:
1. ** = significant at p = 0.01, *** = significant at p = 0.001, NS = not significant at p = 0.005
2. Where σ_c^2, σ_f^2, σ_{pf}^2, σ_{pc}^2 and σ_e^2 = variation between years, families, position x family, position x year and residual variance respectively.

Since all cores were from bark to bark and passed through the pith it would be possible to use either the north or south radius from each tree in future analysis.

3.2.7.4 **Conclusion:**

The high degree of similarity for ring width and weighted density between the north and south side together with lack of significance for σ^2_{pf} and σ^2_{pc} suggests that both ring width and weighted density data are inter-changeable between the north and south radii. Job Description Files were generated for the north radius only for the balance of 27 X-ray plates (435 trees). The north radius was chosen in preference to the south due to the consistently higher number of annual rings following the sawing process.

3.3 STATISTICAL METHODS

When the last RES file had been sent to NRS by OFI, all the data relating to weighted density on the north side (Appendix 3.7) were combined into one large data set for all 690 trees. Each line was identified with the relevant tree, family, replicate, and calendar year.

PROC MEANS within SAS (1982) was used to calculate the mean weighted density by 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 rings together to represent different age spans over the life of the tree to date. These were referred to as ring-groupings (RG). These ring-groupings generally consisted of four annual rings and increased in two-year units from the pith to the cambium. Exceptions to this generality 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.

As with HT, DM and DN assessments in Chapter 2, an abbreviation was adopted to describe the weighted (by area) densities of ring groupings. For example RG6-9 refers to the weighted density of the annual rings 6-years through to and including 9-years from planting and RG19-22 refers to the weighted density of annual rings 19-years through to and including 22-years from planting.

Analysis of the ring-groupings were at the individual tree level using ASReml (Gilmour, 1996; see Chapter 2). As in Chapter 2, Section 2.3.2 all data were standardised prior to analysis by deducting the mean and dividing by the standard deviation. The mixed standard linear model as outlined in Equation 2.1 was again used to generate variance components. As in Chapter 2, analysis of all ring-groupings was in two stages:

i. to estimate heritabilities;

ii. to estimate juvenile:mature correlations (with the breeding goal).

As outlined earlier, in all analyses DN17 and DM16 were included as covariates to ensure minimum bias of estimated variance and covariance components for weighted wood density over the various ring-groupings. Analysis to estimate heritabilities was therefore effectively a trivariate analysis whilst analysis to estimate juvenile:mature correlations involved a quadrivariate analysis.

Although variance and covariance components from the quadrivariate analysis could have been used to estimate heritabilities, it was thought that a two stage analysis would be more satisfactory in practise. This was because the trivariate analysis (which would have to generate 18 variance and covariance components) would process faster than the quadrivariate model (which would have to generate 30 variance and covariance components). Further, estimates obtained from the trivariate analysis could be used as starting values to achieve faster convergence in the quadrivariate analysis. Estimates of

variance and covariance generated in Chapter 2 for DN17 and DM16 were similarly used to assist convergence of the trivariate model.

3.3.1 Analysis to estimate heritabilities:

Single-tree and family heritabilities of each ring-grouping were estimated using trivariate analysis.

A preliminary run of the data for some of the ring-groupings representing very early ages, suggested that h_i^2 may exceed 1.00 if σ_A^2 was calculated indirectly from variation between half-sib family means ($\sigma_A^2 = 4 \times \sigma_f^2$). It is implicit from Equation 2.3, that h_i^2 could exceed 1.00 if $(3 \times \sigma_f^2) > \sigma_e^2$. This problem was avoided by introducing a pedigree file. This had the effect of estimating σ_A^2 directly in the *.asr* file. When σ_A^2 was substituted in Equation 2.3 using the *.pin* file, it was now impossible for h_i^2 to exceed 1.00.

Analysis of ring-groupings without covariates (univariate analysis) was also carried out. This was for comparative reasons to see how estimates of single-tree and family-mean heritabilities (along with associated standard errors) varied when selection for DM17 and DN16 was not taken into account.

3.3.2 Analysis to estimate juvenile:mature correlations:

Since one of the objectives reported in this Chapter was to investigate the possibility of reducing the selection age for mature wood density it was necessary to decide which grouping of annual rings available in this study would best represent mature wood density. The ring-grouping representing the 4 oldest annual rings (i.e. first four rings in from the bark) was taken as the best representative of mature wood density since it should be well removed from the juvenile wood stage. These outer four rings were

considered the breeding goal against which genetic and phenotypic correlations of all the other ring-groupings were estimated using the quadrivariate analysis.

Repeat analysis without covariates was not carried out.

3.3.3 Early selection for wood density:

The efficiency of indirect selection based on young ring-groupings relative to direct selection for the breeding goal was investigated by calculating Q_{gen} (Equation 1.5) and Q_{year} (Equation 1.6) for each ring-grouping. As in Chapter 2, estimation of Q_{year} required knowledge of the generation interval ($T_j + d$). T_j would equate to the oldest growth-ring within a grouping, whilst d was allowed to vary according to the three models used in Chapter 2 (d = variable, d = 5 years, and d = 3 years).

3.4 RESULTS

3.4.1 Mean weighted density

The mean weighted density of annual rings is given by calendar year and age from planting in Table 3.3. The maximum number of annual rings within any sample was 19 (representing 1975-1993). Only 38 trees (5.5% of the sample) grew fast enough to produce a growth ring for 1975 (4th growing season) at the sampling height (1.3 m) although most of the trees (91%) had reached this height by 1979 (8th growing season). The decrease in number of trees containing rings representing 1992 and 1993 (21st and 22nd growing seasons respectively) was due to the occasional breaking off and loss of annual rings during the sample preparation using the twin circular saws.

Figure 3.2 shows how mean weighted density of annual rings started high and reached a peak in 1977 before falling sharply to a minimum in 1982 (11th growing season).

Between 1985 and 1993 the general trend was for weighted density to remain fairly constant with age. Standard deviations (SD) associated with weighted densities fell

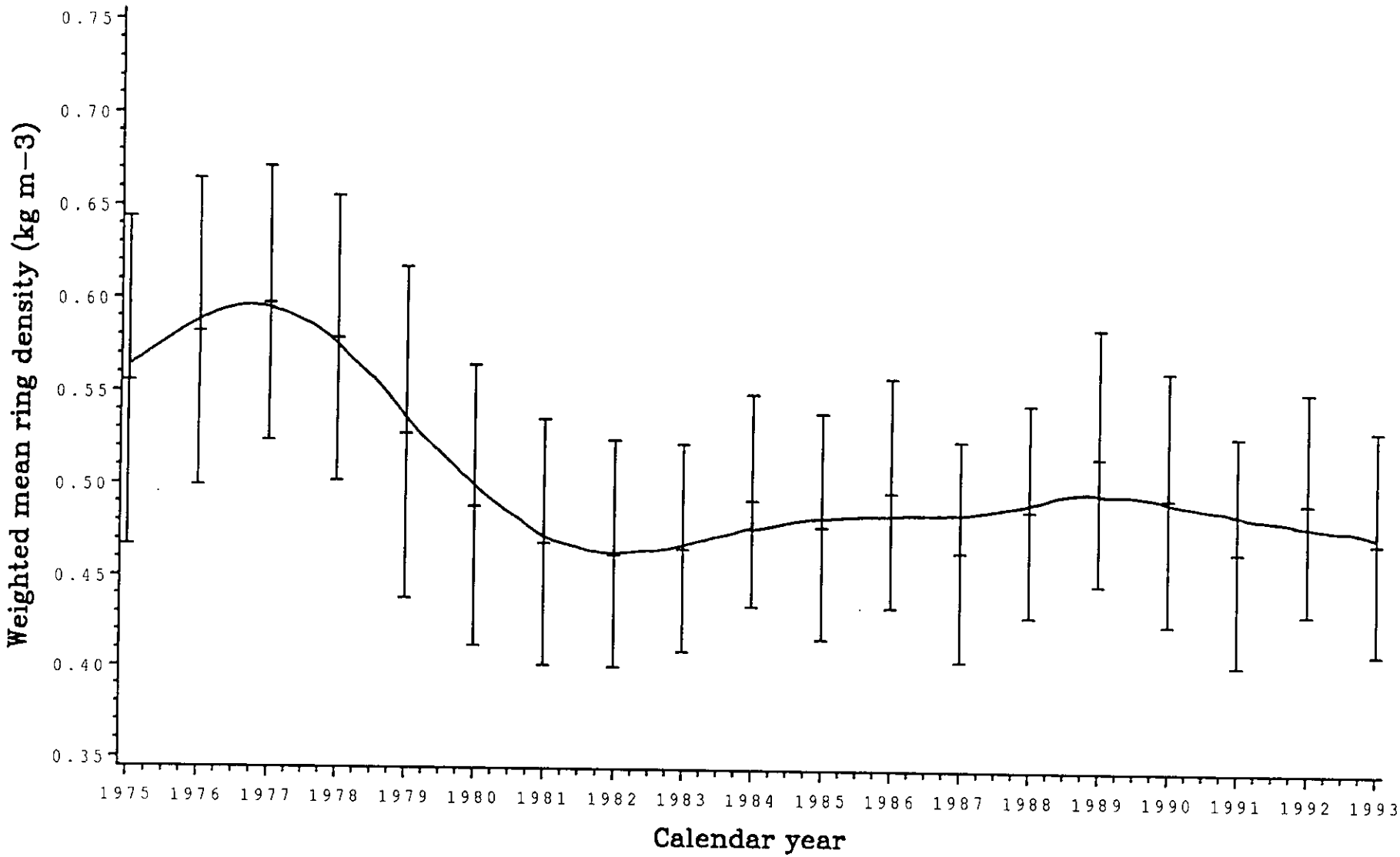
Table 3.3: Mean weighted density, phenotypic standard deviation, and number of trees according to growing season.

Calender Year	Years from Planting	Number of Trees (n/690 x 100%)	Mean Weighted Density	
			kg m^{-3}	SD
1975	4	38 (5.5%)	0.5475	0.1104
1976	5	184 (26.7%)	0.5960	0.1134
1977	6	376 (54.5%)	0.6078	0.1018
1978	7	525 (76.0%)	0.5870	0.0919
1979	8	628 (91.0%)	0.5310	0.0959
1980	9	671 (97.2%)	0.4878	0.0806
1981	10	687 (99.5%)	0.4660	0.0695
1982	11	687 (99.5%)	0.4609	0.0638
1983	12	688 (99.7%)	0.4653	0.0581
1984	13	688 (99.7%)	0.4921	0.0588
1985	14	688 (99.7%)	0.4768	0.0638
1986	15	687 (99.5%)	0.4965	0.0635
1987	16	685 (99.3%)	0.4633	0.0624
1988	17	682 (98.8%)	0.4888	0.0609
1989	18	679 (98.4%)	0.5162	0.0714
1990	19	674 (97.7%)	0.4947	0.0714
1991	20	667 (96.7%)	0.4645	0.0660
1992	21	638 (92.5%)	0.4936	0.0626
1993	22	592 (85.8%)	0.4705	0.0635

Note: Figures in brackets are the percentage of trees containing a growth ring which represented the year in question eg 1975 = (38/690) x 100 = 5.5% therefore only 5.5% of trees gave a growth ring at breast height in 1975. No single calender year was represented by all 690 trees.

sharply between 1975 and 1982 after which they remained relatively steady until rising after the 1988 growing season. Whilst the change in SD will almost certainly be a reflection of the smaller sample size for the earlier rings, it does suggest a reduction in

Figure 3.2 : Variation of weighted mean ring density with calendar year



Note: (i) 1975 = 4 years old; 1993 = 22years old. (ii) Smoothed curve fitted using splines.

variation between trees of weighted density between years 1982 and 1988 (11 to 17 growing seasons after planting).

Combining rings into ring-groupings restricted the sample size of that grouping to the minimum number of trees representing a year within the grouping. The 1975 and 1976 (4th and 5th) growing seasons were represented by only 38 and 184 trees (respectively). Involving either of these years in any ring-groupings would severely restrict the sample size and for this reason they were rejected from any further analysis.

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 3.4. As in Table 3.3, 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 differences in the weighted densities of RG12-15 to RG19-22. Apart from the ring-groupings representing the earlier ages (RG6-9 and RG7-10) the calculated mean weighted densities of the various ring-groupings all vary around 0.4700 kg m^{-3}.

3.4.2 **Analysis to estimate heritabilities:**

Examples of *.as*, *.asr* (edited), *.pin* and *.pvs* files and pedigree file (edited) for the trivariate analysis involving DN17 and DM16 as covariates are given in Appendix 3.10 to 3.14. Appendix 3.15 gives the list of starting values which lead to convergence of the model in the *.asr* file for the respective ring-grouping.

It was common for the model not to converge on the first passage through the ASReml package. On such occasions the variance and covariance components estimated in the penultimate iteration were re-entered as starting values and the model was restarted. This usually led to convergence. On one occasion (RG16-19), the model would not converge despite twice restarting the model with previously generated variance and covariance components. Convergence was finally achieved by substituting the mid-point of the respective cycles which seemed to be operating within each variance and covariance component across interactions.

Table 3.4: Data on 4-ring groupings: Mean weighted density and numbers of trees representing each ring-grouping.

Calender Year																	Ring Grouping (RG) (years)	Number of Trees	Mean Weighted Density (kg m^{-3})	SD
1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993				
X	X	X	X														RG6-9	376	0.5121	0.0659
	X	X	X	X													RG7-10	524	0.4892	0.0640
		X	X	X	X												RG8-11	628	0.4721	0.0606
				X	X	X	X										RG10-13	686	0.4663	0.0536
						X	X	X	X								RG12-15	686	0.4793	0.0501
								X	X	X	X						RG14-17	682	0.4768	0.0510
										X	X	X	X				RG16-19	674	0.4826	0.0525
												X	X	X	X		RG18-21	638	0.4859	0.0551
													X	X	X	X	RG19-22	592	0.4781	0.0546
		X	X	X	X	X	X	X	X								RG8-15	627	0.4731	0.0514
		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	RG8-22	544	0.4732	0.0469
6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22				
Age from planting																				
Juvenile																Mature				

Variance components for each ring-grouping are given in Table 3.5. All variance components and their respective standard errors were calculated from the standardised values generated in the model after rescaling using the square of the standard deviation. The proportion that σ_f^2 contributed to the total phenotypic variance decreased sharply between RG6-9 and RG12-15 (21.26% and 7.87% respectively) after which is varied only slightly. The error term (σ_e^2) increased over the same range from 72.91% (RG6-9) to 86.68% (RG12-15) and was relatively constant thereafter, while σ_{fr}^2 varied only slightly between a maximum of 8.57% (RG7-10) to a minimum of 2.19% (RG16-19).

The equivalent variance components for the ring-groupings representing juvenile wood (RG8-15) and the complete tree (RG8-22) were similar to the ring-groupings for earlier ages with a relatively larger proportion of σ_f^2.

Estimated σ_A^2, σ_P^2, h_i^2 and h_f^2 are given in Table 3.6. Figure 3.3 shows how h_i^2 and h_f^2 decreased 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 (RG8-22) and the complete tree (RG8-22) and were relatively high compared to some of the later-aged ring-groupings.

Point estimates of h_i^2 and h_f^2 without use of covariates are given in Table 3.7. All estimates were inflated relative to the equivalent including covariates. The standard errors for RG6-9, 7-10, 8-11, 8-15 and 8-22 years were very large making a nonsense of the calculated figure. Estimated h_i^2 and associated standard errors for the other ring-groupings were approximately twice the equivalent including covariates. All estimates of h_f^2 were higher than the equivalent including covariates and never fell below 0.95.

Table 3.5: Estimated variance components for the different ring-groupings following trivariate analysis together with DM16 and DN17 as covariates.

Ring-Grouping (years from planting)	σ_f^2 x 10^{-3}	S.E.	$\frac{\sigma_f^2}{\sigma_P^2}$ x 100%	σ_{fr}^2 x 10^{-3}	S.E.	$\frac{\sigma_{fr}^2}{\sigma_P^2}$ x 100%	σ_e^2 x 10^{-3}	S.E.	$\frac{\sigma_e^2}{\sigma_P^2}$ x 100%
RG6-9	0.8567	0.2144	21.26	0.2348	0.1603	5.83	2.9381	1.3305	72.91
RG7-10	0.6213	0.1597	14.85	0.3585	0.1339	8.57	3.2055	1.0043	76.59
RG8-11	0.5440	0.1260	14.79	0.2159	0.0931	5.87	2.9186	0.7912	79.34
RG10-13	0.3441	0.0815	11.69	0.1009	0.0643	3.43	2.4978	0.5250	84.88
RG12-15	0.2068	0.0645	7.87	0.1430	0.0682	5.44	2.2775	0.4253	86.68
RG14-17	0.2166	0.0658	7.98	0.1404	0.0681	5.17	2.3585	0.4354	86.85
RG16-19	0.2007	0.0601	6.97	0.0630	0.0625	2.19	2.6146	0.3260	90.84
RG18-21	0.2544	0.0851	8.36	0.1353	0.0897	4.45	2.6539	0.5588	87.20
RG19-22	0.2413	0.0888	8.40	0.1705	0.0992	5.93	2.4622	0.5786	85.67
RG8-15	0.3588	0.0829	13.15	0.1394	0.0654	5.11	2.2304	0.5268	81.74
RG8-22	0.3087	0.0750	13.46	0.0747	0.0596	3.26	1.9099	0.4795	83.28

Note: 1. σ_e^2 includes all the environment plus ¾ of the additive genetic variance

2. $\sigma_f^2 + \sigma_{fr}^2 + \sigma_e^2 = \sigma_P^2$

Table 3.6: **Total additive and phenotypic variance components and individual tree and family heritabilities for each ring-grouping following trivariate analysis together with DM16 and DN17.**

Ring Grouping (years from planting)	Total $\sigma_A^2 \times 10^{-3}$	S.E.	Total $\sigma_P^2 \times 10^{-3}$	S.E.	h_i^2	S.E.	h_f^2	S.E.
RG6-9	3.4269	0.8575	4.0296	0.3059	0.8504	0.1836	0.9612	0.0711
RG7-10	2.4853	0.6389	4.1853	0.2602	0.5938	0.1385	0.8407	0.0826
RG8-11	2.1761	0.5039	3.6786	0.2089	0.5916	0.1233	0.8308	0.0749
RG10-13	1.3764	0.3262	2.9428	0.2541	0.4677	0.1026	0.7354	0.0804
RG12-15	0.8273	0.2579	2.6273	0.1395	0.3149	0.0944	0.5956	0.1049
RG14-17	0.8665	0.2633	2.7155	0.1432	0.3191	0.0932	0.5995	0.1025
RG16-19	0.8029	0.0601	2.8784	0.0759	0.2789	0.0808	0.7459	0.1854
RG18-21	1.0176	0.3405	3.0436	0.1727	0.3343	0.1073	0.6142	0.1133
RG19-22	0.9651	0.3554	2.8740	0.1712	0.3358	0.1189	0.6203	0.1249
RG8-15	1.4353	0.3315	2.7286	0.1492	0.5260	0.1112	0.7847	0.0769
RG8-22	1.2348	0.2999	2.2934	0.1364	0.5384	0.1197	0.7877	0.0811

Note: 1. Tree per family = 15

2. Number of families = 46

3.4.3 Analysis to estimate juvenile:mature correlations:

Examples of *.as*, *.asr* (edited), *.pin* and *.pvs* files are given in Appendices 3.16 to 3.19. A list of the variance and covariance starting values is given in Appendix 3.20.

Figure 3.3: Variation of single tree and family heritability by ring grouping

Note 1: ★ Single tree heritability ☐ Family heritability Note 2: 46 families; 5 trees per family per replicate; 3 replicates
Note 3: RG = Ring grouping; digits which follow refer to number of years since planting e.g. RG6–9 = rings 6 – 9 years from planting

Table 3.7: Data on ring groupings. Total additive and phenotypic variance components and individual tree and family heritabilities following Univariate analysis without use of covariates.

Ring-Grouping (years from planting)	σ_A^2 x 10^{-3}	S.E.	σ_p^2 x 10^{-3}	S.E.	h_i^2	S.E.	h_f^2	S.E.
6-9	41.7341	186015.3857	42.4464	0.3059	0.9832	****	0.994	****
7-10	40.4563	16813.6553	44.2171	0.2602	0.9149	****	0.9700	****
8-11	37.7260	5910.0505	39.7318	0.2089	0.9495	182.9832	0.9826	65.2604
10-13	2.4517	0.6531	2.8835	0.2541	0.8503	0.2367	0.9817	0.0420
12-15	1.6377	0.4964	2.5215	0.1395	0.6496	0.1745	0.9507	0.0356
14-17	1.9064	0.5468	2.6125	0.1432	0.7297	0.1867	0.9645	0.0328
16-19	1.8683	0.5513	2.7664	0.1523	0.6753	0.1745	0.9598	0.0316
18-21	1.9794	0.6185	3.0542	0.1727	0.6481	0.1809	0.9483	0.0383
19-22	2.0428	0.6524	3.0036	0.1712	0.6801	0.2011	0.9477	0.0451
8-15	3.3386	3.8374	3.5526	0.1492	0.9398	1.1394	0.9869	0.3288
8-22	4.9620	55.7779	5.1291	0.1364	0.9674	7.2381	0.9901	2.3830

Note: 1. **** inestimable by the model, 2. $\sigma_p^2 = \sigma_f^2 + \sigma_{fr}^2 + \sigma_e^2$, 3. Trees per family = 15. Total number of families = 46.

As with the trivariate analysis, the model often had to be restarted using variance and covariance components generated in previous runs of the model. Despite this, the quadrivariate analysis of RG6-9 and RG18-21 with RG19-22 could not be brought to converge. Inspection of the *.asr* files showed very little change in values of the variance components with each iteration or indeed with each succeeding run of the model. It was concluded that the models were very close to convergence and final values within the *.asr* files were analysed by the *.pin* file to give the required phenotypic and genetic correlations. It can be assumed the components finally used were close to the true values since they generated similar correlations to the adjoining ring-groupings, and h_i^2 values similar to those estimated in the trivariate analysis.

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 3.8. All genetic correlations were greater than the equivalent phenotypic correlation although this differential did decrease with mean age of the ring grouping e.g. RG6-9, $r_A = 0.95$ and $r_P = 0.55$; RG18-21, $r_A = 0.95$, $r_P = 0.90$. 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. Estimates of phenotypic correlation increased gradually as the age of the ring-grouping approached that of the breeding value.

Table 3.9 gives the genetic and phenotypic correlations of the different ring-groupings with the covariates DM16 and DN17. All estimates are negative and genetic correlations exceeded phenotypic correlations on all occasions. Estimates of $r_{A_{RG,\ DM16}}$ 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 $r_{A_{RG,\ DN17}}$ 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.

Due to the erratic estimates of variance components and heritabilities with large standard errors associated with some ring-groupings when covariates were excluded from analysis, it was decided there would be little value in analysing genetic and phenotypic correlations without covariates.

Table 3.8: 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 3.9: **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	-0.7001	-0.5884	-0.8227	-0.5511
S.E.	0.1367	0.0347	0.0942	0.0320
RG7-10	-0.7354	-0.6414	-0.8933	-0.5801
S.E.	0.1191	0.0253	0.0812	0.0255
RG8-11	-0.7552	-0.6161	-0.8826	-0.6000
S.E.	0.1092	0.0241	0.0666	0.0228
RG10-13	-0.7811	-0.6309	-0.9013	-0.7406
S.E.	0.1046	0.0432	0.0691	0.0418
RG12-15	-0.7069	-0.5952	-0.9500	-0.6136
S.E.	0.1425	0.0238	0.1251	0.0235
RG14-17**	-0.6403	-0.6294	-0.9500	-0.6650
S.E.	0.1500	0.0222	0.1583	0.0237
RG16-19	-0.6447	-0.6037	-0.9500	-0.6277
S.E.	0.1561	0.0230	0.1983	0.0224
RG18-21	-0.6242	-0.4892	-0.9500	-0.5493
S.E.	0.1798	0.0304	0.1675	0.0289
RG19-22	-0.7968	-0.4568	-0.9500	-0.5361
S.E.	0.1814	0.0334	0.2507	0.0342
RG8-22	-0.7682	-0.6230	-0.9500	-0.6668
S.E.	0.1131	0.0248	0.0989	0.0244
RG8-15	-0.7560	-0.6323	-0.9391	-0.6335
S.E.	0.1045	0.0225	0.0622	0.0209

Note:

1. ##ASReml contains a restriction factor which restrains genetic correlations to a maximum of 0.95

2. **Indicates rings penetrated by the Pilodyn

3.4.4 Early selection for wood density:

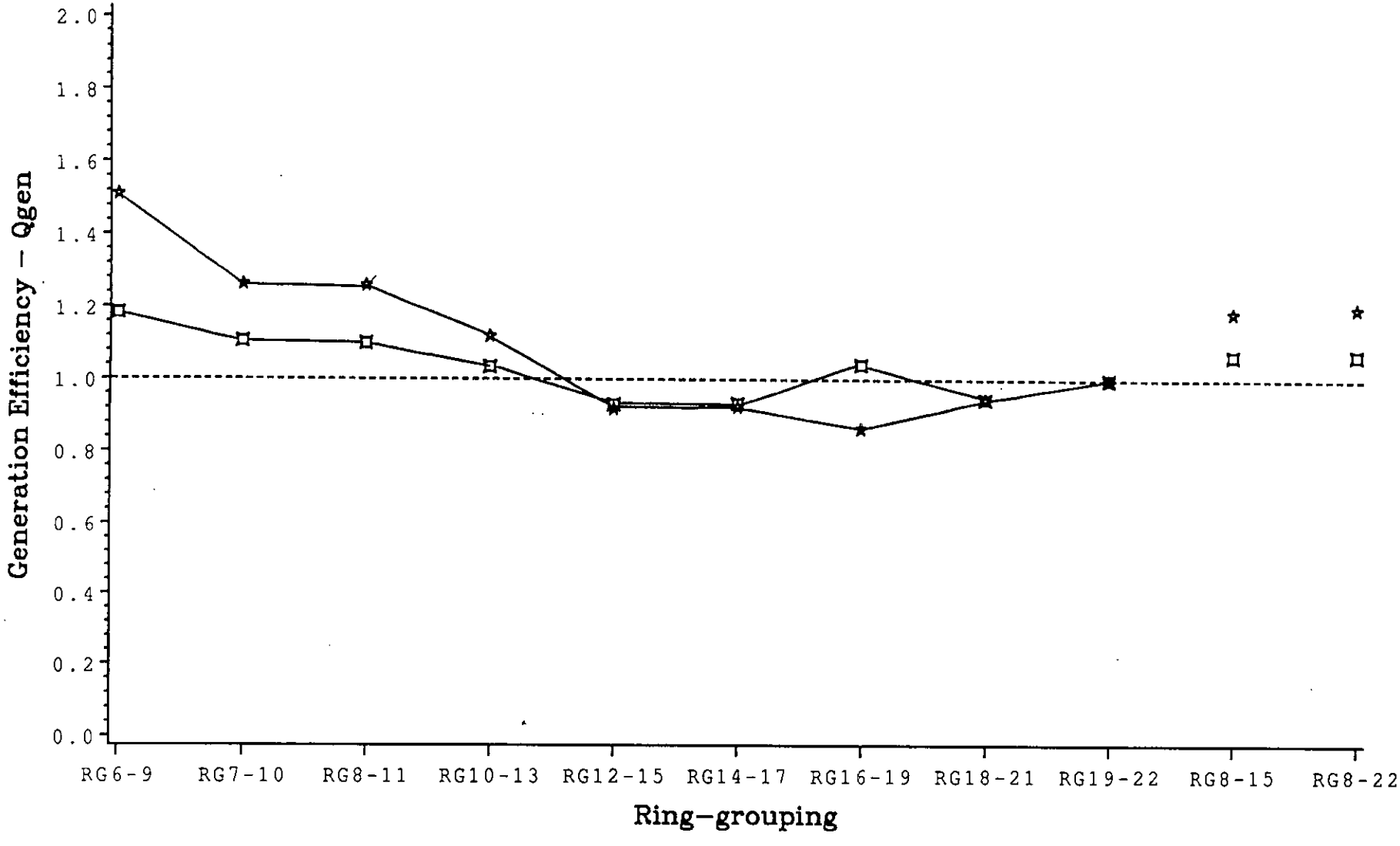
Figures 3.4 and 3.5 show how the generation efficiency (Q_{gen}) and relative genetic gain per year (Q_{year}) were both improved relative to direct selection for the breeding goal (RG19-22) by early, indirect selection for weighted density (data given in Appendix 3.21). This was a feature of the relatively higher single tree and family heritabilities estimated for the more juvenile ring-groupings along with their very high (near unity) 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 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 obtained by indirect selection based on RG6-9; this applied to for 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). Efficiency would be increased to 190% and 214% when $d = 5$ and 3 years respectively.

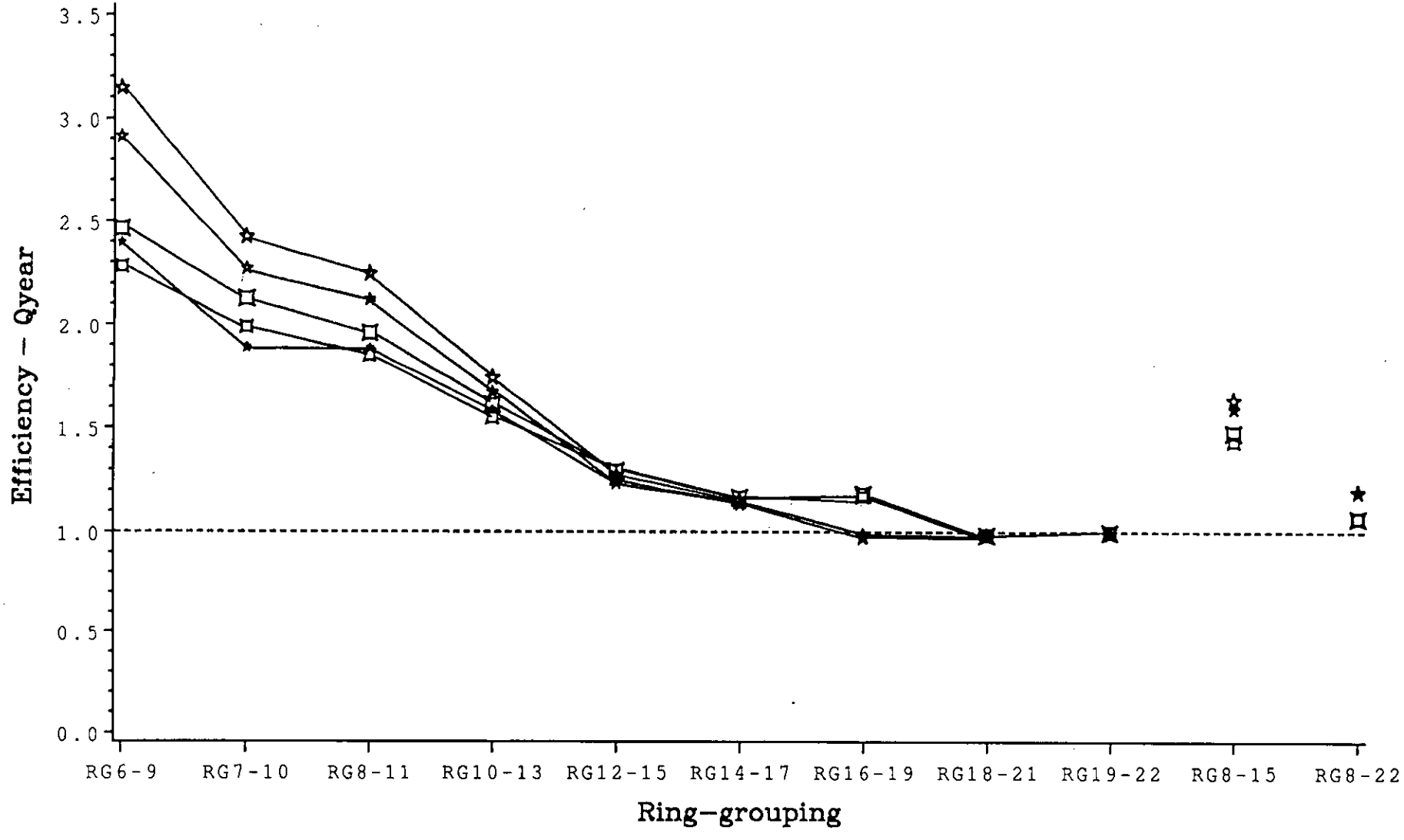
Family selection based on RG6-9 would improve the efficiency of Q_{year} by nearly 130% and 150% when $d = 5$ and $d = 3$ years respectively. The value of (d) decreases in importance as the maximum age of rings within the ring-grouping approaches the breeding goal.

Figure 3.4: Variation of individual tree and family Qgen by ring–grouping



Note 1: ★ = Individual tree Qgen ⌑ = Family Qgen
Note 2: Breeding goal is RG19–22 years. At this point, Qgen is 1.00 for both individual tree and family selection

Figure 3.5: Variation of relative individual tree and family Qyear according to ring–grouping



Note 1: ★ Indiv, d = variable ☆ Indiv, d = 5 years ☆ Indiv, d = 3 years ☐ Family, d = 5 years ☐ Family, d = 3 years
Note 2: Breeding goal is RG19–22 years. At this point Qyear is 1.00 for both individual tree and familyselection

3.5 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 here 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 4 to 5 from the pith before falling quickly to a minimum around 10-15 years, after which there was a slight rise to a plateaux as mature wood density was laid down by the tree.

ii. *Changes of heritability with age*:

This is the first time that time-trend wood density variance and covariance components, and heritabilities have been reported for Sitka spruce from either a selected or non-selected population. 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. This was perhaps too small a sample size to reliable estimate 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 most of the studies mentioned above and listed in Table 1.1. 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 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 (Table 1.4). Talbert, *et al.* (1983), Loo, *et al.* (1984) and Williams and Megraw (1994) all found of $r_{A_{j,m}}$ greater than 0.80 between growth rings within a juvenile wood stage (sometimes as early as 2-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 $r_{A_{j,m}} = 0.90$ and 0.65 between 15-year density with 8-year density in the field and 2-year density in the nursery respectively. Maddern-Harris found $r_{P_{j,m}} = 0.97$ between rings 3 and all rings beyond 15 from the pith in radiata pine, while Corriveau, *et al.* (1991) found $r_{A_{j,m}} = 1.00$ between juvenile wood (1-16 rings) and mature wood (17-23 rings).

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. 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 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. If h_i^2 was found to increase with age as some studies have found with other species (see iii. above) then it becomes quite difficult for indirect selection to be more efficient. Williams and Megraw (1994) found relative gain efficiencies (equivalent

to Q_{gen}) of 84-114% by indirect selection of 12-year density based on selection for 2 or 3-year density. Dean (1990) found an increase in Q_{gen} but not Q_{year} for dry weight (density x surface area) for indirect selection of 15-year dry weight 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 (*op. cit.*).

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 (-0.70, -0.73, -0.76, -0.78, -0.76 and -0.77 for RG6-9, RG7-10, RG8-11, RG10-13, RG8-15 and RG8-22 respectively). This will mean that particular care must be taken in selecting trees with improved diameter for the Sitka spruce breeding programme if the additional objective of preventing a fall in wood density is to be observed.

vii. *Methods*:

There are a number of aspects of the methods used in this study which make it unique:

1. Use of a selection ellipse. This was used to improve the estimates of variance components from a reduced population, relative to random selection. No other studies have been found in the tree breeding literature which selected trees either phenotypically or genetically using this technique.

2. Use of covariates in analysis. The incorporation of the two traits used to calibrate the selection ellipse as covariates in all estimates of variance and covariance components associated with wood density had the effect of further minimising bias due to selection. This effectively linked the reduced population size with the much larger one used to estimate variance components associated with vigour traits and indirect assessment of wood density (Chapter 2).

3. The use of pedigree file to prevent an over estimation of single tree heritabilities.

The combined effect of 1 to 3 (above) was to minimise errors in the estimation of variance components and heritabilities; this was a particular strength of this study. The additional strengths of the study relating to the random selection of the complete population and the fact that all the trees were known to be of the same origin means that for the first time, unbiased genetic variance components are presented for wood density in Sitka spruce.

3.6 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 (r_A close to unity) genetic correlations 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. Heritability estimates are lower than those calculated for Sitka spruce by Wood (1986) and many other studies involving other species. Estimates of age:age genetic correlations are similar to other species for the ages investigated.

vi. 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.

CHAPTER 4

Genetic relationships between ortets, grafted-ramets and progeny — a pilot study

4.1 INTRODUCTION and OBJECTIVES

Amongst the sources of data which could be incorporated with progeny test data in a model designed to estimate breeding values of selected trees are:

i. the original ortet;

ii. grafted-ramets of the ortet growing in clone-banks.

Breeding value estimation based on mass selection of the original ortet is imprecise for traits with low heritabilities (< 0.5). All individuals with a given phenotypic value derive the same estimated breeding value while true breeding values will vary about this point (White and Hodge 1989). It is possible that estimates of true breeding values from grafted-ramets could be more precise than ortets since:

i. ramets are often replicated within clone-banks as opposed to the single representative of an ortet in a forest;

ii. clone-banks are often established on uniform sites whilst the environment between selected ortets can vary considerably within a given forest.

Possible problems associated with calculating additive breeding value based on grafted-ramets include the inability to separate additive and non-additive genetic variance and

unknown amounts of genotype x environment interaction (GxE) due to age of ortet, position of the scion on the ortet and physiological interaction of scion and root stock.

If data collected from grafted-ramets or ortets are to be included in breeding value estimations, it is necessary to know how precise the data from that source will be. Precision could be measured by regression with breeding value estimates derived from the most reliable source (replicated progeny tests). If the precision of grafted-ramets is no greater than that from mass selection of the original ortet there may be little value from including either source of data in the estimation of breeding values.

As outlined in Chapter 1, the literature is limited and often conflicting as to the genetic relationship between either grafted-ramets and ortets or grafted-ramets and progeny. No study has ever been carried out to investigate the genetic relationship between all three sources of data for Sitka spruce. Although the ortets of the Population Study had been measured for total height (amongst other traits) at the time of felling, and measurements for vigour traits and wood density could be collected from grafted-ramets of all 150 ortets growing in a clone-bank, it was decided that a small-scale pilot-study was first necessary to investigate the magnitude of any genetic relationships. Only if a significant relationship was found to exist between grafted-ramets and progeny at a pilot study level would it worth large-scale collection of diameter and wood density data from grafted-ramets representing the population study.

The objectives of the work reported in this Chapter were to estimate the strength of genetic correlations between estimated genotypic values of a small population of Sitka spruce grafted-ramets with (i) those of the original ortet, and (ii) breeding value estimates derived from progeny tests. If significant relationships could be found in this pilot study, data would be collected from grafted-ramets of the individuals from the 'Population Study' already used in the 'Main Study' of wood density described in Chapter 3.

The pilot study differed from similar investigations with other species in that:

i. it employed a Mixed Model Approach involving REML;

ii. it investigated the relationship between grafted-ramets, ortets and progeny and not just grafted-ramets with ortets or grafted-ramets with progeny;

iii it considered stem diameter measured at breast height in addition to wood density.

4.2 MATERIALS AND METHODS

The database of the Tree Improvement Branch (TIB, NRS) was interrogated to identify suitable established grafted-ramets (>15-years since planting) for which there were already wood density and diameter data at both the plus-tree and progeny level. Further restrictions were:

i. the plus-trees should have been identified over a small area of forest during a short time period (1-2 months);

ii. all the grafted-ramets representing the clones from a single forest should have been planted in a single clone-bank over a limited number of years.

Both these restrictions were designed to reduce possible confounding effects due to (a) GxE within the forests and clone-bank and (b) variation of seed origin between selected trees. GxE would be reduced if the environments in the forest and clone-bank were as homogeneous across clones as possible. The assumption was made that if plus-trees were selected over a restricted area and during a small time period, they would more likely be of the same age, size and possibly seed origin.

The data available from the progeny population consisted of progeny-mean values for 15-year diameter breast height and density assessed indirectly using the Pilodyn between 16-21 years from planting. The progeny-mean values for both diameter and density data were adjusted for heterogeneity of site by weighting for family heritability in accordance with the techniques outlined by Lee (1995).

Eleven plus-trees, selected in summer 1964 in each of Ratagan, (Highland Region, Scotland, 57° 13' N, 5° 28' W) and Glenbranter forests (Strathclyde Region, Scotland, 56° 7' N, 5° 3' W), were selected as satisfying the above criteria. Diameter breast height (DBH) of all the plus-trees had been assessed at the time of selection. Twelve-millimetre-diameter pith-to-bark increment cores had also been extracted at the time of selection and the density of rings 20-25 from the pith was assessed gravimetrically as an indicator of the mature wood density (Fletcher and Faulkner 1972).

Grafts of all 22 plus-trees had been planted in Wauchope clone bank (Borders Region, Scotland, 55° 2' N, 2° 39' W) between 1968 and 1974. Planting was 2.5 m between grafts within rows, and 9 m between rows. All rows were orientated in a east/west direction to promote crown development and flower production on the south side.

Although there was overlap of planting ages between the two populations, the Glenbranter grafts tended to be planted before those from Ratagan. No data relating to diameter or density had previously been collected from these grafted-ramets.

Six grafted-ramets had originally been planted adjacently for each of the 22 clones. Three ramets were randomly selected for each clone. Grafts were rejected if they:

i. had been topped (cut off) at or about breast height as part of earlier clone bank management operations;

ii. demonstrated clear graft incompatibility problems.

Occasional death of ramets and the above two restrictions constrained the random selection of ramets. Only two ramets could be selected for four clones, and one clone was represented by just one ramet. A total of 60 ramets were selected from the 22 clones.

In January 1994, when the ramets were 21 to 27 years from planting, bark-to-bark cores were extracted from each ramet in a north to south line at or about breast height using an 8 mm Pressler borer. These cores were taken to the laboratory where segments were assessed directly for wood density by the gravimetric means described below.

Quick, indirect assessments of density were also carried out using the Pilodyn at breast height. Shots were taken from (i) north (ii) south and (iii) east directions to investigate possible variation with cardinal position.

The possibility of elliptical trees in response to a prevailing wind was investigated by measuring DBH with callipers to the nearest 0.5 cm in (i) north/south and (ii) east/west direction. DBH was also assessed using a girthing tape calibrated to the nearest 0.1 cm.

When all assessments were being carried out care was taken to avoid whorls, internode branches, and old girdling scars (from previous flower management operations).

On inspection of the cores in the laboratory, all radii were found to have a minimum of 17 annual rings (counted outwards from the pith). Rings 8-12 and 13-17 were excised from the north and south radii. The assumption was made that rings 8-12 would closely correspond to those rings penetrated by the Pilodyn pin in a 15-year old progeny test, and rings 13-17 were the best available representatives of mature wood which would closely correspond to density assessments of the original ortets. The wood densities of the two 5-ring sections (8-12, and 13-17) were compared within radius (position) and across radii (north and south).

Wood density of each five-ring section was assessed using two different techniques:

a. Standard water displacement:

$$D = \frac{\text{Oven Dry Weight}}{\text{Volume}} \qquad (4.1)$$

where: i. D = density (g cm^{-3});

ii volume (cm^3) is the weight of water (g) displaced by water saturated sections;

ii. Oven dry weight is measured in grams (g).

b. Maximum moisture content (Smith, 1954):

$$D = \frac{1}{\frac{\text{(saturated weight) - (oven dry weight)}}{\text{oven dry weight}} + \frac{1}{1.53}} \qquad (4.2)$$

where: i. 1.53 (g cm^{-3}) is the average value (across species) of the specific gravity of wood substance.

ii. Saturated and oven-dry weights are measured in grams (g).

Sections were saturated with water by submerging them under water in a desiccator and applying a vacuum for 72 hours. Sections were then taken from the desiccator and surface water removed by rolling over blotting paper. Each section was then (i) lowered into a beaker of water resting on an electronic balance of accuracy 0.01 grams and the weight of water displaced recorded; (ii) weighed directly with a similar balance. Sections were then dried by placing them in an oven at 80°C for 48 hours. Following

removal from the oven, sections are allowed to cool in a desiccator where they were stored prior to assessment of oven dry weight. Oven dry weight was assessed directly by placing the sections on the same electronic balance.

4.3 COMPARISON OF ASSESSMENT TECHNIQUES

The objective in measuring the grafted-ramet population was to obtain reliable estimates of wood density and stem diameter. To this end each trait had been assessed or analysed using more than one method, although it was proposed to carry out the subsequent Mixed Model Analysis with only one representative method for each trait. In order to discover if there were significant differences between these methods and which method would be most suitable for further analysis, statistical comparisons were required. Conclusions derived from these investigations would help construct a protocol for assessment of diameter and wood density of grafted-ramets in future work.

PROC GLM within SAS (1982) was used to investigate various positional comparisons:

i. DBH using the calipers in the north/south and east/west directions;

ii. indirect assessment of density using the Pilodyn on the north, south and east sides;

iii. direct assessment of densities between the north and south side;

iv. direct assessment of densities between rings 8-12 and rings 13-17.

An additional comparison was made of:

v. the two forms of direct assessment of wood density.

The same standard linear model was used in a one-way analysis of variance for all the above comparisons:

$$Y_{ij} = \mu + d_i + e_{ij} \qquad (4.3)$$

where: Y_{ij} = observed effect of treatment i on ramet j;

μ = the estimated mean;

d_i = the random effect due to treatment i, Var $(d_i) = \sigma_d^2$;

e_{ij} = the residual effect of ramet j within treatment i, Var $(e_{ij}) = \sigma_e^2$;

and d_i = was respectively (i) to (v) above.

The mean DBH according to the calibrated girthing tape was also calculated.

As the model shows ramets were used as a replication factor in all comparisons.

Depending on the results of these comparisons either data from one method was chosen and the others abandoned, or data were combined across a number of different methods. Decisions for abandoning or combining data were based on what seemed biologically logical following analysis of the data whilst at the same time (i) keeping the data within manageable bands; (ii) preventing replication of analysis by a different method unless there was a perceived biological advantage.

4.3.1. **Results and Discussion**

The ramet-mean values for the various assessment techniques and the statistical significance of their comparison are given in Table 4.1.

i. Diameter Breast Height

Assessment using callipers suggested the ramets were slightly elliptical with a greater diameter in the north/south plane ($p < 0.05$). Elliptical growth in response to a prevailing wind is not uncommon in Britain (Malcolm and Studholm, 1972). Diameter assessed using girthing tape was used in further analysis since this was the only means of assessing the weighted mean diameter of a tree independent of ellipticity which might be detected with callipers. Diameter assessment using the girthing tape was also more precise than with callipers (0.1 cm compared to 0.5 cm).

ii. Density (indirectly)

There was a significant difference between the three cardinal Pilodyn assessments ($p < 0.05$). The north side appeared most dense (least pin penetration) whilst the south and east sides gave very similar results. Since it is unknown if the differences were of any practical significance, further analysis was based on a mean of all three positions.

iii. Density (directly)

The two methods of assessment gave almost identical results. Further analysis was based on the water displacement technique since this was the same technique used to assess the wood density of the original ortets (Fletcher and Faulkner, 1972). There was no significant difference between the mean north and south side density across ramets. Further analysis was based on the mean of each. There was a highly significant difference ($p < 0.01$) between density of rings 8-12 and 13-17. These five-ring sections were kept separate for subsequent analysis.

Table 4.1: Comparisons of the different methods used to assess (i) breast height diameter (ii) pin penetration of the Pilodyn (iii) wood basic density.

Diameter	i. Using girthing tape	= 23.67 cm	
	ii. North/South Callipers	= 23.44 cm	*
	East/West Callipers	= 22.99 cm	
Density (indirectly using the Pilodyn)	South	= 15.62 mm	
	East	= 15.53 mm	*
	North	= 14.50 mm	
Density (directly)	i. Technique : Water Displacement	= 0.3525 kg/m^3	NS
	: Smiths	= 0.3523 kg/mg	
	ii. Position : North	= 0.3497 kg/m^3	NS
	: South	= 0.3551 kg/m^3	
	iii. Position in Core : Rings 8-12	= 0.3664 kg/m^3	**
	: Rings 13-17	= 0.3392 kg/m^3	

Note: NS = not significant at p = 0.05, * = significant at p = 0.05, ** = significant at p = 0.01.

4.3.2 Conclusions

Subsequent Mixed Model Analysis (MMA) involving grafted-ramet data was restricted to:

i. DBH assessed using the girthing tape;

ii. Pilodyn measurements as a mean of all three cardinal points;

iii. density assessed using the standard method of water displacement; north and south radius data combined by five-ring section; and wood density of rings 8-12 separate from rings 13-17.

4.4 STATISTICAL METHODS

The following linear mixed model was fitted to the grafted-ramet diameter and density data and analysed using the REML directive (Patterson and Thompson, 1971) within the GENSTAT (1993) computer software package.

$$Y_{ijk} = \mu + f_i + c_{ij} + r_{ijk} \qquad (4.4)$$

where Y_{ijk} = observed trait value (diameter or density) of ramet k from clone j within forest i,

μ = a fixed general mean;

f_i = the fixed effect of forest i (Ratagan or Glenbranter), Var $(f_i) = \sigma^2_f$;

c_{ij} = the random effect of clone j within forest i (j = 1, 2 ..... 11), Var $(c_{ij}) = \sigma^2_c$;

r_{ijk} = the random effect of ramet k within clone j and forest i, (k = 1, 2 or 3), Var $(r_{ijk}) = \sigma^2_{c(r)}$.

The effect of forest was considered to be fixed whilst the effect of clone and ramet within forest were considered to be random.

The model was run for each of the traits under consideration (DBH, density rings 8-12, density rings 13-17 and Pilodyn) in two progressive ways:

i. in order to investigate any differences between grafted-ramet populations, the grafted-ramet data were analysed at the combined and individual population level;

ii. as in the first run but with the introduction of density and diameter data collected from ortets and progeny to act as covariates. The covariates used were (a) progeny-mean Pilodyn score; (b) ortet density; (c) progeny-mean

diameter; (d) ortet diameter. This was done in order to identify those covariates which would significantly reduce the estimated genetic variance between clones (σ_c^2) following regression with the variate. A large reduction in σ_c^2 would indicate a worthwhile relationship between variate and covariate. This would suggest that either variable could be used to estimate breeding values and that the two traits used in combination would lead to an increase in precision of variance component and breeding value estimation.

Since the limited literature on the relationships between grafted-ramets and original ortets or progeny has tended to calculate simple correlation co-efficients of ortets or grafted-ramet means against progeny means for wood density, these were also calculated for comparative purposes.

4.5 RESULTS

4.5.1 Progeny and Ortet

Details of ortet-mean age, diameter and wood density together with family-mean diameter and indirect assessment of wood density (Pilodyn) for the open-pollinated progeny are presented by forest in Table 4.2. The Glenbranter ortets and progeny had significantly more dense timber than the Ratagan population. The Glenbranter ortets also had a significantly larger diameter than the Ratagan ortets, although there was no significant difference between forests for diameter assessed in progeny tests.

Table 4.2: Comparison of forest mean values for diameter and wood density traits of ortets and progenies.

		Glenbranter	Ratagan	SE	
Ortet:	Age (years)	39	37	± 0.91	NS
	DBH	48.80 cm	41.67 cm	± 2.6146	*
	Density	0.3115 kg/m^3	0.2849 kg/m^3	± 0.0119	*
Progeny:	DBH at 15 years	13.12 cm	13.03 cm	± 0.2949	NS
	Pilodyn pin penetration	14.61 mm	15.73 mm	± 0.3896	*

Note: NS = not significant at p = 0.05, * = significant at p = 0.05

4.5.2 Grafted Population

4.5.2.1 Mean values:

The basic model was run at the combined and separate population levels. The combined model allowed a comparison of predicted means for the Glenbranter and Ratagan populations which are presented in Table 4.3. There were no detectable differences between the two forests (at the 5% level) for any of the traits under investigation except DBH which was probably a reflection of the earlier planting date for the Ratagan grafted-ramets.

Table 4.3: Population mean values for density (assessed gravimetrically), diameter at breast height and density assessed indirectly using the Pilodyn for grafted clones from Glenbranter and Ratagan forests.

	Glenbranter	Ratagan	SE	
Density - rings 8-12 (g cm^{-3})	0.3651	0.3682	± 0.014	NS
Density - rings 13-17 (g cm^{-3})	0.3431	0.3360	± 0.015	NS
Pilodyn (mm)	15.01	15.43	± 1.114	NS
Diameter breast height (cm)	22.07	25.18	± 1.826	*

Note: NS = not significant p = 0.05, * = significant p = 0.05.

It is interesting that the density of rings 8-12 was higher than rings 13-17 in each population. This was opposite to the trend reported by Brazier (1967) who found that the density of mature selected trees started high and then decreased to a minimum between 10-15 years after which the density started to rise again. A possible explanation for the difference found here is that the grafts in the clone bank were open-grown, often with their crown extending to ground level. It is possible that the very wide plant spacing (2.5 m within rows x 9 m between rows) extended the juvenile-wood phase such that the minimum density was reached beyond 15-years, despite the mature age of the scion material.

4.5.2.2. **Variance components and heritabilities:**

Variance components and broad sense heritabilities (H^2) for both the combined and individual populations are presented in Table 4.4.

Table 4.4: Variance components and broad sense heritability for diameter and density traits of the combined and individual grafted-ramet populations.

Combined Populations	σ_c^2	$\sigma_{c(r)}^2$	H^2
Density - rings 8-12	0.00070	0.00100	0.41 ± 0.14
Density - rings 13-17	0.00104	0.00037	0.74 ± 0.09
Diameter	15.78	6.77	0.70 ± 0.10
Pilodyn	6.022	2.114	0.74 ± 0.08

Glenbranter	σ_c^2	$\sigma_{c(r)}^2$	H^2
Density - rings 8-12	0.00090	0.00135	0.40 ± 0.20
Density - rings 13-17	0.00136	0.00028	0.83 ± 0.09
Diameter	23.22	7.43	0.76 ± 0.11
Pilodyn	7.005	2.183	0.76 ± 0.11

Ratagan	σ_c^2	$\sigma_{c(r)}^2$	H^2
Density - rings 8-12	0.00052	0.00062	0.45 ± 0.2
Density - rings 13-17	0.00069	0.00046	0.60 ± 0.17
Diameter	8.42	6.03	0.58 ± 0.17
Pilodyn	5.004	2.045	0.71 ± 0.13

Note: $H^2 = \dfrac{\sigma_c^2}{\sigma_c^2 + \sigma_{c(r)}^2}$ calculated together with standard errors within the GENSTAT Model.

where σ_c^2 = variation between clones and $\sigma_{c(r)}^2$ = variation of ramets within clone.

Broad sense heritability for the combined populations were high for all traits except density of rings 8-12 which also had a high standard error (SE). Wood density H^2

compared favourably with those reported by Velling (1974) for two populations of Scots pine clones, 10-13 years after grafting (H^2 = 0.72 ± 0.04 and 0.88 ± 0.04) and were generally higher than those reported by Zobel *et al* (1962) who looked at specific gravity in 3-year-old grafted clones of slash pine (H^2 = 0.458 to 0.625). No reports of H^2 for DBH measured on grafted-ramets have been found in the literature.

The variation across traits of H^2 in each forest closely reflected those found at the combined forest level . Values of H^2 tended to be lower (with higher SE) at Ratagan for all traits except density of rings 8-12.

A possible confounding factor in the calculation of H^2 was the inability to remove any G x E between ortet selection site and the clone-bank, and the scion with the rootstock. Effects of interaction between the scion and root-stock could well be small since Nichols and Brown (1971) found the variation in levels of wood density between grafted-ramets and open-pollinated progeny planted at the same spacing were due more to the effect of age of the shoot rather than any scion:root-stock interaction.

4.5.2.3 **Introduction of covariates:**

Although the model was initially tested at the combined and individual forest levels, the trends between forests were very similar. The difference between forests was investigated by regressing each of the variates on the covariates at the combined population level and investigating the forest by covariate interaction using the Wald statistic generated by the model within the GENSTAT programme. A high value of the Wald statistic would indicate a significant difference between regression slopes for the two forests. In all cases the difference in slope was found to be very small ($p > 0.05$, Table 4.5). Further analysis was carried out at the combined forest level.

Table 4.5: Wald statistics for the forest by covariate interaction.

Grafted-Ramets	COVARIATES			
	Progeny Density	Ortet Density	Progeny Diameter	Ortet Diameter
Density (rings 8-12)	1.5	1.3	0.6	0.0
Density (rings 13-17)	0.1	0.6	0.4	2.0
Pilodyn	0.0	0.1	0.5	0.3
Diameter	0.3	0.0	0.5	1.3

Note: 1 Degree of Freedom. There are no significant differences (when p = 0.05, Wald statistic = 3.84) for any of the above combination of variate and covariate.

Table 4.6 shows the proportion of σ_c^2 which remained following regression with each of the covariates. Results are presented as a proportion of σ_c^2 which existed *before* the regression. A Wald test was used to measure the significance of the regression co-efficient obtained. The only covariate which caused a highly significant ($p \leq 0.001$) reduction in σ_c^2 following regression with any of the variates was progeny density when regressed with grafted-ramet densities (rings 8-12 and 13-17) and Pilodyn. There was evidence of a significant regression between progeny diameter and grafted-ramet density, and between ortet density and grafted-ramet Pilodyn but in each case the decrease in σ_c^2 was only small and in the range of 14-18% compared to the much larger 39-61% associated with progeny density.

Table 4.6: Proportion of variation between clones (σ_c^2) remaining after regression with covariates.

Grafted-Ramets	No Covariates	COVARIATES			
		Progeny Density	Ortet Density	Progeny Diameter	Ortet Diameter
Density - σ_c^2 Rings 8-12	100%	39%	107%	86%	102%
Wald Test		12.7	0.1	3.4	0.5
Significance		***	NS	*	NS
Density - σ_c^2 Rings 13-17	100%	47%	99%	82%	106%
Wald Test		17.7	1.1	4.9	0.1
Significance		***	NS	*	NS
Pilodyn - σ_c^2	100%	61%	82%	99%	99%
Wald Test		11.5	5.0	1.2	1.1
Significance		***	*	NS	NS
Diameter - σ_c^2	100%	100%	104%	106%	89%
Wald Test		1.0	0.3	0.0	3.1
Significance		NS	NS	NS	NS

Note: NS = not significant at p = 0.05, * = significant at p = 0.05, *** = significant at p = 0.001

Further analysis was carried out on those variate/covariate combinations which gave a significant ($p \leq 0.05$) regression to estimate the genetic correlations between the breeding value of the covariate and the genotypic value of the grafted-ramet ($r_{g,\ BV}$). The method of estimating genetic correlations employed here is somewhat crude since it employs estimates of accuracy based on single tree heritabilities for wood density and diameter derived from other studies involving Sitka spruce. It merely represents the best possible estimate of genetic correlations (with no standard errors attached) based on the available data. Results are presented in Table 4.7. The estimated values of $r_{g,\ BV}$ were highest when progeny density was the covariate in combination with grafted-ramet density of rings 8-12, rings 13-17, and density assessed using the Pilodyn. Values of $r_{g,\ BV}$ when progeny diameter and ortet density were the covariates, were lower than those for progeny density alone but may still be of some value in the determination of variance components and breeding values.

Table 4.7: Estimated genetic correlations between breeding value of the covariate and genotypic value of the grafted clones ($r_{g,\ BV}$).

	Progeny Density	Ortet Density	Progeny Diameter	Ortet Diameter
Density (rings 8-12)	0.86	--	-0.48	--
Density (rings 13-17)	0.80	--	-0.54	--
Pilodyn	-0.69	-0.66	--	--
Diameter	--	--	--	--

Note: Details of calculations involved given in Appendix 4.1.

The estimated accuracy of breeding values for progeny and ortet are given in Appendix 4.1. The relative values of estimated accuracy increase from ortet to progeny and from diameter to density.

4.5.2.4 Simple correlations:

Following the results of the comparison of forests carried out under the REML analysis simple correlations were only calculated at the combined forest level. Results are presented in Table 4.8.

Table 4.8: Simple treatment-mean correlations between density of the ortets, progeny and grafted-ramets at the combined forest level.

		Progeny Density	Ortet Density	Grafted-ramet Pilodyn	Grafted-ramet density	
					Rings 8-12	Rings 13-17
Progeny Density		-	0.64 **	-0.56 **	0.44 *	0.62 **
Ortet Density			-	-0.45 *	0.00 NS	0.23 NS
Grafted-ramet Pilodyn				-	-0.52 *	-0.72 ***
Grafted-ramet density	**Rings 8-12**				-	0.73 ***
	Rings 13-17					-

Note: NS = not significant at p = 0.05, * = significant at p = 0.05, ** = significant at p = 0.01, *** = significant at p = 0.001.

Relationships between grafted-ramet and either ortet or progeny traits were found to be similar to those found using REML following the introduction of covariates. There were significant correlations between density of the progeny and grafted-ramet density of rings 8-12, rings 13-17 and density assessed using the Pilodyn. Ortet density was poorly correlated with grafted-ramet density of either set of rings although there was an unexpected correlation ($p \leq 0.05$) with grafted-ramet density assessed indirectly using the Pilodyn. There was a highly significant correlation ($p \leq 0.01$) between ortet and progeny density. Within the grafted-ramet population, rings 8-12 were highly significantly correlated with rings 13-17 ($p \leq 0.001$).

4.6 DISCUSSION

4.6.1 Analysis using the mixed model approach:

One of the main limitations of this pilot study was the small number of clones representing each population and the fact that within a population, the selected ortets were dispersed over a large area of forest. Any correlations between grafted-ramets and covariates exist through genotypic relationships between ramets and either ortets or progeny. The strength of such an association will *a priori* depend on how well the covariates used estimated the ortet genotype. These estimates may be poor in this study due to the unknown variation in environment and possibly seed origin between ortets selected within a forest. In the case of progeny, the strength of the relationship may also be influenced by the extent of non-additive genetic variance since the progeny mean estimates only the breeding value.

Despite these possible sources of error, certain associations have been found. The covariate offering the greatest reduction in σ_c^2 following regression with density variables within the grafted-ramet populations was progeny density; the most precisely estimated breeding value. This covariate had particularly high values of genetic correlation with all density traits measured in the grafted-ramets. Progeny diameter, the

second most precisely estimated breeding value, made a small contribution to σ_c^2 reduction for density of rings 8-12 and 13-17 but none for Pilodyn or diameter. The indirect effect of the diameter covariate on grafted-ramets density is not surprising since Wood (1986) found a significant, negative phenotypic correlation of r_P = -0.34 up to -0.69 between 15-year progeny-mean density and diameter. However, since Pilodyn and basic density are not perfectly correlated (r_P = - 0.69, Wood *op. cit.*) the link between progeny diameter and grafted-ramet Pilodyn is perhaps rather tenuous.

Although the reduction of σ_c^2 and the value of the genetic correlation between grafted-ramet density (rings 8-12 and 13-17) with progeny diameter as a covariate were relatively low, it may still be worthwhile including those sources of data in a multi-level estimation of density and diameter breeding values and estimates of variance components.

The significant reduction of σ_c^2 for grafted-ramet density, assessed using the Pilodyn, when regressed with ortet density as a covariate is difficult to explain. Pilodyn assessment of wood density is less precise than gravimetric methods (Wood, 1986) and so any relationship between grafted-ramet Pilodyn and ortet density should be more pronounced for the gravimetrically assessed outer rings (13-17) of the grafted-ramets. Since this was not found to be the case, it perhaps highlights the possible errors associated with these small datasets. Conclusions relating to areas of genetic overlap and worthiness of inclusion in genetic models are probably better restricted to higher levels of statistical significance.

Ortet diameter makes no significant reduction to σ_c^2 for any of the traits in the grafted-ramet populations suggesting it is of low value in estimating genotypic values.

The high estimates of $r_{g,\ BV}$ values for genotype of grafted-ramets for density (rings 8-12 or 13-17) with the ortet breeding value assessed using the progeny density data suggests clone banks may be a useful source of genetic information. The Wald statistic values

were similar for rings 8-12 and 13-17 but the higher broad sense heritabilities (H^2) associated with rings 13-17 suggest it may only be necessary to measure the outer rings in further studies.

It is worth remembering that wood density of the progeny was assessed indirectly using the Pilodyn. It is probable that the more accurate gravimetric assessment of wood density would be better correlated with the true breeding value for wood density and therefore further increase the significance of regression of grafted-ramet and progeny density.

4.6.2 **Analysis based on simple correlations:**

The level of correlation coefficients between ortet and grafted-ramet mean (i.e. clone mean) calculated in this study falls between the high correlations reported by Ericson (1960) and Gislerud (1973) of r = 0.80-0.76, and r = 0.51 respectively and the lower ones of Zobel *et al* (1962; r = 0.28). These differences most probably reflect the relative effort and success in trying to remove the possible confounding effects due to variation of seed source and environment between the selected ortets i.e. estimates of fixed effects. Comparisons of relative diameter and density of the ortets (compared to local population means) would increase not only the correlations but also the regressions evaluated in the Mixed Model Analysis.

4.6.3 **General trends based on combined analysis:**

The often large and significant reduction in σ_c^2 following the introduction of covariates and calculated genetic correlations between breeding values as assessed from the progeny and genetic value (additive and non-additive genetic contribution combined) of the grafted-ramets does give an idea of the value of including different generation levels in estimation of variance components and breeding values. Wood density assessment of grafted-ramets may well be useful in providing additional information on breeding

values of ortets based primarily on data collected in progeny tests. Clone banks may therefore act as links between geographically separated populations by removing the need to estimate unknown fixed effects associated with each of those populations. In this effect, the clone-bank becomes synonymous with a progeny test in that the effects of the environment are minimised allowing a more accurate assessment of genotype.

There would appear to be less benefit from including wood density data from the original ortet in any model in the absence of data enabling the estimation of fixed effects. Density data from grafted-ramets can also contribute to final estimated diameter breeding values derived from progeny tests due to the strong (negative) genetic correlation between diameter and density.

4.7 CONCLUSIONS

This pilot study was designed to investigate the degree of simple and genetic correlations between ortet breeding value for wood density and stem-diameter assessed using traditional progeny tests, with data collected from the original ortet and grafted-ramets of those ortets growing in a clone-bank.

The main findings were:

1. A significant relationship exists between the estimates of genotypic values for density of grafted-ramets and ortet breeding value estimated from the family mean performance in a progeny test.

2. Density data collected from grafted-ramets growing in a clone bank should add more precision to density breeding values and variance component estimates derived from progeny test data.

3. In the absence of progeny tests, density assessed on grafted-ramets would give a more precise indication of genotypic value than ortets alone.

4. Including data from the original ortets for wood density added little additional information.

5. There was no benefit from including either ortet or grafted-ramet diameter data in estimation of diameter breeding value.

6. Simple correlations between ortet and progeny-mean wood density reflect the results calculated in the mixed model approach and compare well with the limited published data.

The above conclusions were encouraging. The pilot study demonstrated the possible benefits of including wood density data from a grafted-ramet population in the estimation of breeding values, suggesting that variance components could also be estimated with reduced error.

It is quite possible that the strength of genetic relationships between ortet, progeny and grafted-ramets in the Population Study could be further improved relative to this pilot study since in the former:

1. The ortets were of known single origin (QCI);

2. The ortets were not disparate over the forest, but concentrated in one compartment allowing a better estimate of fixed effects;

3. Density assessment of the progeny would be carried out by X-ray densitometry as well as indirect (Pilodyn) methods.

4. The grafted-ramets were all planted in a clone-bank in the same year.

Future assessments of DBH, Pilodyn and gravimetric assessment of wood density for grafted-ramets from the Population Study should be rationalised as follows:

i. DBH: since trees may be elliptical, assessment should be by girthing tape.

ii. Pilodyn: since pin penetration may vary with cardinal position, more than one shot is necessary from different cardinal positions. Analysis should be based on a mean of the positions.

iii. Basic density: collect the outer five-ring sections either the north or south side only and assess using either the standard water displacement method or maximum moisture content method.

CHAPTER 5

Introduction of data from ortet and grafted-ramet populations.

5.1 INTRODUCTION AND OBJECTIVES

The 'Pilot Study' was carried out to investigate the magnitude of correlations between progeny test data with ortets or grafted-ramets data for wood density or stem diameter. That study was considered to be successful in that it demonstrated high estimates of genetic correlations between wood density breeding values assessed in progeny tests and genotypic values of grafted-ramets growing in a clone-bank. This was encouraging since it indicated the possible value of including grafted-ramet wood density data in the estimation of variance components and breeding values involving a multiple-data source in REML and BLUP analyses.

A number of reasons were presented in the 'Pilot Study' as to why the equivalent correlations for wood density and also vigour should be greater for the randomly selected single-origin trees that constitute the 'Population Study' relative to the selected trees from possibly more than one origin that composed the 'Pilot Study'.

The objectives of work reported in this Chapter were:

i. To estimate correlations between ortet breeding values for wood density and certain vigour traits estimated from the 'Main Study' with data collected from the original 'Population Study' ortets and grafted-ramets growing in a clone-bank.

ii. To investigate the response in breeding value of the progeny as a result of selection for height in the ortet population and diameter and density in the grafted-ramet population, thereby further demonstrating at a more practical level the correlation between traits from different genetic sources.

iii. To make recommendations regarding data collection from ortet and grafted-ramet populations in future estimation of variance components and breeding values.

5.2 MATERIALS AND METHODS

In order to carry out the investigation outlined above, wood density and vigour data were required from (i) The 'Main Study' (ii) the original ortets and (iii) grafted-ramets.

5.2.1 The 'Main Study':

Progeny test data for each trait were readily available from the 'Main Study' as a result of previous analysis described in Chapters 2 and 3. The breeding goals of DM23 and RG19-22 along with their respective optimum indirect selection traits (HT09 and RG6-9) were chosen as suitable representatives for vigour and wood density against which data from ortets and grafted-ramets could be correlated.

5.2.2 Grafted-ramet data:

Scion material had been collected from all 150 ortets of the 'Population Study' at the time of felling and grafted onto juvenile root-stock in January 1973. Three grafted-ramets of each ortet were planted adjacent to each other in a sequential pattern within the Ledmore clone-bank (Central Region, Scotland, 56° 28' N, 3° 32' W) in Spring 1975. Ramets were planted in an east/west direction at a spacing of 2 m between grafts and 3 m between rows. There were 12 clones (36 grafts) to a row and 12.5 rows.

In November 1995, when the grafted-ramets were 21-years from planting, stem diameter and Pilodyn data were collected and 8 mm cores were extracted with a Pressler borer to allow gravimetric assessment of wood density.

Many of the conclusions from the 'Pilot Study' with respect to how the grafted-ramets should be measured and subsequent samples analysed, were implemented in this study as follows:

i. Diameter at breast height was only assessed using a girthing tape to an accuracy of 0.1 cm;

ii. Pilodyn data were collected at breast height from more than one cardinal position (north and west side of each tree). The mean of these data were used in analysis;

iii. Cores were taken at breast height from the north radius of the tree only;

iv. Only the outer 5 rings were assessed for wood density;

v. The standard water displacement method was used to assess wood density of the outer 5-ring samples as described in Chapter 4.2.

Not all clones were assessed for the above traits. Measurements were only carried out on those 46 clones which acted as mother trees to the open-pollinated families analysed for wood density and reported in Chapter 3. This was done in an attempt to retain balance with the 'Main Study'.

As in the 'Pilot Study', data were collected from all live ramets representing a clone which did not express clear incompatibility problems. These restrictions lead to the total rejection of four clones and a further three clones were represented by just one ramet.

Increment cores, Pilodyn readings and breast height diameter data were collected from a total of 107 grafted-ramets (2.55 grafts/clone) as listed in Appendix 2.2. On arrival at the laboratory, three cores were found to be badly shattered and were rejected for gravimetric assessment. Wood density data assessed by gravimetric means was therefore restricted to 104 ramets (2.47 ramets/clone).

5.2.3: **Ortet data:**

All 150 ortets were felled in November 1972. Total tree height was calculated to the nearest centimetre as the combination of stump height and felled tree length. These data are presented along with the dominance class of the tree in Appendix 5.1.

Wood density, either directly (gravimetrically) or indirectly (Pilodyn), was unfortunately not assessed before the trees were felled and disposed of.

Trees within each dominance class had been selected from across the entire survey site which was found to be quite heterogenous in topography ranging from 30 m to 130 m height above sea level (h.a.s.l.). The location of each tree had been previously identified on a 1:2,100 map traced from local forest compartment stock-maps. The h.a.s.l. of each individual tree had not been recorded at the time of selection.

Decline in total tree height with increase in h.a.s.l. (leading to increased exposure and reduced growing season) has been documented in Britain (Worrell, 1987). It was therefore not surprising that some dominant trees at high elevation were found to be smaller than sub-dominant trees at lower elevations. This was acceptable in terms of allocating a tree to a dominance class based on relative height amongst immediate neighbours. It was however, quite unacceptable in terms of describing relative breeding values for height unless an adjustment was possible for h.a.s.l.

A study was carried out with the following objectives:

i. to investigate if a significant relationship existed between tree height and h.a.s.l. at this site;

ii. to use h.a.s.l. as a co-variate if a relationship did exist in order to calculate adjusted tree heights for a unified h.a.s.l. which could be used in further analysis involving ortet height data.

5.2.3.1: **Method:**

The study area within South Strome Forest, was identified on a 1:10,000 ordinance survey map (sheet NG 83 SE) which gave contours every 10 m. The map was photo-enlarged by 400% onto an acetate sheet so that the size and scale of the study area now equated as closely as possible with the original traced map giving the location of all 150 ortets. The acetate sheet was then placed over the traced map allowing the h.a.s.l. of each ortet to be estimated to the nearest 5 metres.

5.2.3.2: **Statistical Methods:**

Analysis involved regression of h.a.s.l. with total tree height and calculation of the regression coefficient (slope) using PROC REG within SAS (1982). A significant regression between the two traits would allow adjusted total tree height to be calculated for a unified h.a.s.l. according to the equation:

$$Y_i = y_i - b\ (X_i - A) \qquad (5.1)$$

where: Y_i = adjusted height for tree *i*;

y_i = original height for tree *i*;

X_i = h.a.s.l. for tree *i*;

b = regression coefficient of h.a.s.l. against original tree height;

A = unified h.a.s.l.

Analysis was carried out (i) on the complete population of 150 trees and (ii) sub-divided by dominance class. A significant difference between slopes across dominance class would mean that co-variate adjustment would have to be carried out at the individual dominance class level.

A comparison of mean h.a.s.l. by dominance class was also carried out to see if all trees within a dominance class were equally distributed over the site or were biased to higher or lower elevations. PROC GLM within SAS (1982) was used in the analysis according to the following model:

$$Y_{ij} = u + D_j + e_{ij} \qquad (5.2)$$

where: Y_{ij} = h.a.s.l. tree i within dominance class j;

u = estimated mean tree height for the site;

D_j = the random effect due to dominance class j;

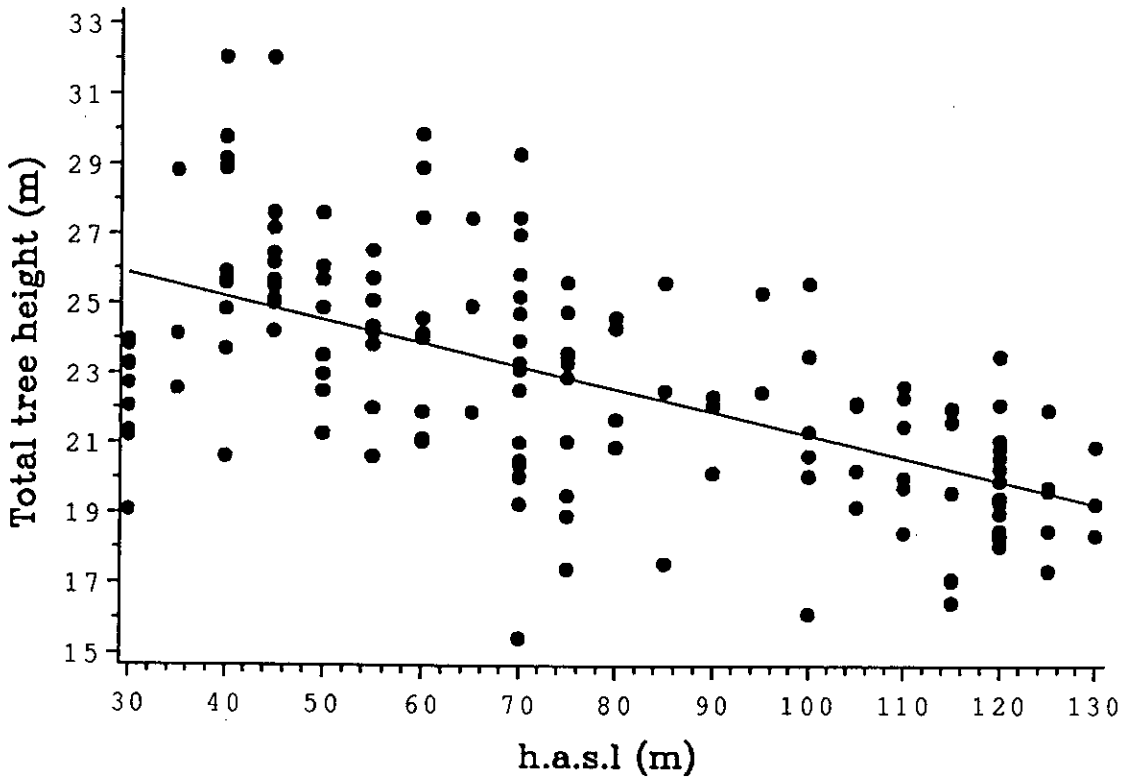
e_{ij} = the residual effect of tree i within dominance class j.

5.2.3.3 **Results and Discussion:**

Appendix 5.2 is the map of the original study area in South Strome Forest constructed using the original tracing, super-imposed with 10 metre contours. There would seem to be an even spread of selected trees across the entire study site which increases in h.a.s.l. at a fairly constant rate.

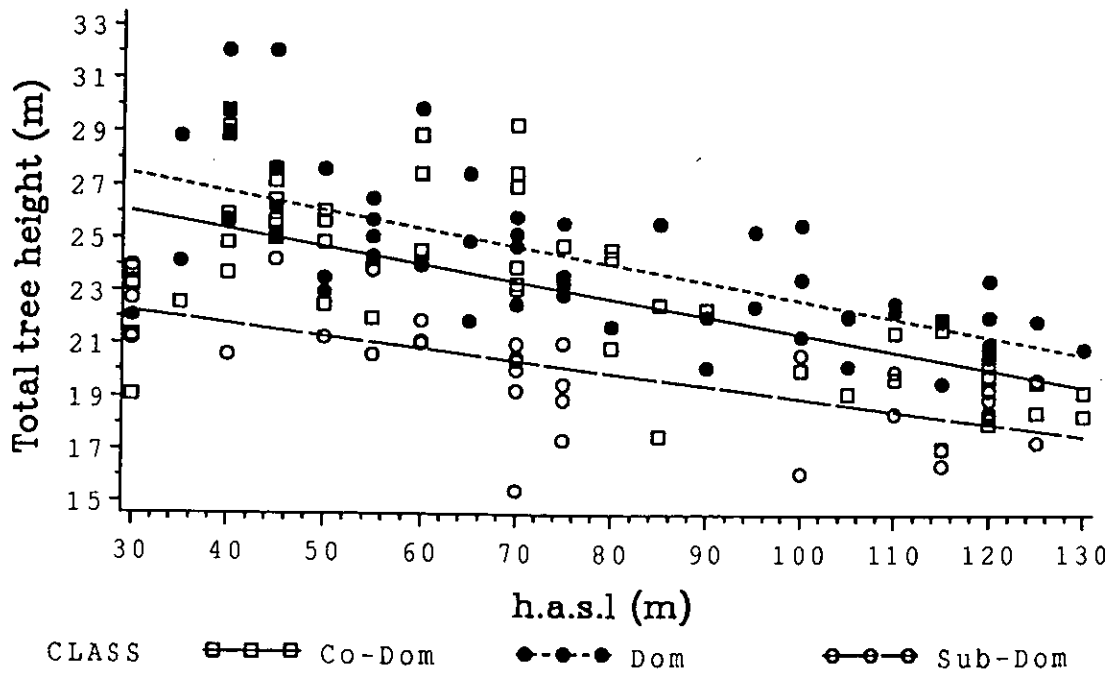
Figure 5.1 is a graph of tree height against h.a.s.l. for the complete population of 150 trees; Figure 5.2 is the equivalent graph sub-divided by dominance class. In each case there was a highly significant relationship ($p < 0.0001$) between the total tree height

Figure 5.1: Original ortet tree height against h.a.s.l.



Note: No distinction made between trees of different dominance classes.
Regression line: Tree height = 27.8338 – 0.06197 * h.a.s.l. r = 0.60 p = 0.0001

Figure 5.2: Original ortet tree height against h.a.s.l. by dominance class



Note : Dom = dominant, Co–dom = Co–dominant, Sub–dom = Sub–dominant
Regression lines: Dom = 29.4721– 0.0679 * h.a.s.l r = 0.67 p = 0.0001
Co–Dom = 27.9796– 0.0658 * h.a.s.l. r = 0.64 p = 0.0001
Sub–Dom = 23.6223– 0.0467 * h.a.s.l. r = 0.67 p = 0.0001

and h.a.s.l. There was no significant difference (p= 0.35) between slopes of the regression equations when analysis was sub-divided by dominance class (Table 5.1), and although standard deviations for adjusted tree heights were high within dominance classes, there was no significant difference (p = 0.36) between mean h.a.s.l. across dominance class (Table 5.2). All subsequent analysis were therefore carried out at the complete population level.

The mean h.a.s.l. of the 150 selected trees was 75.60 m (Table 5.2); this height was chosen as the unified h.a.s.l. Adjusted tree heights were then calculated according to Equation 5.1 with b = -0.06197 (Figure 5.1). Original and adjusted total heights together with the h.a.s.l. for each tree are give in Appendix 5.1.

Original and adjusted dominance-mean tree heights are also given in Table 5.2. Although there were only small differences at the mean dominance-class level, standard deviations for adjusted heights were smaller than the original at both the complete population and dominance class level. Individual tree changes between original (Or) and adjusted heights (Aj) were often considerable e.g. 4002: Or = 19.08 Aj = 16.25; 4149: Or = 18.49 Aj = 21.55 (Appendix 5.1).

There was a highly significant difference between dominance classes for both original and adjusted tree heights (Tables 5.1 and 5.2) indicating clear phenotypic differences between the classes across the site. According to Assman (1970), co-dominant and sub-dominant trees should be 84-95% and 74%-84% the height of dominant trees respectively. From Table 5.2, it would appear both the co- and sub-dominants are at the top end of the Assman definition.

Even following adjustment of tree height for h.a.s.l., Figure 5.3 shows there was a considerable range of heights within each dominance class and over-lap of ranges between dominance classes. This range was greatest within the co-dominant class where adjusted tree height varies from 16.25 m to 29.9 m.

Table 5.1: Comparison of slope between original total tree height and h.a.s.l. by dominance class.

Source	df	MS	Significance
Class	2	47.0033	p = 0.0001 (***)
h.a.s.l.	1	473.9089	p = 0.0001 (***)
h.a.s.l.* class	2	5.1041	p = 0.3510 (NS)
Error	144	4.8394	

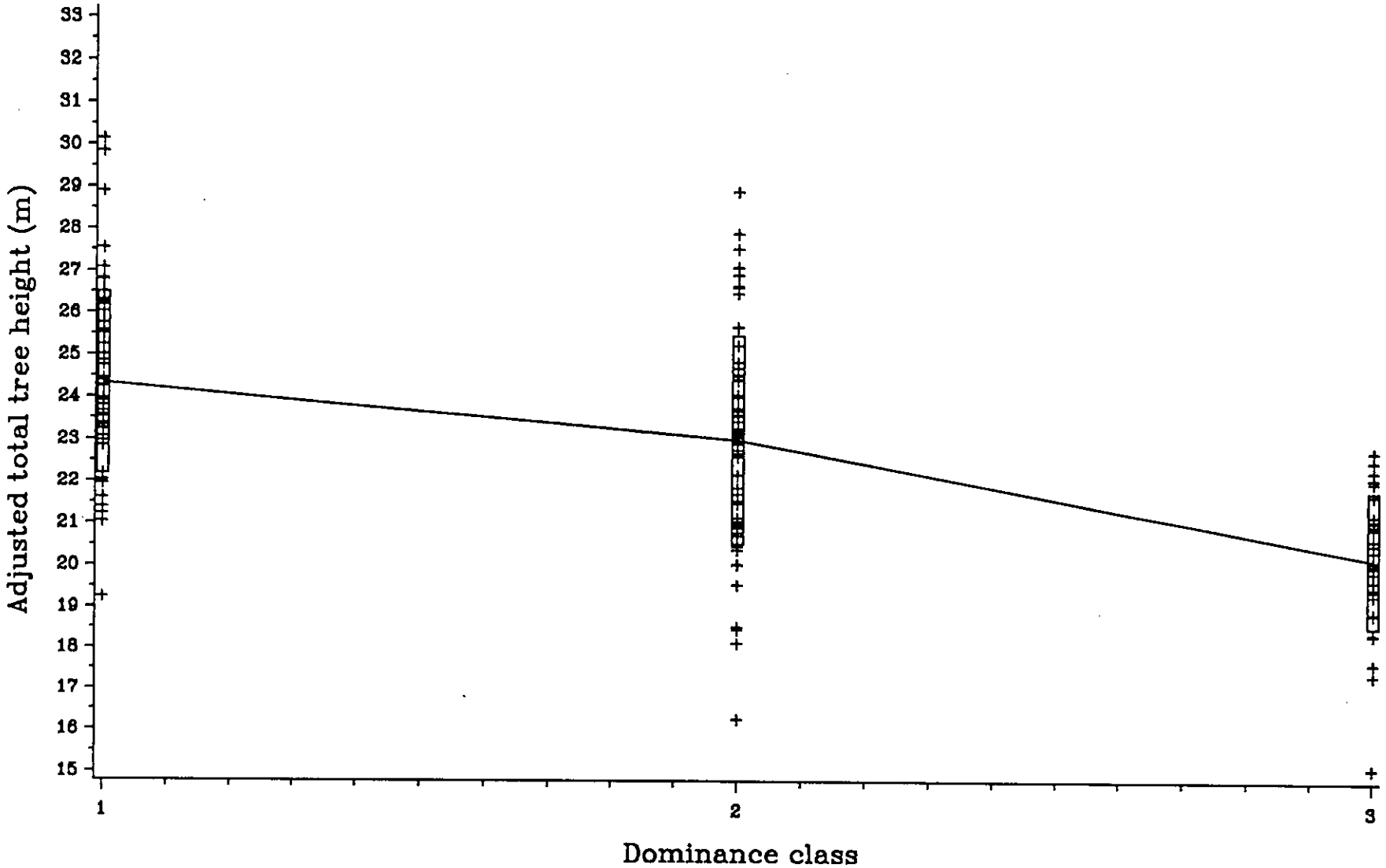
Note: h.a.s.l. = height above sea level.

Table 5.2: Original and adjusted tree height and height above sea level by dominance class and for all tree combined.

	Original height (m)	Adjusted height (m)	Adjusted class-mean height relative to dominant trees	Height above sea level (m)
Dominant	24.34 ± 2.9	24.34 ± 2.2	100%	75.56 ± 29.0
Co-dominant	23.23 ± 3.3	23.02 ± 2.5	95%	72.21 ± 32.4
Sub-dominant	19.82 ± 2.13	20.19 ± 1.6	83%	81.57 ± 31.1
Significance between treatment means	p = 0.0001 ***	p = 0.001 ***	—	p = 0.36 NS
All trees	22.83 ± 3.4	22.83 ± 2.7	—	75.60 ± 30.9

Note: ± indicates Standard Deviation.

Figure 5.3 : Adjusted tree height by dominance class



Note 1. Dominance class: 1 = Dominant, 2 = Co-dominant, 3 = Sub-dominant
Note 2. Each box indicates one standard deviation about the mean

5.2.3.4 Conclusions

Tree height of the original ortets selected within the South Strome study area was highly influenced by height above sea level.

By using h.a.s.l. as a covariate adjusted tree heights have been calculated assuming a unified h.a.s.l. equal to the mean for the 150 selected trees. Covariate adjustment was carried out at the complete population level as there were no significant difference between slopes at the individual dominance class level.

5.3 STATISTICAL METHODS

Analysis involved bringing together the data from the different genetic sources. Quadrivariate analysis was necessary for all analyses involving RG19-22 and RG6-9 since, as before, in order to avoid selection bias the two traits used to calibrate the original selection ellipse (DM16 and DN17) were included as covariates. All other regressions involved bivariate analysis. As before, all data for use in analysis were standardised by subtracting the mean and dividing by the standard deviation for that trait.

Datasets for grafted-ramet and ortet traits required information regarding male and female parents, plot, replicate and tree number (within plot). Both parents were unknown and therefore equal to zero. All trees within each site were considered to be from the same plot and replication for that site. Individual grafted-ramets within each clone were presented to the analytical software as repeat measurements of the various traits. Since it was not possible to sub-divide either the clone-bank or the forest, each site was associated with just one fixed effect. As before, all data from the 'Main Study' contained information regarding known female and unknown male parents, three different fixed effects associated with replicates and either 25 trees (HT09), 12 or 13 trees (DM23) or 5 trees (RG6-9, RG19-22) per plot.

All analysis was carried out using ASReml (Gilmour, 1996). As in previous analysis, a parameter (*.as*) file described the bi- or quadrivariate model and gave information on the description and location of the data and pedigree files. Relative to previous *.as* parameter files used to analyse exclusively the data from the 'Main Study', it was necessary to introduce an additional site referring to either the forest or clone-bank as appropriate. Since there was no relationship between random residual effects and family by replicate interaction between the two different sites, these variance components could not be estimated by the *.as* file although 'dummy' data were generated. The covariance for genetic effects across sites could however be estimated by virtue of the $Z_l a_l$ matrix and vector in Equation 2.2.

Estimates of variance and covariance components were generated to the *.asr* output file. As in the quadrivariate analysis described in Chapter 3, if it was not possible to achieve convergence on the first run of the model, estimates of variance and covariance components generated in the penultimate iteration of the model were used as starting values in subsequent runs.

Certain estimates of the different variance and covariance components were further used to calculate a number of statistical functions as follows:

i. *Clonal heritability*

As reported in Chapter 4, clone-mean heritability (H_c^2) was estimated for all grafted-ramet traits according to the following equation:

$$H_c^2 = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{G(n)}^2} \qquad (5.3)$$

where: H_c^2 = clone-mean heritability;

σ_G^2 = variance between clones;

n = number of repeat measures;

$\sigma_{G(n)}^2$ = variance due to clone x repeat measure interaction.

ii. *Simple correlation coefficients*

The simple correlation between ortet height and grafted-ramet mean (i.e. clonal mean) diameter, density and Pilodyn score with progeny-mean values were estimated according to the following equation:

$$r = \frac{COV_{\overline{X}\,\overline{Y}}}{\sqrt{\sigma_{\overline{X}}^2\ \sigma_{\overline{Y}}^2}} \qquad (5.4)$$

where: r = simple correlation coefficient;

$COV_{\overline{X}\,\overline{Y}}$ = Covariance between mean values of Trait X and Trait Y;

$\sigma_{\overline{X}}^2$ = variance of mean values of Trait X;

$\sigma_{\overline{Y}}^2$ = variance of mean values of Trait Y;.

Trait X = ortet or clonal mean;

Trait Y = progeny mean.

As in Chapter 4, it was not possible to estimate the phenotypic correlation between Traits X and Y since sites were not common.

iii. *Genetic correlations*

Genetic correlations between Trait X and Trait Y ($r_{g,\ BV}$) were estimated to allow a comparison with similar estimates reported in Chapter 4. As in the 'Pilot Study', the estimates of genetic correlations were only an approximation as it involved correlating the genotypic values (additive and non-additive) of the clonal data with the breeding values (additive only) of traits derived from the progeny test as follows:

$$r_{g,\ BV} = \frac{COV_{G_{XY}}}{\sqrt{\sigma^2_{G_X}\ \sigma^2_{G_Y}}} \qquad (5.5)$$

where: $r_{g,\ BV}$ = genetic correlation between Trait X and Trait Y;

$\sigma^2_{G_X}$ = genetic variance of Trait X;

$\sigma^2_{G_Y}$ = genetic variance of Trait Y;

$COV_{G_{XY}}$ = genetic covariance between Trait X and Trait Y.

The model assumes non-additive genetic variance = 0.

Since $\sigma^2_{G_X}$ could not be estimated for ortet height, the phenotypic variance was substituted and weighted by the same value of single tree heritability used to calculate $r_{g,\ BV}$ as reported in Chapter 4 ($h_i^2 = 0.15$).

iv. *Correlated response*

The response in breeding value for certain traits within the progeny population (Trait Y) following selection for a specific trait within the ortet or grafted-ramet population (Trait X) was estimated as follows:

$$b_{YX} = \frac{COV_{G_{XY}}}{\sigma^2_{P_X}} \qquad (5.6)$$

where: b_{YX} = correlated response of Trait Y on Trait X;

$\sigma^2_{P_X}$ = phenotypic variance of Trait X.

In order to estimate the above functions of variance and covariance components it was necessary to construct 3 different *.pin* files as follows:

i. ortet:progeny data;

ii. grafted-ramet:progeny data (bivariate);

iii. grafted-ramet:progeny data (quadrivariate).

As before, the *.pin* file acted on estimated variances and covariances from the *.asr* file and generated the output to *.pvs* file. Since the data were all standardized prior to analysis, it was necessary to 'scale-up' variance and covariance components by multiplying the generated figure by the $S.D^2$ (variance) or the product of the respective standard deviations of the two traits (covariance).

Investigations across data sources were restricted to those thought to be of greatest potential value based on experience from the 'Pilot Study'. Thus ortet height and all grafted-ramet traits were involved in bivariate analysis with DM23, ortet height and grafted-ramet diameter were involved in bivariate analysis with HT09 and grafted-ramet density and Pilodyn were involved in quadrivariate analysis with RG6-9 and RG19-22.

5.4 RESULTS

Individual grafted-ramet values for gravimetrically assessed wood density, Pilodyn and diameter are given in Appendix 5.3. Trait-mean values, standard deviations and number of trees representing each trait are given in Table 5.3. Details of traits from the Main Study first reported within Chapters 2 and 3 are repeated here for ease of reference.

Examples of *.as*, *.pin* and *.pvs* files used or generated in the bi- and quadri-variate analysis are given in Appendices 5.4 to 5.12. Examples of *.asr* files are not presented since they can extend to many pages and are similar in principle to those present in Chapter 3, whilst all the relevant variance and covariance components (with standard errors) are repeated in the *.pvs* file.

Convergence in the *.asr* file was not achieved for all the quadrivariate analyses using the ASReml software. Whilst successful convergence was achieved between RG6-9 (including covariates DM16 and DN17) with grafted-ramet Pilodyn and wood density data, convergence of RG19-22 (including covariates) with the same grafted-ramet traits proved impossible. Negative sums of squares were constantly generated at the family (σ_f^2) level. Many fruitless runs of the model were carried out with different starting values using observations from the *.asr* file before negative sums of squares were generated. Attempts were made to observe each iteration to learn how the variance and covariance components were changing and perhaps prevent a negative sum of squares from being generated by amending the starting values. All attempts were unsuccessful.

Further attempts were made to (i) fix all covariances which were similar to variance components; (ii) then fix the variance and covariance components relating to the error (σ_e^2) and family (σ_f^2) level in order to achieve good estimates of σ_{fr}^2; (iii) then run the model one iteration at a time with σ_{fr}^2 fixed at its newly estimated value and σ_e^2 and σ_f^2 reverted to random effects. Again convergence was not achieved. This time the analysis was abandoned.

Table 5.3: Mean value, standard deviations and number of trees per trait according to genetic source and trait.

Trait		Mean	Standard Deviation	Number of Trees
Progeny:	**HT09 (cm)**	359.64	75.1060	9227
	DM23 (cm)	15.08	3.4022	4438
	RG6-9 (g cm^{-3})	0.5121	0.0659	376
	RG19-22 (g cm^{-3})	0.4781	0.0546	592
Ortets:	**Adjusted Height (m)**	22.83	2.6880	150
Grafted-ramets:	**Diameter (mm)**	175.66	42.1510	129
	Pilodyn (mm)	18.44	2.7769	107
	Density (g cm^{-3})	0.3416	0.0363	104

i. *Variance components*

Estimates of the phenotypic variance (σ_p^2), genotypic variance (σ_G^2) and clonal or family mean variance ($\sigma_{\bar{c}}^2$ and $\sigma_{\bar{f}}^2$) are given in Table 5.4. Estimates of covariance between treatment means ($COV_{\bar{X}\,\bar{Y}}$) and genetic covariance ($COV_{Gen_{XY}}$) between Traits X and Y are presented in Table 5.5. Figures of σ_p^2 and σ_G^2 for the progeny traits are nearly identical to estimates of σ_p^2 and σ_G^2 reported in Tables 2.6 and 3.6, any differences are due to the different combination of genetic relationships between traits involved in the bi- or quadrivariate analysis, causing the ASReml model to modify estimates slightly. Estimated values of σ_p^2 and σ_G^2 for Traits X and Y also varied slightly across the different bi- or quadrivariate analyses carried out. The figures reported here are the means of the estimates generated in the different runs.

Table 5.4: **Phenotypic, genotypic and treatment-mean (clonal or family) variance components (complete with standard errors) for all traits involved in the investigation into genetic relationship across genetic sources (ortet, grafted-ramets or progeny).**

Trait		Phenotypic Variance σ_p^2	Genotypic Variance σ_G^2	Clonal or Family Variance σ_c^2 or σ_f^2
ORTET	Height (m)	7.2250 ± 0.7283		$7.2250^{\#}$ ± 0.7283
GRAFTED RAMET	Diameter (mm)	1812.24 ± 44.9862	970.62 ± 275.02	1216.7 ± 41.2196
	Density (g cm^{-3})	0.1262×10^{-2} ± 0.2098×10^{-3}	0.6940×10^{-3} ± 0.2056×10^{-3}	0.7390×10^{-3} ± 0.2014×10^{-3}
	Pilodyn (mm)	7.5585 ± 1.3161	4.6807 ± 1.2970	4.8087 ± 1.2815
PROGENY	DM23 (cm)	11.3180 ± 0.2463	1.6610 ± 0.3910	0.5733 ± 0.9368×10^{-1}
	HT09 (cm)	5372.4 ± 145.15	1862.7 ± 471.00	879.98 ± 112.07
	RG6-9 (g cm^{-3})	0.4134×10^{-2} ± 0.3384×10^{-3}	0.3388×10^{-2} ± 0.1007×10^{-2}	0.1214×10^{-2} ± 0.9610×10^{-4}

Note: 1. Trait units given in brackets.

2. $^{\#}\sigma_p^2$ = mean variance for ortet height since n = 1.

3. ± indicates standard error.

Table 5.5: **Estimation of treatment-mean (clonal or family) and genotypic covariance (complete with standard errors) between Traits X (ortet height; grafted-ramet diameter, density and pilodyn) and Trait Y (selected traits measured on progeny).**

Trait X		Trait Y					
		TRAITS MEASURED ON PROGENY					
		$COV_{\bar{X}\,\bar{Y}}$			$COV_{Gen_{XY}}$		
		DM23 (cm)	HT09 (cm)	RG6-9 ($g\ cm^{-3}$)	DM23 (cm)	HT09 (cm)	RG6-9 ($g\ cm^{-3}$)
ORTET	Height (m)	0.6401 ± 0.2081	20.9153 ± 7.1974		1.2821 ± 0.4131	41.8100 ± 14.3948	
GRAFTED RAMET	Diameter (mm)	6.4088 ± 3.9055	106.47 ± 148.08		12.8176 ± 7.8114	212.96 ± 296.13	
	Density ($g\ cm^{-3}$)	$-0.7729 \times 10^{-2} \pm 0.3535 \times 10^{-2}$		$0.3947 \times 10^{-3} \pm 0.5870 \times 10^{-4}$	$-0.1546 \times 10^{-1} \pm 0.1711 \times 10^{-1}$		$0.7894 \times 10^{-3} \pm 0.2975 \times 10^{-3}$
	Pilodyn (mm)	0.4230 ± 0.2808		$-0.1987 \times 10^{-1} \pm 0.1168 \times 10^{-1}$	0.8458 ± 0.5616		$-0.3977 \times 10^{-1} \pm 0.2336 \times 10^{-1}$

Note:
1. Grafted-ramet mean (i.e. clone mean) based on n = 3; progeny mean based on n = 75 (HT09), n = 37.5 (DM23) or n = 15 (RG6-9).
2. Trait units given in brackets.
3. ± indicates standard error.
4. $COV_{\bar{X}\,\bar{Y}}$ = covariance of treatment mean for Trait X and treatment mean for Trait Y.
5. $COV_{Gen_{XY}}$ = covariance of genetic effects for Trait X and Trait Y.

ii. *Clonal Heritability*

Estimates of clonal heritability (H_c^2) for the traits measured on the grafted-ramets are given in Table 5.6. All estimates were similar across traits with similar standard errors. The range is from $H_c^2 = 0.53$ (diameter) to 0.62 (Pilodyn). Direct assessment of density had a lower value ($H_c^2 = 0.55$) than indirect which is surprising, although the respective standard errors gave considerable overlap between these two methods of density assessment.

Table 5.6: Grafted-ramet clone-mean heritabilities (H_c^2) assuming 3 ramets per clone.

Grafted-ramet trait	σ_G^2	$\sigma_{G(n)}^2$	H_c^2
Diameter (mm)	935.258	843.137	0.5259 ± 0.0866
Density (g cm^{-3})	0.6940×10^{-3}	0.5676×10^{-3}	0.5501 ± 0.0932
Pilodyn (mm)	4.6807	2.8786	0.6192 ± 0.0825

Note: 1. ± indicate standard error.

2. Trait units given in brackets.

iii. *Simple correlation coefficients (r) and genetic correlations ($r_{g,\ BV}$).*

Estimates of r and $r_{g,\ BV}$ are given in Table 5.7. On all occasions $r_{g,\ BV}$ exceeds r. This is particularly the case for bivariate analysis of ortet height with progeny DM23 and HT09; ($r_{g,\ BV} = 0.95$, $r = 0.32$ and $r_{g,\ BV} = 0.93$, $r = 0.26$ respectively). This probably reflects the errors associated with introducing an assumed value of individual tree heritability for mature height of $h_i^2 = 0.15$. The value of $h_i^2 = 0.15$ was selected in the 'Pilot Study' as being a typical value of heritability for juvenile (up to 10 years old) height in Sitka spruce reported by Lee (1994). A re-calculation of the data with $h_i^2 = 0.30$ gave estimates of $r_{g,\ BV}$ for ortet:DM23 and ortet:HT09 of 0.6756 ± 0.1969 and

0.6580 ± 0.2059 respectively, thus demonstrating how estimates of $r_{g,\ BV}$ assessed using this method can drop as the heritability increases to what may be a true value for mature tree height.

Table 5.7: Treatment-mean correlations (r) and genetic correlations ($r_{g,\ BV}$) between Traits X and Y (complete with standard errors).

Trait X			Trait Y		
			PROGENY		
			DM23 (cm)	HT09 (cm)	RG6-9 (g cm^{-3})
ORTET	Height (m)	r s.e.	0.3150 ± 0.0900	0.2622 ± 0.0827	
		$r_{g,\ BV}$ s.e.	0.9500 ± 0.2785	0.9306 ± 0.2912	
GRAFTED RAMET	Diameter (mm)	r s.e.	0.2425 ± 0.1405	0.1014 ± 0.1394	
		$r_{g,\ BV}$ s.e.	0.3246 ± 0.1876	0.1581 ± 0.2171	
	Density (g cm^{-3})	r s.e.	-0.3429 ± 0.1426		0.4167 ± 0.1320
		$r_{g,\ BV}$ s.e.	-0.4537 ± 0.1882		0.5788 ± 0.1832
	Pilodyn (mm)	r s.e.	0.2348 ± 0.1489		-0.2603 ± 0.1441
		$r_{g,\ BV}$ s.e.	0.3024 ± 0.1914		-0.3482 ± 0.1926

Note: 1. r calculated according to Equation 5.4.

2. $r_{g,\ BV}$ calculated according to Equation 5.5.

3. A single-tree heritability (h_i^2) of 0.15 was assumed for ortet height.

4. Trait units given in brackets.

5. ASReml has a restriction factor which prevents correlations from exceeding 0.95.

Values of r and $r_{g,\ BV}$ involving grafted-ramet diameter and Pilodyn with either progeny DM23, HT09 or RG6-9 were very low and had large standard errors indicating there would be no value from including either of these grafted-ramet traits in the estimation of ortet breeding values. Values of r and $r_{g,\ BV}$ for grafted-ramet density and RG6-9 were quite large (0.42 and 0.58 respectively) suggesting a good genetic relationship and therefore a possible benefit of combining these traits in the estimation of ortet breeding values.

Grafted-ramet density and progeny DM23 gave moderate values of r and $r_{g,\ BV}$ (- 0.34 and -0.45 respectively).

iv. *Correlated response*

Regression coefficients (b_{YX}) of the breeding value of Trait Y (progeny) on the genotypic value of Trait X (ortet or grafted-ramet) are given in Table 5.8. The value of b_{YX} indicates the unit increase in Trait Y following a unit increase in the selection differential of Trait X. For example an increase in selection differential of ortet height of 1.00 m causes a 0.1701 cm increase in the breeding value of progeny DM23. Similarly, if the selection differential of ortet height was 5% relative to the mean, this would cause an increase in the mean breeding value of DM23 by 1.38%.

The largest values of correlated response were grafted-ramet density with RG6-9 (3.6%), and DM23 (-2.0%), and ortet height with HT09 (2.0%). These figures reflect the estimates of simple (r) and genetic ($r_{g,\ BV}$) correlations and also the value of adjusting ortet tree height for h.a.s.l.

Table 5.8: **(i) Regression coefficients (b_{YX}) of the breeding value of Trait Y on the genotypic value of Trait X (complete with standard errors) and (ii) correlated response in Trait Y following a 5% selection differential for Trait X.**

Trait X		Trait Y		
		PROGENY		
		DM23	HT09	RG6-9
ORTET	**Height:**			
	b_{YX}	0.1701 cm/m	5.8300 cm/m	
	s.e.	±0.0547	± 2.3107	
	5%	1.38%	2.0%	
GRAFTED RAMET	**Diameter:**			
	b_{YX}	0.1054×10^{-1} cm/mm	0.1701 cm/mm	
	s.e.	± 0.6231	± 0.2344	
	5%	0.63%	0.45%	
	Density:			
	b_{YX}	-17.498 cm/g cm^{-3}		1.0680 g cm^{-3}/g cm^{-3}
	s.e.	± 7.1043		± 0.3664
	5%	-2.00%		3.6%
	Pilodyn:			
	b_{YX}	0.1450 cm/mm		-0.8270×10^{-2} g cm^{-3}/mm
	s.e.	$\pm 0.9690 \times 10^{-1}$		$\pm 0.4697 \times 10^{-2}$
	5%	0.89%		-1.5%

Note: 1. b_{YX} calculated according to Equation 5.6.

2. The value of b_{YX} indicates the unit increase in Trait Y follow a unit increase in selection differential of Trait X.

3. Selection differential calculated as (0.05 x Trait X_{mean}).

4. Correlated response in Trait Y = $\left[b_{YX} \times \frac{\text{(selection differential for Trait X)}}{\text{(Trait } Y_{mean})} \times 100\%\right]$

There is often great scope for increasing the selection differential when choosing ortets with which to commence a breeding programme. A selection differential of one tree out of 1000 (selection intensity = 2.633; Becker, 1984) would give a correlated increase in DM23 breeding value of 8.0%. It indicates the gain that can be achieved at the stage of plus-tree selection despite low single tree heritabilities, if there is potential for a high selection intensity.

5.5 DISCUSSION

i. *Ortet Height*

Despite relatively low values of simple treatment-mean correlations (r), genetic correlations ($r_{g,\ BV}$) were high between adjusted ortet height and the direct (DM23) and indirect (HT09) breeding goals from the 'Main Study'. The absolute values of $r_{g,\ BV}$ were undoubtedly dependent on the assumed value of h_i^2 for mature tree height, but it does at least reflect a strong general relationship between adjusted tree height and progeny breeding goals for diameter.

Values of $r_{g,\ BV}$ between ortet and progeny height or diameter were not estimated in the 'Pilot Study' due to an insignificant reduction of σ_c^2 (equivalent here to σ_G^2) following regression between the two traits. It would seem therefore that when ortets are all from the same origin and ortet height is adjusted according to a well correlated environmental variable, it may be worthwhile combining ortet height along with progeny test data in the assessment of breeding values.

There are many factors which can influence the growth rates of trees across a site or forest. At the South Strome site, h.a.s.l. was considered to be the most restrictive factor; at other sites it may be one or more independent or interacting variables. Provided the height of trees selected within each forest or geographic area were adjusted according to measurable and well correlated site variables, then that whole forest or geographic

area could be attributed with a fixed effect in future bivariate analysis with progeny tests data to increase the precision of breeding value estimates.

Estimates of the correlated response (b_{YX}) are independent of the assumptions regarding single tree heritability for mature tree heights. Correlated response combined with the selection differential for Trait X gives an indication of expected gain in Trait Y. Figures presented here indicate that a large selection differential at the time of plus-tree (ortet) selection (the tallest from every 1000 trees) will give a worthwhile (8.0%) increase in the breeding value of DM23 (selection goal for diameter) relative to a random selection of ortets.

ii. *Grafted-ramets*

Grafted-ramet density correlated with RG6-9 resulted in the largest value of $r_{g,\ BV}$ (0.58). This confirms the findings of the 'Pilot Study' that grafted-ramet density would be worthwhile including in bivariate analysis with density data collected in progeny tests to assess estimates of density breeding values. This combination of traits also gave the highest percentage increase in a Trait Y (3.6%) following a 5% increase in the selection differential of Trait X.

There was a moderate negative genetic correlation between grafted-ramet density and progeny diameter ($r_{g,\ BV}$ = -0.45). In addition correlated response in DM23 was greater following a 5% increase in grafted-ramet density (-2.00%) than a 5% increase in ortet height (1.38%). Simple treatment-mean correlations were also larger between grafted-ramet density with DM23 (r = -0.45) relative to ortet height (r = 0.32). Values for $r_{g,\ BV}$ were greater between ortet height with DM23 relative to grafted-ramet density but were less precisely estimated since the latter was based exclusively on data generated within this study. The general findings confirm those of the 'Pilot Study' in that grafted-ramet density would assist in the estimation of diameter breeding values.

The relatively low estimates of $r_{g,\ BV}$ between grafted-ramet diameter and Pilodyn with either DM23 (0.32 and 0.30), HT09 (0.16 and N/A) or RG6-9 (N/A and -0.34) suggests little value from including either of these traits in the assessment of the respective breeding values.

Estimates of clonal heritability reported here for grafted-ramet diameter and density were very similar to those found in the 'Pilot Study' although grafted-ramet Pilodyn was higher (with larger standard errors) in the 'Pilot Study' ($H_c^2 = 0.71 \pm 0.13$) compared to here ($H_c^2 = 0.62 \pm 0.08$). The clonal heritability of grafted-ramet density (0.55) suggests a large proportion of non-additive genetic variance when compared to the single tree heritability for similar aged ring-groupings from the 'Main Study' (RG18-21; $h_i^2 = 0.33$).

iii. *Data from alternative sources*

Progeny-tests will remain the most reliable source of breeding value estimation and, whereas neither of these alternative sources of data would ever replace progeny tests, they could prove useful by:

a. increasing the accuracy of estimated breeding values relative to progeny tests alone;

b. reducing the size and cost of progeny tests if the existing accuracy of breeding value estimation is considered acceptable.

Breeders should therefore consider including data on (i) grafted-ramet density along with data collected in progeny tests when estimating breeding values and variance components for selection goals of both wood density and diameter, (ii) ortet height adjusted according to well correlated site variable(s) when estimating breeding values and variance components of selection goals for diameter. It is also likely that further

benefit would derive from use of the grafted-ramet data if each individual graft was planted randomly in a complete block design within the clone bank.

iv. *Convergence not achieved*

It was unfortunate that convergence was not achieved between grafted-ramet density and Pilodyn with RG19-22, since the evidence of similar regressions with RG6-9 and density of rings 13-17 with progeny density in the 'Pilot Study' was that values of $r_{g,\ BV}$ would be high. It is worth considering why convergence was not achieved.

When the ASReml software calculates values of variance and covariance it does so by assuming the starting values are the correct estimates. It uses these estimates to assist in the estimation of fixed effects. Once the fixed effects have been calculated, the variance and covariance components are recalculated according to the fixed effects. The programme moves back and forth between calculation of fixed effects and variance and covariance components until the change in value of all the variance and covariance components is minimal according to pre-programmed thresholds. If this point is achieved within the permissible maximum number of iterations (19) convergence is achieved. If not, the model must be re-run with updated estimates of variance and covariance values.

It becomes more difficult to achieve convergence as the number of variables and levels of analysis increases (Hill and Thompson, 1978). As in the studies reported in Chapter 3, there were a total of 30 variance or covariances to be estimated in the quadrivariate analysis reported here, involving 3 levels of variance. This means that at each iteration, the model is updating the components in a 30 dimensional space with complex boundary conditions. If this is further complicated by introducing highly imbalanced data in terms of number of trees representing each trait (Table 5.3), the software and genetic theory are operating at the extremes of their capabilities. It would seem that quadrivariate analysis involving grafted-ramet density and Pilodyn with

RG19-22 was beyond that level of capability. The lack of convergence could therefore be considered beneficial in illustrating the limitation of the analytical software under complex conditions.

A further problem could have arisen due to high genetic correlations between traits. Under these circumstances, variances and covariances are close to each other on a very flat plane and it becomes easy for negative sums of squares to be generated as one of the 30 components moves out of bounds beyond the limits of this flat plane. It may still be possible to achieve convergence if there is a good number of trees representing each trait with a relative balance between traits. If the number of trees representing some of the traits becomes very small with great imbalance between traits as it does here, the likelihood of convergence is reduced.

Given the above restrictions, it was surprising that convergence was achieved for RG6-9 in quadrivariate analysis and not RG19-22; especially since the latter was represented by an additional 200 trees. One explanation is that the genetic correlation between RG19-22 with grafted-ramet density and Pilodyn may be even greater than it was for RG6-9.

5.6 CONCLUSIONS

The main findings of this investigation were:

i. genetic correlations were high between genotypic values of (a) grafted-ramet density with breeding values of juvenile wood density (RG6-9) and the direct selection goal for diameter (DM23) assessed from a progeny test and (b) adjusted ortet height and breeding values of the direct (DM23) and indirect (HT09) selection goals for diameter from a progeny test;

ii. genotypic correlations were low between grafted-ramet diameter and breeding values of the direct (DM23) and indirect (HT09) selection goals for diameter from a progeny test;

iii. it would be beneficial to include grafted-ramet density and adjusted ortet height along with wood density and vigour data collected within replicated progeny tests in the calculation of wood density and vigour breeding values and variance components;

iv. calculated estimates of correlated response in progeny traits following a selection intensity of 1 in 1000 trees for ortet height illustrate the value of a high selection intensity when identifying plus-trees.

CHAPTER 6

DISCUSSION

6.1 INTRODUCTION

This study investigated the variance and covariance components for vigour and wood density operating within a sample of Sitka spruce trees known as the 'Population Study' selected in South Strome Forest in 1969. Data analysis was based predominantly on the progeny raised from open-pollinated seed collected from the parent trees and planted in Garcrogo Forest ('Main Study') in 1972. Height data collected from the original ortets and diameter and density (direct and indirect) data collected from grafted-ramets of the ortets growing in a clone-bank were subsequently regressed against certain traits assessed in the progeny test to investigate their potential contribution towards breeding value estimation.

The study was unique in a number of different areas.

I. Data from a randomly selected population:

Data collected from the 'Population Study' have two important strengths:

i. all the original selections were of a single known origin (QCI);

ii. all the selections were randomly chosen across all dominance classes.

Previous investigations into variance and covariance components for wood density and vigour traits beyond 6-years from planting have been based on data collected from progeny tests of ortets selected for vigour across an unknown range of origins.

This means that, for the first time, this study presents variance and covariance components for wood density and vigour ranging over the first half of a Sitka spruce rotation which are independent of bias due to selection and unknown amounts of confounding of variation between families due to variation between origins. The study becomes the definitive work into variance and covariance components operating for these traits within unselected Sitka spruce of QCI origin.

II. Age: age trends for vigour and wood density:

Vigour and wood density data from one to twenty-three years after planting were presented from the 'Main Study'. No other study has investigated variance components for either of these traits for Sitka spruce growing in Britain over such a prolonged time-period .

This was also the first study into genetic age:age correlations for wood density in Sitka spruce in Britain.

III. Investigating the value of alternative genetic sources:

This was the first time that the genetic correlations between ortets, grafted-ramets and progeny for certain traits of wood density, diameter and height have been reported for Sitka spruce in Britain.

IV Use of Mixed Model Analysis:

REML was used to generate the variances and covariances within the progeny test and investigate the genetic relationship of data from different genetic sources. This is the first time that mixed model analysis techniques have been used to analyse variance components of Sitka spruce in Britain. REML gave more precise estimates of fixed effects operating within the progeny test and prevented bias due to selection of a reduced

sample size in investigations for wood density variance components and genetic relationships across genetic sources.

6.2 DATA FROM A RANDOMLY SELECTED POPULATION

Previous studies into the variance and covariance components operating within Sitka Spruce in Britain have been restricted in one of a number of ways. They have either been biased due to selection of the ortets for vigour combined with an unknown element of confounding variation between origins (Gill, 1987 and Lee, 1993), or if randomly selected, published data have been restricted to 1 to 6-year height (Samuel and Johnstone, 1979). Although all the previous studies used analysis of variance for data collected across a range of sites, none adjusted the data for fixed effects (sites and replicates within sites).

If variance components are known for a randomly selected population of trees, the effects of selection for one or more traits can be simulated by investigating the correlated response i.e. the change in correlated character Y as a result of selection for character X (Falconer, 1981). This could be important in considering the selection intensity for a primary trait in order to prevent an unacceptable fall in the breeding value (BV) of a secondary trait.

Variance components from populations selected for a particular character are biased according to the value of the genetic regression between the phenotypic value of the selected ortet with the breeding value of that ortet based on progeny test evaluation. If there are further genetic correlations between the primary trait and other traits of economic value, they too will be subject to bias. The degree of bias will be unknown unless variance and covariance components from a randomly selected population are available for comparison.

Estimates of genetic parameters from selected local populations are usually biased to that population and location. Better estimates can be obtained by combining many such estimates across sites and populations (Koots and Gibson, 1996). However, genetic parameters collected from a randomly selected population growing on a site to which it is well adapted will give better estimates of precision with less bias.

Variance components from a randomly selected population such as the 'Population Study' presented here, can be considered as base or datum values for Sitka spruce of QCI origin growing on a well adapted site. By having such base values for QCI origin material, it will be possible to monitor changes for variances and covariances, heritabilities and genetic and phenotypic correlations between and within traits according to selection differentials, across generations.

6.3 AGE:AGE TRENDS FOR VIGOUR AND WOOD DENSITY

6.3.1 Vigour traits:

A weakness of this study was that vigour was not assessed exclusively in terms of height or diameter. Height was assessed at the end of the first growing season and then annually for 11-years from planting after which diameter was substituted as a measure of vigour on the grounds that it was less expensive and more convenient to collect. Both height and diameter were collected at the end of the tenth growing season (HT10 and DM10) enabling a correlation of the two traits ($r_A = 0.9037$; $r_P = 0.8361$).

i. Heritability

It is not possible to state conclusively the variation in heritability of height beyond 11-years from planting or of diameter before 10-years and beyond 23-years from planting. It is however possible to say that whereas the family heritability of height and diameter varied only slightly between HT01 (0.60) and DM23 (0.71), single tree heritability fell

from a maximum of 0.38 (HT07) to a minimum of 0.12 (DM17) before increasing again slightly to 0.15 (DM23), possibly in response to thinning.

The values of h_i^2 for 1 to 6-year height are almost exactly the same as those reported by Samuel and Johnstone (1979). This reflects the relative lack of GxE interaction if all trees are known to be of the same origin and are well adapted to the sites on which they are planted. The values of family heritability found in this study were lower than those reported by Gill (1987) who looked at multiple-site analysis of selected populations of trees of possibly mixed origins. It is quite possible that an element of variation between origins was confounded with variation between family means thereby inflating the estimates of additive genetic variation and so family heritability.

The high values of h_i^2 for early height traits in this study made a major contribution towards lowering the age of optimum indirect selection for the DM23 breeding goal in terms of genetic gain per year.

ii. Juvenile:mature correlations

This was the first time that juvenile:mature phenotypic and genetic correlations have been presented for a randomly selected Sitka spruce population. Genetic correlations were generally larger than phenotypic correlations particularly when the differential of ages was large (e.g. HT02:DM23; $r_A = 0.62$ s.e. 0.1382; $r_p = 0.43$ s.e. 0.0124) although standard errors attached to genetic correlations routinely exceeded those for phenotypic correlations. Estimates of genetic correlations are usually subject to large sampling errors, are therefore seldom very precise and can vary markedly between different populations (Falconer, 1981). This again makes estimation of such parameters from a randomly selected single-origin population a particularly important reference point.

Genetic correlations with DM23 increased rapidly between HT02 and HT03 ($r_A = 0.38$ and 0.62 respectively) as the plants became established, after which there was a more

gradual increase with increasing age of the trees and therefore a reduction of the juvenile:mature differential. The next significant increase in genetic age:age correlations with DM23 was when assessments for vigour were changed from height to diameter ($r_{A_{HT10:DM23}} = 0.81$; $r_{A_{DM10:DM23}} = 0.90$) suggesting that if this had been made at an earlier age, genetic age:age correlations would have been more advanced giving an even younger optimum juvenile selection age.

iii. Optimum selection ages

The estimation of heritability and genetic age:age correlations allowed the calculation of optimum selection ages for vigour based on generation efficiency (Q_{gen}) and genetic gain per year (Q_{year}) relative to direct selection for the breeding goal when both Q_{gen} and $Q_{year} = 1.0$. Both estimates of efficiency were dependent on the ratio of heritability at the younger and older ages and the genetic correlations between traits at the two ages. Q_{gen} could only exceed 1.00 if $r_{Ajm}\, h_j > h_m$ and, whilst this did occur for earlier ages of individual tree selection, it never occurred at the family selection level due to the relatively constant values of h^2_f with time.

Q_{year} was often > 1.0 since this was effectively calculated as the product of Q_{gen} and the ratio of the older and the younger selection ages after allowing for the delay to induce flowering. Q_{year} was calculated for both individual tree and family selection using (i) heritability and genetic juvenile:mature correlation estimates taken from the actual data, assuming DM23 to be the selection goal and (ii) equal heritabilities across ages, with juvenile:mature correlations derived from various Lambeth regression equations (Lambeth, 1980) and an assumed breeding goal of 40-year height or diameter.

In all cases, the optimum age for individual tree selection exceeded that for family selection by around 4 to 5 years. This differential was mainly a feature of the extra delay required between selection of the juvenile trees and when those trees could be brought to flower. There were savings of 3 to 4 years and 4 to 7 years (depending on the

Lambeth regression equation based on genetic correlations which was adopted) if the forward selected tree could be brought to flower in 5 or 3-years from selection respectively. This emphasises the importance to the efficiency of Sitka spruce breeding in Britain of further research into reducing the age of flower initiation.

There was remarkably little difference between the optimum selection ages estimated assuming the two different breeding goals. Optimum selection age for individual tree selection was found to be HT07 to HT09 using both techniques, whilst the optimum age for family selection was between HT03 (breeding goal DM40) and HT05 (breeding goal of DM23).

These optimum family selection ages correspond closely with HT03 and HT06 recommended by Gill (1987), assuming a breeding goal of diameter fifteen years from planting. Individual tree selection was not considered by Gill (*op. cit.*).

Jensen *et al* (1996) in their investigation into the variance components of a small (N = 15), highly selected Sitka spruce population growing in Denmark again only reported optimum selection ages for family selection. They stated HT09 to be the optimum family selection trait based on correlated response and a breeding goal of 21-year basal area. This was a somewhat older age than either this study or Gill (1987) suggested. The conclusions of Jensen *et. al.*(*op. cit.*) are somewhat surprising since figures of efficiency per year were presented which suggested HT02 to be the optimal age although delay due to flowering was not considered.

The optimum selection ages presented in this study have been in terms of either individual tree or family selection. In practice an index would be constructed to select the best families and the best individuals within those families. In a similar way to that in which REML and BLUP call upon data from different sources and weight them according to variances and covariances between all the collected data, an index would weight family information prior to selecting the individual with the largest within family

deviation. Individual trees would not be selected independently of their parental pedigree. Index selection using family and within family information would help reduce optimum individual tree selection ages from the maximum of HT09 closer to the optimum family selection age of HT06.

iv. Use of the Lambeth regression equation:

The preferred Lambeth regression equation from this study was based on genetic juvenile:mature correlations of height with diameter. Lambeth (1980) predicted from phenotypic correlations of height that the optimum selection age for a conifer species on a 40-year rotation should be 8-years from planting. That prediction turned out to be remarkably close to the 7 to 9-years from planting predicted by the preferred regression equation in this study. This may be coincidental since the delay before flowering (d) in this study was 9-years whilst Lambeth (*op. cit.*) assumed $d = 5$ years. When $d = 5$ years in this study, the optimum selection ages fall to HT03 and HT04 which are more optimistic than those predicted by Lambeth (*op. cit.*).

There were clear advantages to tree breeding progress (Table 2.10) in terms of optimum selection ages of using a Lambeth equation based on the theoretically appropriate genetic rather than phenotypic juvenile:mature correlations. This benefit, whilst still real, did diminish as the age range of the data on which juvenile:mature correlations were estimated increased i.e the r_{HD} option compared to r_{DD} or r_{HH}. This further illustrates the need to obtain as wide an age-range as possible when using data to construct a Lambeth regression equation. Height or diameter collected over a restricted age-range (e.g. HT02 to HT11 and DM10 to DM23) may lead to too many errors in terms of ultimate selection age.

A possible restriction of the Lambeth method used here, could have been the assumed constant heritability with age. Yet the optimum individual tree selection ages predicted with the preferred Lambeth equation compared favourably with those estimated from the

actual data (breeding goal of DM23) and by Lambeth (1980). The data show that family heritabilities are likely to remain constant with age whilst single tree heritabilities fall within the age-range investigated but could be influenced by the timing of thinning operations. With so many factors including crop development and competition possibly influencing estimates of heritability, the assumption of constant heritability with age remains the safer option, with unknown but assumed low error estimates.

6.3.2 **Wood density:**

i. Heritability

This is the first study to report the variation with age of variance components and heritability for wood density of Sitka grown in Britain. There was a sharp decline in both single-tree and family heritability between RG6-9 and RG19-22. It is important that when statements are made regarding the heritability of wood density in Sitka spruce that the age of the tree since planting is made clear because h_i^2 can vary from 0.85 (RG6-9) to 0.34 (RG19-22).

Comparison of heritability estimates and associated standard errors (s.e.) for ring-groupings with and without the two traits used to calibrate the selection ellipse as covariates illustrates the possible errors which can occur due to selection bias. The only previous reports of wood density heritability for Sitka spruce in Britain were Wood (1986) and Lee (1993), both of whom reported variance components from selected populations. Neither study included estimates of standard error for heritability, which, based on evidence presented here, could be very large.

The value of $h^2_i = 0.73$ estimated by Wood (1986) was the same as the heritability for the equivalent ring-grouping in this study (RG14-17) when analysed *without* the covariates ($h_i^2 = 0.73 \pm 0.19$) although the equivalent estimate of h_i^2 *with* the covariates was 0.32 ± 0.09. This demonstrates the value of the covariates and the REML analysis

in preventing bias and increasing precision, something that was omitted in previously reported heritability estimates.

ii. Juvenile:mature correlations and optimum selection ages

This has been the first study to present genetic juvenile:mature correlations of wood density for Sitka spruce grown in Britain. For the first time it can be stated that the density of juvenile wood is a very good indicator of the density of mature wood in Sitka spruce.

Genetic correlations of juvenile ring-groupings with ring-groupings used to represent mature wood density were close to unity. High juvenile:mature correlations between ring-groupings and the relatively higher heritability values of more juvenile ring-groupings combine to demonstrate the efficiency of selecting for wood density at an early age based on both Q_{gen} and Q_{year}. Selection based on RG6-9 was the optimum indirect selection trait for mature wood laid down between 19 and 22 years from planting (RG19-22).

Since the most juvenile ring-grouping investigated in the study (RG6-9) also gave the highest value of Q_{year} against the selection goal (RG19-22), it is quite likely that similar high values of Q_{year} would be found for even more juvenile ring-groupings i.e. for annual rings laid down earlier and closer to the pith. It is clear that the optimum selection age for wood density in Sitka spruce progeny tests can be lowered from the current practise of 15-years from planting to at least 9-years from planting.

As far as possible, cores were collected at 1.3 m above the ground (breast height). It is quite possible that if cores had been removed closer to the ground (1.0 m or 0.75 m), then (based on the mean annual height figures given in Table 2.4) an extra one or two annual rings would have appeared in the extracted cores. Consequently, more trees would have contained annual rings laid down just 4 or 5 years from planting, enabling

a more juvenile ring-groupings (e.g. RG4-7) to be composed and correlated with the breeding goal. This would have helped in deciding if indirect selection for mature wood density could be carried out at even younger ages.

The high genetic correlations between wood density assessed using the X-ray densitometer and the Pilodyn means that the latter can continue to be used as an effective screening tool for wood density in Sitka spruce progeny tests. However, since in this study the average 9-year old Sitka spruce tree is approximately 360 cm tall with a DBH of around 7 cm, the tree would flex away from the vertical whenever a Pilodyn pin was shot in 1.3 m above the ground. If the Pilodyn is to be used as a screening tool for wood density at just 9-years from planting it will be necessary to shoot the Pilodyn pin into the tree at a point closer to the ground where the diameter will be greater. Further studies would be required to investigate the suitability of, for example 1.0 m or 0.75 m above the ground.

The conclusions regarding early selection ages for wood density are not too surprising when compared with studies on other species reported in the literature. Work with loblolly pine (Loo *et al*, 1984; Williams and Megraw, 1994), radiata pine (Maddern-Harris, 1965) and Douglas fir (McKimmy and Campbell, 1982) all indicated high phenotypic or genetic correlations between juvenile and mature wood as early as 2-years from planting.

6.3.3 **Relationship between vigour traits and wood density:**

Wood (1986) found phenotypic correlations of -0.34 to -0.69 between 15-year diameter and whole-tree density. Lee (1995) reported a genetic correlation of -0.66 between 15-year diameter and pin penetration of the Pilodyn at similar ages. Sitka spruce breeders have therefore been aware for a number of years of the need to consider wood density when selecting for diameter, if the existing value of wood density is to be maintained.

Results from this study, however, suggest even higher negative genetic correlations between diameter and wood density than had previously been considered ($r_{A_{DN17,\ DM23}}$ = -0.81; $r_{A_{RG19-22,\ DM16}}$ = -0.80). This further emphasises the problem of attaining concurrent improvement of wood density and diameter.

Greater selection emphasis has been placed on the genetic improvement of vigour rather than any other trait in the first generation of selection in the Sitka spruce breeding strategy (Lee, 1993). Table 6.1 gives the correlated genetic response (b_{YX}) for the vigour breeding goal (DM23), the wood density breeding goal (RG19-22) and the optimum indirect selection trait for the wood density breeding goal (RG6-9) following selection of the optimum indirect selection trait for the vigour breeding goal (HT09). Values of b_{YX} were estimated using ASReml (Gilmour, 1996) in the same way that similar estimates were reported in Chapter 5. As before, analysis involving RG19-22 and RG6-9 were quadrivariate since DM16 and DN17 were included as covariates whilst regressions of breeding values for DM23 with HT09 involved bivariate analysis.

Table 6.1 also presents the consequent change of the correlated trait from increasing the breeding value of HT09 by 5%. Every 1 cm increase in HT09 gives a 0.2356 x 10^{-1} cm increase in DM23 and 0.3083 x 10^{-3} g cm^{-3} fall in RG19-22; a 5% increase in HT09 causes DM23 to increase by 2.8% and RG19-22 to fall by 1.1%. The same increases for HT09 causes the density of RG6-9 to fall by 0.7199 x 10^{-3} g cm^{-3} and 2.5% respectively. These estimates of correlated response are particularly worrying since they mean that juvenile wood density falls at a faster rate than mature wood density as a consequence of selecting for vigour based on HT09. Nearly all batons of timber cut from Sitka spruce logs will contain an element of juvenile wood and since the density of juvenile wood tends to be lower than mature wood (Brazier, 1967), it is important to ensure that juvenile wood density does not become unacceptably low for construction timber as a consequence of selecting for HT09. These findings confirm the conclusion of Thompson (1992) when he stated that it becomes important to screen for wood density at an early age not only as an indicator of mature wood density, but also in an attempt

Table 6.1: Regression coefficients (b_{YX}) and consequent changes in DM23, RG19-22 and RG6-9 (Traits Y) as a result of selection for vigour at the optimum individual tree selection age (HT09; Trait X).

Correlated Trait	b_{YX}	Percentage increase in correlated trait following a 5% increase in BV of HT09
DM23	0.2356×10^{-1} cm/cm $\pm 0.3751 \times 10^{-2}$	2.8%
RG19-22	-0.3083×10^{-3} g cm^{-3}/cm $\pm 0.1827 \times 10^{-3}$	-1.1%
RG6-9	-0.7199×10^{-3} g cm^{-3}/cm $\pm 0.2598 \times 10^{-3}$	-2.5%

Note: 1. $b_{YX} = \frac{COV_{G_{XY}}}{\sigma_{G_X}}$ where Trait X = HT09, Trait Y = correlated trait.

2. Estimated value of b_{YX} from the ASReml *.pvs* file must be scaled up by multiplying by $\frac{\text{Trait } X_{SD} \times \text{Trait } Y_{SD}}{(\text{Trait } X_{SD})^2}$ where SD = standard deviation.

3. HT09:DM23 $COV_{G_{XY}} = 49.61 \pm 10.03$, $\sigma^2_{G_X} = 2106.5 \pm 463.8$;

   HT09:RG19-22 $COV_{G_{XY}} = -0.5728 \pm 0.3339$, $\sigma^2_{G_X} = 1858.94 \pm 39.45$;

   HT09:RG6-9 $COV_{G_{XY}} = -1.3511 \pm 0.5332$, $\sigma^2_{G_X} = 1876.99 \pm 38.47$.

4. $\pm$ indicates standard error.

to identify those rare genotypes which combine above average vigour with above average juvenile wood density. It is the value and duration of juvenile wood density and not the value of mature wood density which will become the limiting factor in dictating timber strength if selection was to be exclusively for HT09.

In practice, a multi-trait selection index approach is used to identify Sitka spruce genotypes for the various breeding populations (see Chapter 1.1). A Kempthorne restriction (Kempthorne and Nordskog, 1959) is used in the General Breeding Population to maximise diameter and stem straightness whilst preventing a fall in wood density. The data presented here highlight that it will be particularly difficult to improve diameter and wood density concurrently. It may however be possible to improve both

traits if the number of trees from which selection is made is large enough to allow the identification of 'correlation breakers' (Kleinschmit, *et al.*, 1993) which go against the general trend.

The practical effect of this study on the breeding and selection of Sitka spruce for diameter and wood density will be significant and immediate. A first assessment of family-mean performance for vigour will now be carried out 5-years from planting. This will be followed by measurement of 9-years height and wood density. Straightness and branching characteristics are most likely to be assessed 9-years from planting after which forward selection of the best individual trees in the best families can take place (based on multi-trait index selection) and the progeny tests can be closed.

6.4 INTRODUCTION OF OTHER GENETIC SOURCES

The Mixed Model Analysis approach of the 'Pilot Study' (Chapter 4) and inclusion of other genetic sources from within the 'Population Study' (Chapter 5) allowed the estimation of genetic correlations and correlated responses of parent trees and grafted-ramets with breeding values from progeny tests. Absolute values of simple treatment-mean correlations and genetic correlations varied slightly between 'Pilot' and 'Population' studies. This is not surprising given the important differences between the two populations:

i. the trees in the 'Pilot Study' were highly selected for vigour whilst those in the 'Population Study' were not;

ii. the sample size of the 'Pilot Study ' was smaller than the 'Population Study' and the former were selected and analysed without the benefit of a selection ellipse preventing bias;

iii. the breeding value of each parent tree in the 'Pilot Study' had not been assessed following a BLUP analysis with unbiased estimation of fixed effects.

Despite the differences in absolute values, similar trends did emerge between the two samples of trees. In each case high values of $r_{g,BV}$ were estimated between grafted-ramet wood density and density assessed in progeny tests. There would therefore seem to be some value in including grafted-ramet wood density data with progeny test wood density data in the estimation of variance components and breeding values. The 'Population Study' also suggested that grafted-ramet density may be suitable for combining with DM23 in the estimation of variance components and breeding values of the selection goal for vigour. Indirect wood density assessment of the grafted-ramets using the Pilodyn did not seem to give quite the same benefits.

A major difference between the two studies was that whereas ortet diameter made no contribution towards breeding value estimates of vigour in the 'Pilot Study', adjusted ortet height did make a significant contribution in the 'Population Study'. This suggests that ortet height, adjusted according to a measurable environment variable, would be a valuable addition to breeding value estimation in a BLUP analysis involving data collected from different sources. Since plus-trees tend to be selected across a large number of forests, some measure of the performance of the plus-trees for height relative to the site mean would be required if tree breeders were to take advantage of this ortet:progeny relationship. Attaching additional fixed effects for each forest would enable the BLUP program to help further in removing variation between forest due to location e.g. length of growing season. This element of the study confirmed the value to the tree breeder of the standard practice of imposing a high selection differential for ortet height when selecting plus-trees. This was also the conclusion of Cornelius (1994) in his review of the effectiveness of plus-tree selection for yield. A selection differential of the tallest from every one thousand plantation trees should increase DM23 breeding value by 8%.

There would seem to be no benefit from including grafted-ramet diameter in estimation of either diameter or wood density breeding values.

Although the pilot study showed no benefit from including ortet density in BV estimation, it is perhaps unfortunate that ortet wood density was not estimated in the 'Population Study'. Based on the example of ortet height adjusted according to a covariate, it is possible that the single-origin source of the trees could have made a contribution towards estimation of wood density breeding values provided it too was adjusted according to a correlated environmental variable such as h.a.s.l.

6.5 USE OF MIXED MODEL ANALYSIS

i. Estimation of unbiased variance components within a single data source.

Much of the analysis reported in Chapter 2 did not require the sophisticated REML analysis incorporated in the package of ASReml (Gilmour, 1996). All the variance components, heritabilities and genetic and phenotypic correlations (with associated standard errors) could have been estimated using a standard linear model and least square means in a standard statistical package such as SAS (1982), GENSTAT (1993) or MINITAB (1992).

The principles of REML were essential however in the estimation of unbiased variance and covariance components for wood density reported in Chapter 3. All the trees, from each of the 125 families which provided data for the two traits used to construct the selection ellipse (Cameron and Thompson, 1986), were always included as covariates when ever analysis was performed involving any of the ring-groupings. Comparative analysis without the covariates resulted in much higher estimated values of both single tree and family heritabilities and their associated standard errors.

One alternative method to achieve unbiased estimates of variances and covariances for wood density would have been to sample all 125 families in the complete progeny test which represented the Main Study. This would have increased field work and interpretation of the resulting X-ray densitometry data by 255%!

ii. Estimation of genetic correlations between data sources

Although the study did not compare variance component and breeding values estimated by REML and BLUP with and without the additional genetic sources, it did use REML to estimate genetic correlations between genotypic values from the ortets and grafted-ramets with breeding values from the 'Main Study'. This would not have been possible without the principles of REML. Previous studies (e.g. Zobel, *et al.*, 1962; Velling, 1974; Ericson, 1960) merely investigated the simple treatment-mean correlations between genetic levels which were often very low.

iii. Increasing the precision of breeding value estimates

The single-trait breeding value of an individual can be estimated from data collected from a number of different genetic sources, the most reliable of these being a progeny test (Appendix 4.1). By introducing data from other levels (ortets, grafted-ramets, other progeny tests), further information is gathered regarding the breeding value of the individual. The value of each different genetic source is expressed as a regression of the predicted breeding value on phenotypic values. By including different sources of data and combining them together to form an index, a more reliable estimate is obtained of the breeding value of an individual. The phenotypic value from each source will have a weighting attached to it according to its genetic regression with the breeding value.

The objective is to maximise the regression of the index values with the breeding values:

$$I = b_1 \underset{\sim}{P}_1 + b_2 P_2 + b_3 P_3 + ... \qquad (6.1)$$

where: I = index value;

P_1 = phenotypic value for measurement 1 etc;

b_1 = weighting factor for measurement 1 etc.

The maximising of the regression leads to a set of simultaneous equations, with as many equations as there are measurements (Falconer, 1981). For example, for just three measurements:

$$b_1 P_{11} + b_2 P_{12} + b_3 P_{13} = A_{11} \qquad (6.2)$$
$$b_1 P_{21} + b_2 P_{22} + b_3 P_{23} = A_{21}$$
$$b_1 P_{31} + b_2 P_{32} + b_3 P_{33} = A_{31}$$

where: P_{11} = the phenotypic variance of measurement 1;

P_{12} = the phenotypic covariance of measurements 1 and 2;

A = the variance and covariance of the respective breeding values.

Any BLUP software calculates the values of P and A using the matrices given in Equation 2.2. If there is no pedigree relationship between two measurements from the same or different sources, then the covariance has a value of 0 in the matrix. If there is a pedigree relationship, then a covariance value will appear and will contribute towards the estimation of the breeding value. A reliable source of data is one with a high pedigree relationship as well as more precise estimates of the breeding values (other fixed effects being equal).

iv. Practical use of MMA techniques by tree breeders

It follows that some data sources will have little or no contribution towards the index value and these can be discarded. As described above, wood density of grafted-ramets and adjusted heights of the ortets would be worthy of inclusion with progeny test data in breeding value estimation of wood density and vigour for first generation selections.

In second and subsequent generations, data from grafted-ramets and ortets are most likely to be replaced with more reliable (higher genetic correlations) related progeny test data from the first generation.

The BLUP analysis estimates the breeding value of each individual tree present in the data sets regardless of generation level or genetic source. This means that tree breeders will have the opportunity to rank trees for breeding values across generations if necessary. Each year the constituent clones of the breeding population could be up-dated following analysis of data collected during the previous 12 months. It will not be necessary to wait until a generation of progeny testing has been fully assessed before the constitution of clones in the breeding population is revised.

The theory and value of the MMA techniques may be clear and convincing but practical application could prove a daunting task for breeders. It would require each tree in all existing and future progeny tests to be given a unique ID number. The ID number would appear in a pedigree file along with details of the mother and father of each tree (0 if unknown). If analysis was to be at the individual tree level and assuming 3 sites with 40 trees per family at each site, the Sitka spruce first generation progeny testing programme in Britain of 2,500 plus-trees would involve approximately 300,000 lines in a data set and associated pedigree file. As data are included from grafted-ramets and the next generation of progeny tests, the dataset would continue to increase in size. The dataset could be reduced by a factor of 40 if analysis was at the family site-mean level and, whereas that may be possible for the backward selection of the first generation, it will not be possible for forward selection in the second generation.

The problems experienced in achieving convergence reported in Chapter 5 demonstrate the problems associated with quadrivariate REML analysis if the data are very unbalanced across datasets. If analysis had to be at a quadrivariate level in routine progeny test analysis (diameter, density, stem-straightness and branching) to estimate individual tree breeding values (BLUP) for a multi-trait selection index, computation

loading could be very high. Quadrivariate analysis in this study often took over 60 minutes to run, (9,500 lines of data) assuming convergence. It is likely that convergence would eventually be achieved in the example stated above since data will most probably be relatively balanced across datasets.

These are practical problems with which animal breeders have become familiar. Once a pedigree file has been constructed it is relatively easy to add new individuals as new progeny tests are established and computer programs can be run over night or at week-ends when loading from other users is low.

There is a tendency for tree breeding data to be more balanced than animal breeding data. Tree breeders establish large (20-40) numbers of trees over a small number of sites (3-5) in order to estimate breeding values. Conversely, animal breeders can often only measure a few animals (1- 5) over a large number of sites (20+). The importance of estimating fixed effects and making full use of the available data, whilst important to both disciplines of breeders, is more pronounced for the animal breeders. White and Hodge (1989) feel tree breeders are well able to estimate fixed effects before analysis and that analysis could be at the plot mean level. Both these measures would reduce computational loading considerably but may introduce more errors in the estimation of breeding values.

The value of REML has been demonstrated in estimating unbiased variance components with restricted amounts of data. The short comings of the data and software reported in Chapter 5 will probably be short lived as new statistical techniques, computer software, and more powerful computers are developed. Computer loading is no longer a real problem and, as such, tree breeders should employ BLUP rather than BLP to obtain the most precise estimates of fixed effects and REML to obtain unbiased estimates of variance components.

6.6 SUGGESTIONS FOR FUTURE WORK

The study has identified the need for further work in the following areas:

i. An investigation into the variance components and heritability for the wood density for very young (less than 6 years from planting) trees and the correlated response of such early wood density traits with early selection traits for vigour. Such a study would most likely involve the destructive sampling of trees by taking discs close to the ground.

ii. The optimum position on the tree at which the Pilodyn can be used to screen for juvenile wood density.

iii. How do breeding value estimates for selected ortets actually vary as data are added from alternative sources? This would involve estimating breeding values from a progeny tests, adding grafted-ramet data (wood density only) and ortet data (adjusted height only) where available, and then adding any additional progeny-test data.

iv. What is the potential for reducing the number of trees representing a family in a progeny test (and therefore, cost of progeny testing) if data are available from alternative genetic sources? This would assume BLUP analysis to bring all these sources together and that existing levels of precision attached to breeding values are acceptable.

CHAPTER 7

CONCLUSIONS

7.1 INTRODUCTION

This study involved a detailed analysis into the variance and covariance components operating for vigour and wood density for a randomly selected Sitka spruce population of trees of Queen Charlotte Islands origin known as the 'Population Study'. The original parent trees were identified in a stand in North West Scotland although most assessments were made on the open-pollinated progeny collected from the parent trees growing in a progeny test in South West Scotland. The genetic parameters and functions of variance components estimated from the progeny test enabled the calculation of optimum selection ages for both vigour and wood density.

Genetic correlations between vigour and wood density traits assessed in progeny tests with similar traits from both the original ortets and grafted-ramets growing in clone-banks were estimated initially in a pilot study and latterly for the 'Population Study'. The genetic correlations estimated were used to determine which traits from alternative genetic sources, when combined with progeny tests data, would give more precise estimates of breeding values and variance components.

Restricted Maximum Likelihood (REML) was used in the generation of all fixed effects, variances and covariances across all ages in the progeny test and for the combined genetic sources. All estimates of genetic parameters were therefore unbiased by either selection or analysis. The unbiased nature of all variance and covariance components as well as functions of variance components makes this the definitive study for vigour and wood density variance components for Sitka spruce growing in Britain.

The objectives of this study as stated in Chapter 1 and repeated here, were to:

i. Investigate the variance components and heritability for height, diameter and wood density in a randomly selected Sitka spruce population;

ii. Determine age:age correlations and optimum selection ages for vigour traits and wood density;

iii Investigate the genetic correlations for vigour and wood density across different genetic populations and make recommendations as to which could be included along with progeny test data in the future evaluations of breeding values and variance components;

iv. Make recommendations regarding the use of MMA techniques in the multi-trait selection and breeding of Sitka spruce in Britain.

Conclusions relative to the above objectives are given below.

7.2 VARIANCE COMPONENTS AND HERITABILITY

Variance components:

Wood density is under more additive genetic control than height or diameter at an equivalent age. The variation between family means (σ_f^2) for the wood density and vigour breeding goals (RG19-22 and DM23) is 13.5 % and 3.5% respectively. Similarly, height as an indicator trait for DM23 is under slightly more genetic control than diameter at the same age (HT10 = 8.93%; DM10 = 7.74%).

The degree of genetic control within vigour and wood density traits varies with age. Variation between family means reaches a maximum at HT07 for vigour traits (9.57%)

whilst wood density starts at a maximum for RG6-9 (21.26%) and then falls gradually with age. A systematic thinning of the progeny test 18-years from planting resulted in a slight increase in genetic control of diameter and wood density. It essential that the precise trait (height or diameter, number of annual rings in a grouping), age and state of crop development are stated when quoting the variance components operating within Sitka spruce.

Heritability:

Family heritability for height and diameter do not vary much with age (HT01 = 0.61; DM23 = 0.57). Single tree heritability however, is much more variable with the values for height tending to exceed those for diameter.

Single tree heritability for height is initially high (HT01 = 0.32) and then falls in response to planting shock (HT03 = 0.14) before rising again to a maximum at HT07 (0.38). It then remains constant about this value (HT10 = 0.36). When assessments change from height to diameter, values of h_i^2 gradually fall with age (DM12 =0.27; DM17 = 0.12) although a thinning operation causes a slight increase (DM19 = 0.19; DM23 = 0.15).

Family heritability for wood density starts high and far exceeds height or diameter at equivalent ages (RG6-9 = 0.96) but falls with age to values similar to those calculated for diameter (RG12-15 and RG14-17 = 0.60). Single tree heritability is consistently higher than equivalent aged vigour traits although it also tends to fall with age. It is a maximum at RG6-9 (0.85) and falls with age to a minimum at RG16-19 (0.28) before increasing slightly following the thinning operation (RG19-22; $h_i^2 = 0.34$).

The fall off with age of σ_f^2, h_i^2 and h_f^2 does mean that juvenile wood (RG8-15; $\sigma_f^2 = 13.15\%$, $h_i^2 = 0.53$, $h_f^2 = 0.78$) is under more genetic control than mature wood (RG19-22; $\sigma_f^2 = 8.4\%$; $h_i^2 = 0.34$, $h_f^2 = 0.62$).

The Pilodyn was used as an indirect assessment of wood density after 17-years. Both h_i^2 and h_f^2 for Pilodyn are higher than the equivalent aged (RG14-17), direct assessment of wood density (0.44, 0.71 and 0.31, 0.60 respectively).

7.3. AGE:AGE CORRELATIONS AND OPTIMUM SELECTION AGES

Age:age correlations:

Genetic correlations between early height and diameter assessments with the breeding goal of DM23 tend to exceed equivalent phenotypic correlations. Values of genetic correlation between height and DM23 rise sharply from HT01 (r_A = 0.28) to HT03 (r_A = 0.62). All genetic correlations between diameter traits and DM23 exceed r_A = 0.90. Diameter is a better correlated indicator trait for DM23 than height at the same ages (r_A HT10 = 0.81; DM10 = 0.90).

Genetic correlations between indicator traits and the mature wood breeding goal (RG19-22) are all very high; in all cases r_A = 0.95. Values of genetic correlations always exceed those of phenotypic correlations although the differential does decrease as the age difference between indicator traits and breeding goal decreases e.g. RG6-9, r_P = 0.55; RG18-21; r_P = 0.90. Juvenile wood density (RG8-15) is highly correlated with mature wood density (r_A = 0.95, r_P = 0.68), as is the youngest indicator trait assessed (RG6-9).

Optimum selection ages:

Optimum family and individual tree selection ages were chosen by maximising efficiency of early selection relative to selection for the breeding goal using generation efficiency (Q_{gen}) and genetic gain per year (Q_{year}). This was carried out assuming breeding goals of DM23 (the oldest assessment of vigour in the progeny test) and 40-year diameter. The latter breeding goal involved using juvenile:mature correlations generated from the data to construct Lambeth regression equations which enabled

estimation of genetic correlations for juvenile vigour traits with breeding goals extrapolated beyond the range of the original data.

Due to little variation in h_f^2 with age or trait, Q_{gen} for family selection is most efficient at DM23, but Q_{gen} for individual tree selection is maximised at HT09. Q_{gen} was not estimated when the breeding goal was DM40. This was because constant values of heritability were assumed across age and traits, therefore Q_{gen} was always equal to the value of r_A from the Lambeth equation and could not exceed 1.00.

The optimum family-mean indirect selection traits for DM23 and DM40 in terms of maximum Q_{year} are height at 5 years and 3 years from planting respectively. The equivalent traits for individual tree indirect selection are height at 9 years and height at 7 years respectively.

The optimum indirect selection trait for RG19-22 is the weighted density of annual rings 6 to 9 from planting (RG6-9). This is the optimum selection age for both family-mean and individual tree selection in terms of Q_{gen} and Q_{year}.

The Pilodyn assessment of wood density was found to be highly negatively correlated with X-ray densitometry assessments of wood density (RG6-9, r_A = -0.82; RG19-22, r_A = -0.95). The Pilodyn can continue to be used as an effective tool for screening wood density.

7.4 RELATIONSHIP BETWEEN VIGOUR AND WOOD DENSITY

Wood density has a high negative genetic correlation with vigour traits (e.g. $r_{A_{DM16,\ RG19-22}}$ = -0.80, r_P = -0.46). Concurrent improvement of vigour and wood density seems impossible without identifying rare genotypes which go against the general trend. Investigations into genetic correlated response show that a 5% increase in the breeding value of the optimum indirect selection trait for vigour (HT09) will cause

mature wood (RG19-22) and the optimum indicator trait for mature wood density (RG6-9) to fall by 1.1% and 2.5% respectively. This means that wood density must be screened at a early age if juvenile wood density is to remain at acceptable levels to satisfy Machine Stress Grading regulations.

7.4 VALUE OF DATA FROM OTHER GENETIC SOURCES

Grafted ramets:

Genetic correlations between breeding values assessed in progeny tests and genotypic values from grafted-ramets ($r_{g,\ BV}$) are always higher than the equivalent treatment-mean correlations (r).

Genetic correlations for wood density breeding values assessed in progeny tests and the genotypic values for wood density of the outer five rings collected from grafted-ramets in a clone bank are high. This was found to be the case in both the pilot study and the 'Population Study' ($r_{g,\ BV}$ = 0.80 and 0.58; r = 0.73 and 0.42 respectively). Grafted ramet wood density is also (negatively) well correlated with progeny breeding goals for diameter ('Population Study' DM23, $r_{g,\ BV}$ = -0.45; pilot study DM15, $r_{g,\ BV}$ = 0.54).

These level of correlations indicate that combining wood density data from grafted-ramets in a clone bank with wood density and diameter data from a progeny test, will result in better estimates of breeding values and variance components for each trait than progeny test data alone can do.

Grafted-ramet diameter and Pilodyn data did not give good genetic correlations with diameter or density traits assessed in progeny tests. There is no value from including either of these grafted-ramet traits in the assessments of breeding values or variance components if progeny tests data are already available.

Ortets:

There are high genetic correlations between ortet height and 23-year diameter ($r_{g,\ BV}$ = 0.95; r = 0.32) if the former is adjusted for a well correlated environmental variable (in this case height above sea level). Combining ortet height and progeny tests data for vigour will result in better estimates of breeding values for vigour provided the ortet data are adjusted in this way.

7.5 USE OF MIXED MODEL ANALYSIS

Estimation of wood density variance components:

By including the two traits used to calibrate the selection ellipse as covariates in all estimates of wood density variance components, REML successfully gives more precise estimates with reduced associated standard errors than when the effects of selection were not taken into account. For example h_i^2 for RG6-9 with and without the covariates are 0.85 (s.e.= 0.1836) and 0.98 (s.e. = out of range of programme) respectively; equivalent values for RG19-22 are 0.34 (s.e.= 0.1189) and 0.68 (s.e. = 0.2011). Such quadrivariate analysis linking the selected portion of the population to the complete randomly selected population is not possible without the genetic covariances exploited within the matrices of REML.

Genetic correlations across genetic sources:

REML is also essential in investigating genetic correlations between traits across genetic sources where the environment is not common. In the absence of such analysis, results would have been in terms of simple treatment-mean correlations alone which often do not reflect the potential of an alternative genetic source. For example, adjusted ortet height with DM23, r = 0.32 but $r_{g,\ BV}$ 0.95; grafted-ramet density with RG6-9, r = 0.42, but $r_{g,\ BV}$ = 0.58.

There are problems in achieving convergence with the REML software during quadrivariate analysis when some of the data originates from alternative genetic sources and there is great imbalance of trees across datasets. Tree breeders need to be aware of the limitations of genetic theory and computer software if they are to successfully employ data from alternative genetic sources to generate breeding values and variance components using BLUP and REML (respectively).

7.6 RECOMMENDATIONS

The study has demonstrated the following:

i. Selection of the best families for vigour based on progeny test data can take place based on HT05; individual tree selection can follow based on HT09.

ii. Selection of the best families and best individuals within those families for wood density can take place by assessing the density of the outer 4 annual rings at age 9 from planting.

iii. The Pilodyn can be used to assess wood density indirectly when selection takes place at 9-years old.

iv. If mature grafted-ramets are available, they should be assessed for wood density to assist in the estimation of breeding values and variance components for diameter and wood density.

v. As far as possible REML should be used to estimate all variance components. This will ensure that breeding values are subsequently estimated more precisely using BLUP allowing a more accurate selection of individuals for breeding and production populations based on multi-trait index selection.

7.7 SUGGESTED IMPROVEMENTS FOR FUTURE SIMILAR STUDIES

i. Cores for wood density studies could have been extracted lower down the tree. In this way more annual rings would have been present in each core allowing correlations with RG19-22 of more juvenile ring groupings;

ii. The cores could have been used to estimate tree diameter back to 6-years from planting. This would have enabled the estimation of genetic and phenotypic correlations between more juvenile diameter traits than the DM10 presented here, with the breeding goal of DM23. It would also have allowed the construction of a more complete diameter:diameter Lambeth regression equation which may have affected the optimum selection age.

iii. The study should have been repeated over all 'Main Study' sites to give a complete review of variance and covariances independent of possible confounding due to GxE effects.

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Appendix 2.1: South Strome Population Study - Site Details

Species:	Sitka spruce.
Origin:	Queen Charlotte Islands
Year Planted:	1935.
Location:	Ross and Cromarty District, Highland Region. Approximately 12 km north east of Kyle of Lochalsh.
Map Reference:	NG 874 334, Sheet 24 - 57° 21' North, 6° 32' West.
Compartment:	27-28 (old) 26 (new).
Area:	8 hectares.
Elevation:	30 m to 130 m.
Aspect:	South West.
Topography:	Uneven shallow burn gullies. Small sheltered, narrow and steep glen running east to west for 2 km.
Rainfall:	1780 mm.
Soil:	Brown earth, surface water gley.
Geology:	Lewisian gneiss.

Appendix 2.2: Site Details of Garcrogo 3 - the 'Main Study'

Main study:	Population study open-pollinated progeny test.
Species:	Sitka spruce.
Origin:	Queen Charlotte Islands.
Location:	Nithsdale, Dumfries and Galloway Region, Scotland. Approximately 30 km north west of Dumfries.
Map references:	NX 786 814, sheet 78. 55° 6' north, 3° 54' west.
Previous land use:	Sheep grazing until ploughed by Forestry Commission in December 1971.
Compartments:	117 and 122.
Total area:	9.5 hectares.
Elevation:	230-240 m.
Topography:	Even, uniform and gentle slope.
Rainfall:	1440 mm.
Soil:	Hill peat, generally 30 cm or more in depth.
Geology:	Silurian. Tarannon and Llandovery slates and shales.
Length of growing season:	*195 days.
Site preparation:	Ploughed with a single mould-board to a depth of approximately 30 cm. Ridges 2 m apart. Phosphate fertiliser applied at planting; a phosphate/potassium mix was applied in 1979.
Spacing:	2 x 2 m equivalent to 2,500 trees/hectare.
Original plot size:	7 x 7 (49) trees/plot. Measurements restricted to inner 5 x 5 (25) trees.
Replication:	3 complete and randomised.

*Calculated according to the method of Fairbairn (1968)

Appendix 2.3: **List of open-pollinated families, ortets and grafted-ramets analysed within each genetic source.**

List of Parent identities	MAIN STUDY		OTHER GENETIC SOURCES	
	Open-pollinated		Ortets	Grafted Ramets
	Chapter 2	*Chapter 3*	*Chapter 5*	
SS 4001	x		x	
SS 4002	x		x	
SS 4003	x		x	
SS 4004	x		x	
SS 4005	x	x	x	x
SS 4006	x		x	
SS 4007	x	x	x	x
SS 4008	x	x	x	
SS 4009	x		x	
SS 4010	x	x	x	x
SS 4011	x		x	
SS 4012	x	x	x	x
SS 4013				
SS 4014	x		x	
SS 4015	x		x	
SS 4016	x	x	x	x
SS 4017	x	x	x	x
SS 4018	x		x	
SS 4019	x		x	
SS 4020	x		x	
SS 4021	x		x	
SS 4022	x	x	x	x
SS 4023	x		x	
SS 4024	x		x	
SS 4025	x		x	
SS 4026	x	x	x	x
SS 4027	x		x	
SS 4028	x		x	
SS 4029	x	x	x	x
SS 4030	x	x	x	x
SS 4031	x		x	
SS 4032	x		x	
SS 4033	x	x	x	x
SS 4034	x		x	
SS 4035	x	x	x	x
SS 4036	x		x	
SS 4037	x	x	x	x
SS 4038	x		x	

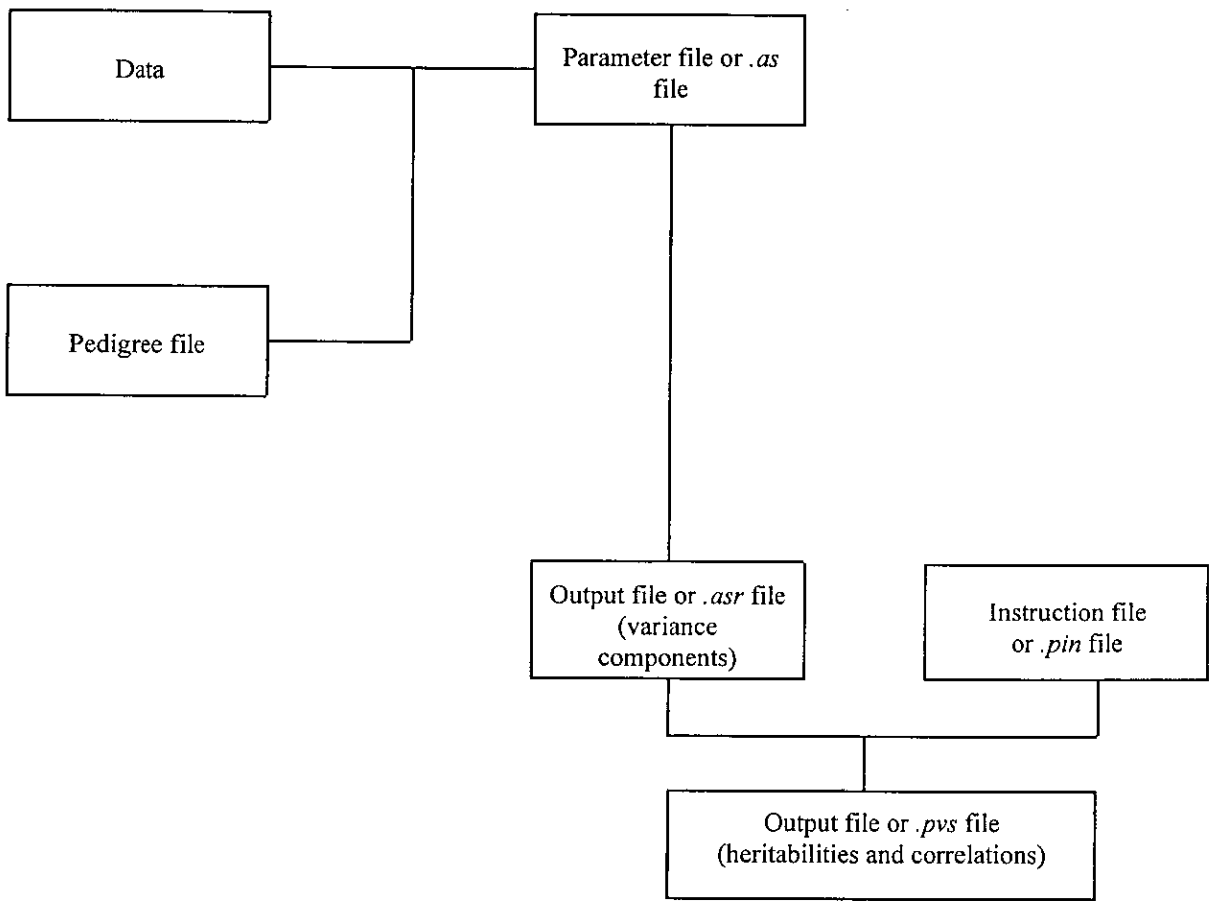
List of Parent identities	MAIN STUDY		OTHER GENETIC SOURCES	
	Open-pollinated		Ortets	Grafted Ramets
	Chapter 2	*Chapter 3*	*Chapter 5*	
SS 4039			x	
SS 4040	x		x	
SS 4041	x		x	
SS 4042	x	x	x	x
SS 4043	x	x	x	x
SS 4044	x	x	x	x
SS 4045	x		x	
SS 4046	x		x	
SS 4047	x		x	
SS 4048	x		x	
SS 4049	x		x	
SS 4050	x	x	x	x
SS 4051	x	x	x	x
SS 4052	x	x	x	x
SS 4053	x		x	
SS 4054	x	x	x	x
SS 4055	x		x	
SS 4056	x		x	
SS 4057	x	x	x	x
SS 4058	x	x	x	x
SS 4059	x		x	
SS 4060	x		x	
SS 4061	x		x	
SS 4062	x		x	
SS 4063	x		x	
SS 4064	x	x	x	x
SS 4066	x		x	
SS 4067	x		x	
SS 4068	x		x	
SS 4069	x	x	x	x
SS 4071	x		x	
SS 4072	x		x	
SS 4073	x		x	
SS 4074	x		x	
SS 4075	x	x	x	x
SS 4076			x	
SS 4077			x	
SS 4078	x		x	
SS 4079	x	x	x	x
SS 4080	x	x	x	x
SS 4081			x	

List of Parent identities	MAIN STUDY		OTHER GENETIC SOURCES	
	Open-pollinated		Ortets	Grafted Ramets
	Chapter 2	*Chapter 3*	*Chapter 5*	
SS 4082			x	
SS 4083	x		x	
SS 4084	x		x	
SS 4085	x		x	
SS 4086	x		x	
SS 4087	x		x	
SS 4088	x		x	
SS 4089			x	
SS 4090	x		x	
SS 4091	x	x	x	x
SS 4092	x	x	x	x
SS 4093	x	x	x	x
SS 4096	x		x	
SS 4097			x	
SS 4098	x	x	x	
SS 4099			x	x
SS 4100	x		x	
SS 4101			x	
SS 4102			x	
SS 4103	x	x	x	x
SS 4104	x	x	x	x
SS 4105	x		x	
SS 4106	x		x	
SS 4107	x		x	
SS 4108			x	
SS 4109			x	
SS 4110			x	
SS 4111			x	
SS 4112	x		x	
SS 4113	x		x	
SS 4114	x	x	x	x
SS 4115	x		x	
SS 4116	x	x	x	x
SS 4117	x	x	x	x
SS 4118	x	x	x	
SS 4119	x		x	
SS 4120	x		x	
SS 4121	x	x	x	x
SS 4122	x		x	
SS 4124	x		x	
SS 4125			x	

List of Parent identities	MAIN STUDY		OTHER GENETIC SOURCES	
	Open-pollinated		Ortets	Grafted Ramets
	Chapter 2	*Chapter 3*	*Chapter 5*	
SS 4126			x	
SS 4127			x	
SS 4128	x		x	
SS 4129	x		x	
SS 4130	x		x	
SS 4131	x		x	
SS 4132	x		x	
SS 4133	x	x	x	x
SS 4134	x		x	
SS 4135	x		x	
SS 4136	x	x	x	x
SS 4137	x		x	
SS 4138	x		x	
SS 4139	x		x	
SS 4140	x	x	x	x
SS 4141	x		x	
SS 4142	x	x	x	x
SS 4143	x		x	
SS 4144	x		x	
SS 4145			x	
SS 4146	x		x	
SS 4147	x	x	x	x
SS 4148	x	x	x	x
SS 4149	x	x	x	x
SS 4150			x	
	125	**46**	**150**	**46**
Sites:	**Garcrogo 3**	**Garcrogo 3**	**South Strome**	**Ledmore Clone Bank**
Assessments:	**HT01-HT11 DM10-DM23 DN17**	**Density from 4-22 years from planting**	**Height at Felling**	**Density Pilodyn DBH**

Note: x = data collected from this genetic unit and used in analysis.

Appendix 2.4: Flow chart of the sequence of data analysis involved using the ASReml software.



Appendix 2.5: Typical ASReml.*as* input (or parameter) file for Univariate Analysis

Analysis of Garcrogo 3 height data:

```
1    id     1      0
2    dam    1    150   # coded 1 to 150
3    sire   1      0   # open pollinated
4    rep    1      3   # coded 1 to 3
5    plot   1    375   # coded 1 to 375
6    tree   1     25   # coded 1 to 25
7    HT01   1      1   !M-9
8    HT02   1      1   !M-9
9    HT03   1      1   !M-9
10   HT04   1      1   !M-9
11   HT05   1      1   !M-9
12   HT06   1      1   !M-9
13   HT07   1      1
14   HT08   1      1
15   HT09   1      1
16   HT10   1      1
17   HT11   1      1
allht1.dat
12 1 1 0 0
-9
4 5 2
0 .1 .05
0 0 0 0 0
```

Note:

1. In this example HT06 (line 12) has been identified for analysis from dataset 'allht1.dat'. which contains all the height data from HT01 to HT11.
2. A pedigree file has not been called upon in this analysis.
3. Replicate, dams (families) and plots have been identified for analysis (third last line).
4. Replicates have been identified as fixed (0 variances second last line).
5. Starting values are 0.1 and 0.05 for family (dams) and family*replication (plots) variances respectively.

Appendix 2.6: Typical ASReml.*asr* output file for Univariate Analysis.

```
 ASREML Thu Oct 24 13:55:35 1996 analysis of garcrogo 3 height data       HT06.asr

Univariate analysis of HT06
 Data being read from allht1.dat
 Model term      Size Type      COL  Minimum      Mean         Maximum   # zero
  1 id              1 Covariate  1  151.00       5482.5       11325.        0.
  2 dam           150 Factor     2  1.0000       71.597       149.00        0.
  3 sire            1 Covariate  3 0.10000E+25 0.00000E+00-0.10000E+25 9239.
  4 rep             3 Factor     4  1.0000       1.9994       3.0000        0.
  5 plot          375 Factor     5  1.0000       188.78       375.00        0.
  6 tree           25 Factor     6  1.0000       12.998       25.000        0.
  7 HT01            1 Covariate  7  1.0000       26.436       59.000      411.
  8 HT02            1 Covariate  8  11.000       46.687       95.000        7.
  9 HT03            1 Covariate  9  7.0000       69.444       141.00       14.
 10 HT04            1 Covariate 10  4.0000       100.35       197.00       14.
 11 HT05            1 Covariate 11  15.000       149.80       295.00        8.
 12 HT06            1 Variate   12  23.000       189.65       357.00        0.
 13 HT07            1 Covariate 13 -9.0000       255.07       460.00        0.
 14 HT08            1 Covariate 14 -9.0000       323.84       530.00        0.
 15 HT09            1 Covariate 15 -9.0000       358.88       590.00        0.
 16 HT10            1 Covariate 16 -9.0000       435.62       690.00        0.
 17 HT11            1 Covariate 17 -9.0000       510.67       780.00        0.
      9375 records read,        9239 records retained
 Forming          529 equations:             4 dense
NOTICE:    25 (more) singularities,
LogL=-39297.2     S2=  1715.      9236 df   0.10000   0.05000   1.00000

LogL=-39261.3     S2=  1675.      9236 df   0.16419   0.07758   1.00000

LogL=-39256.6     S2=  1661.      9236 df   0.20280   0.09869   1.00000

LogL=-39256.4     S2=  1659.      9236 df   0.21094   0.10525   1.00000

LogL=-39256.4     S2=  1659.      9236 df   0.21122   0.10565   1.00000

Final parameter values                      0.21122   0.10565   1.00000


  Source       Model  terms     Gamma     Component    Stnd error
 plot            375    375  0.211219      350.316       37.5375
 dam             150    125  0.105652      175.228       41.8560
 Variance       9239   9236   1.00000      1658.55       24.9136
Variance of Variance components
  1409.06
 -468.838       1751.93
 -25.3586     -0.738190E-01   620.687
            Solution       Standard Error    T-value     T-prev
  4 rep              3     4805.08
          1    199.576        2.17793         91.64
          2    196.543        2.17785         90.25      -1.17
          3    172.575        2.17812         79.23      -9.27
Finished: Thu Oct 24 13:56:25 1996   LogL Converged
```

Note:
1. In this example the variance components are generated for HT06.
2. The model took 5 iterations to converge.
3. Final values of random effects are repeated in the breakdown by 'Source' along with SE.
4. Estimates of the fixed effects (replicates) are given at the end of the output file.

Appendix 2.7: Typical (1) instructions (ASReml.*pin*) and (2) output (ASReml.*pvs*) files used in Univariate Analysis to calculate (i) Single tree and (ii) Family heritabilities.

1. **ASReml.*pin* files**:

(i) Single Tree Heritability (h^2_i):

```
P phen          1       1       1
P va            0       4       0       0
H h2            5       4
```

(ii) Family Heritability (h^2_f):

```
P phen          0.3333          1               0.0135472
P va            0               1               0               0
H h2f           5               4
```

2. **ASReml.*pvs* files**

(i) Single Tree Heritability (h^2_i):

```
Label           Seq     HT06.pvs        SE

   4 phen         2184.       914.9       1283.       595.3       2793.

   5 va           700.9      -1875.       7008.      -0.2953      5132.
                  0.2803E+05

     h2           = va        /phen       =          0.3209  0.0724
```

(ii) Family heritability (h^2_f):

```
Label           Seq     HT06.pvs        SE

   4 phen         314.5       0.4582      1596       -0.1173      1596

   5 va           175.2      -468.8       1752       -0.7382E-01  1596

     h2f          = va        /phen       =           0.5572      0.0689
```

Note: In this example h^2_i and h^2_f are calculated for HT06.

Appendix 2.8: Typical ASReml.*as* input (or parameter) file for Bivariate Analysis.

Analysis of Garcrogo 3 height, diameter and density data

```
1   id     1     0
2   dam    1   150  # coded 1 to 150
3   sire   1     0  # open pollinated
4   rep    1     3  # coded 1 to 3
5   plot   1   375  # coded 1 to 375
6   tree   1    25  # coded 1 to 25
7   HT06   1     1  !M-9 !P8
8   DM23   1     1  !M-9
9   Trait  0     1
10  pl     0  0905  !L1
coll6+23.dat
7 1 1 0 19            # analyse HT06, normal distr, link, filter maxit
-9
9.4 9/2 10
0 .1 .1 .1
1 2 1
9375 0 0
2 0 9 1 .01 1 !GP
12 2
2 0 9 0.05 .00001 0.035 !GP
150 0
```

Note:

1. In this example the variances and covariances between HT06 and DM23 will be generated and output to the ASReml.*asr* file.
2. Data for HT06 and DM23 have been brought together and are stored in file coll6+23.dat.
3. A pedigree file has not been called upon.
4. !P8 on line 7 indicates bivariate analysis with the trait identified on line 8.
5. Line 14 gives details of the random effects to be estimated.
6. Starting values for variance and co-variance components preceed !GP on the second last line and are 1 0.01 1 and 0.05 0.00001 0.035.

Appendix 2.9: Typical ASReml.*asr* output file for Bivariate Analysis.

```
 ASREML Tue Jun 11 17:01:11 1996 analysis of garcrogo 3 height, diameter
coll6+23.asr
 Bivariate analysis of HT06          and DM23
  Data being read from coll6+23.dat
  Model term      Size Type      COL  Minimum      Mean         Maximum    £ zero
   1 id              1 Covariate  1  151.00       5459.4       11325.          0.
   2 dam           150 Factor     2  1.0000       71.288       149.00          0.
   3 sire            1 Covariate  3 0.10000E+25 0.00000E+00-0.10000E+25 9375.
   4 rep             3 Factor     4  1.0000       2.0000       3.0000          0.
   5 plot          375 Factor     5  1.0000       188.00       375.00          0.
   6 tree           25 Factor     6  1.0000       13.000       25.000          0.
   7 HT06            1 Variate    7 -3.4584      0.14232E-05  3.4730        136.
   8 DM23            1 Variate 2  8 -3.3933      0.23376E-02  3.9662       4937.
   9 Trait           2 Traits/Variat
  10 pl            375 Conditional  9 Trait :     1    5 plot      :  375
  11 Tra.rep         6 Interaction  9 Trait :     2    4 rep       :    3
  12 Tr_1.dam      150 Conditional  9 Trait :     1    2 dam       :  150
  13 Tr_2.dam      150 Conditional  9 Trait :     2    2 dam       :  150
       9375 records read,        9375 records retained
  9375  identity
     2  Unstruct    1.00    0.01    1.00
     2  Unstruct    0.05    0.00    0.04
   150  identity
 Structure of Tr_1.dam     has   300 levels defined
  Forming          682 equations:            7 dense
 LogL=-797.383     S2=  1.000     18744 df   0.10000   1.00000   1.00000
     0.01000   1.00000   0.05000   0.00001   0.03500
 LogL=-17932.0     S2=  1.000     18744 df   0.13956   1.00000   0.20856
     0.11000   0.32279   0.04784   0.00011   0.01856
 LogL=-8522.14     S2=  1.000     18744 df   0.14587   1.00000   0.35341
     0.21640   0.52399   0.04459   0.00121   0.02295
 LogL=-3807.32     S2=  1.000     18744 df   0.13779   1.00000   0.52799
     0.37788   0.74942   0.04836   0.01331   0.02338
 LogL=-1877.40     S2=  1.000     18744 df   0.13119   1.00000   0.66407
     0.52755   0.92396   0.06619   0.03161   0.02788
 LogL=-1381.30     S2=  1.000     18744 df   0.12845   1.00000   0.71218
     0.58647   0.99236   0.08057   0.03871   0.03261
 LogL=-1339.87     S2=  1.000     18744 df   0.12780   1.00000   0.71643
     0.59296   1.00071   0.08301   0.04007   0.03341
 LogL=-1339.46     S2=  1.000     18744 df   0.12774   1.00000   0.71647
     0.59321   1.00110   0.08308   0.04010   0.03342
 LogL=-1339.46     S2=  1.000     18744 df   0.12774   1.00000   0.71647
     0.59322   1.00112   0.08308   0.04010   0.03342
 Final parameter values                      0.12774   1.00000   0.71647
     0.59322   1.00113   0.08308   0.04010   0.03342

   Source        Model  terms     Gamma      Component    Stnd error
  pl               375    375  0.127740      0.127740      0.132775E-01
  Residual    Unstruct      2  0.716473      0.716473      0.107503E-01
  Residual    Unstruct      2  0.593220      0.593220      0.130285E-01
  Residual    Unstruct      2   1.00113       1.00113      0.205346E-01
 Tr_1.dam     Unstruct      2  0.830763E-01  0.830763E-01  0.177542E-01
 Tr_1.dam     Unstruct      2  0.401034E-01  0.401034E-01  0.886745E-02
 Tr_1.dam     Unstruct      2  0.334234E-01  0.334234E-01  0.694477E-02
 Variance of Variance components
  0.176291E-03
 -0.351200E-05  0.115569E-03
 -0.158210E-05  0.949175E-04  0.169742E-03
  0.171567E-06  0.770816E-04  0.213695E-03  0.421670E-03
 -0.586523E-04 -0.412263E-06 -0.755246E-06 -0.107563E-05  0.315211E-03
 -0.287700E-07 -0.126981E-05 -0.224865E-05 -0.275254E-05  0.105138E-03  0.786316E-04
 -0.794719E-07 -0.102642E-05 -0.300405E-05 -0.773873E-05  0.373741E-04  0.424274E-04
  0.482298E-04
 Degrees of Freedom     6   150   150   375
             Solution       Standard Error    T-value     T-prev
```

```
 11 Tra.rep          6        25.58
            1    0.205424        0.438100E-01       4.69
            2    0.143243        0.438084E-01       3.27      -1.24
            3   -0.355015        0.438133E-01      -8.10      -9.95
            4    0.114752E-01    0.277601E-01       0.41       8.10
            5    0.436915E-01    0.280624E-01       1.56       1.01
            6   -0.810091E-01    0.276954E-01      -2.93      -3.91
Finished: Tue Jun 11 17:01:51 1996    LogL Converged
```

Note:
1. In this example, the variances and covariances are generated for HT06 and DM23
2. Of the triplicate of values under a given heading 'Source' e.g. Residual, the first and third lines are the variance of Traits 1 and 2 respectively the second line is the covariance of Traits 1 and 2.
3. This model took 9 interactions to converge.

Appendix 2.10: Typical (1) ASReml.*pin* input and (2) ASReml.*pvs* output files for Bivariate Analysis.

1. ASReml.*pin* file:

```
#           Residual Dam     Plot
#           A AB B   A AB B  A AB B
P phenA     1 0 0    1 0 0   1 0 0
P phenAB    0 1 0    0 1 0   0 1 0 0
P phenB     0 0 1    0 0 1   0 0 1 0 0

P damA      0 0 0    4 0 0   0 0 0 0 0 0
P damAB     0 0 0    0 4 0   0 0 0 0 0 0 0
P damB      0 0 0    0 0 4   0 0 0 0 0 0 0 0

H direct_herit_A  13 10
H direct_herit_B  15 12
H plot_csqA       7  10
H plot_csqB       9 12

R direct_corr     13 14 15
R plot_corr       7 8 9
R Phen_corr       10 11 12
```

Note: 1. In this example individual tree heritabilities and genetic, phenotypic and environmental correlations will be calculated using variances using covariances generated from the ASReml.asr file
2. direct_herit relates to single tree heritability.
3. direct_corr relates to genetic correlations.
4. Phen_corr relates to phenotypic correlation.

2. ASReml.*pvs* output file.

```
Label              Seq    coll6+23.pvs     SE
  8 phenA           0.9273      0.1141E-03  0.1116E-03  0.9258E-04  0.7618E-04
                    0.2561E-03  0.1038E-03  0.3627E-04  0.4819E-03
  9 phenAB          0.6333     -0.1611E-05  0.9365E-04  0.1675E-03  0.2109E-03
                    0.1044E-03  0.7638E-04  0.3942E-04  0.1964E-03  0.2439E-03
 10 phenB            1.035      0.9210E-07  0.7606E-04  0.2107E-03  0.4139E-03
                    0.3630E-04  0.3967E-04  0.4049E-04  0.1124E-03  0.2504E-03
                    0.4544E-03
 11 damA           0.3323      -0.2346E-03 -0.1649E-05 -0.3021E-05 -0.4303E-05
                    0.1261E-02  0.4206E-03  0.1495E-03  0.1025E-02  0.4175E-03
                    0.1452E-03  0.5043E-02
 12 damAB          0.1604      -0.1151E-06 -0.5079E-05 -0.8995E-05 -0.1101E-04
                    0.4206E-03  0.3145E-03  0.1697E-03  0.4154E-03  0.3055E-03
                    0.1587E-03  0.1682E-02  0.1258E-02
 13 damB           0.1337      -0.3179E-06 -0.4106E-05 -0.1202E-04 -0.3095E-04
                    0.1495E-03  0.1697E-03  0.1929E-03  0.1451E-03  0.1577E-03
                    0.1620E-03  0.5980E-03  0.6788E-03  0.7717E-03
    direct_herit = damA          /phenA        =          0.3584   0.0713
    direct_herit = damB          /phenB        =          0.1292   0.0262
    plot_csqA    = pl            /phenA        =          0.1378   0.0134
    direct_corr  = damAB    /SQR[damA     *damB     ]=    0.7611   0.0920
    Phen_corr    = phenAB   /SQR[phenA    *phenB    ]=    0.6466   0.0091
```

Note: 1. This example is the output from an investigation into the genetic and phenotypic correlations between HT06 and DM23

2. Extreme right-hand column gives Standard Errors asscociated with the calculate value to the left of this column.

Appendix 2.11: Selection goal of 23-year diameter: variation of Q_{gen} and Q_{year} with selection age and delay before generation turn-over.

	T_j	h_i^2	h_f^2	$r_{A_j, DM23}$	Q_{gen}		Q_{year}				
							Individual			Family	
					Individual	Family	d = variable	d = 5 years	d = 3 years	d = 5 years	d = 3 years
HT01	1	0.3194	0.6062	0.2766	0.4061	0.2844	1.0336	1.8950	2.6394	1.3273	1.8488
HT02	2	0.1533	0.5194	0.3810	0.3875	0.3626	0.9042	1.5500	2.0150	1.4506	1.8858
HT03	3	0.1440	0.4256	0.6204	0.6115	0.5345	1.3172	2.1404	2.6500	1.8709	2.3163
HT04	4	0.2204	0.4710	0.7048	0.8595	0.6388	1.7190	2.6740	3.1924	1.9875	2.3728
HT05	5	0.2642	0.5259	0.7537	1.0063	0.7219	1.8785	2.8177	3.2706	2.0212	2.3461
HT06	6	0.3209	0.5573	0.7611	1.1200	0.7504	1.9599	2.8508	3.2354	1.9101	2.1678
HT07	7	0.3828	0.5673	0.7430	1.1941	0.7391	2.0897	2.7863	3.1047	1.7246	1.9217
HT08	8	0.3649	0.5497	0.7737	1.2140	0.7576	1.9996	2.6149	2.8696	1.6318	1.7907
HT09	9	0.3477	0.5295	0.8497	1.3015	0.8166	2.1436	2.6030	2.8199	1.6332	1.7693
HT10	10	0.3571	0.5480	0.8142	1.2639	0.7960	1.9660	2.3592	2.5277	1.4859	1.5921
HT11	11	0.3673	0.5576	0.8264	1.3010	0.8150	2.0238	2.2767	2.4161	1.4263	1.5136
DM10	10	0.2734	0.5576	0.9033	1.2269	0.8908	1.9085	2.2902	2.4538	1.6629	1.7817
DM12	12	0.2283	0.5746	0.9335	1.1586	0.9346	1.7074	1.9083	2.0083	1.5393	1.6199
DM14	14	0.1719	0.5764	0.9460	1.0188	0.9486	1.4264	1.5014	1.5582	1.3979	1.4507
DM16	16	0.1321	0.5962	0.9620	0.9082	0.9810	1.2110	1.2110	1.2429	1.3080	1.3425
DM17	17	0.1246	0.5969	0.9630	0.8830	0.9826	1.1238	1.1238	1.1479	1.2506	1.2774
DM23	23	0.1482	0.5733	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
DN17	17	0.4389	0.7131	0.8142	1.4012	0.9081	1.7833	1.7833	1.8215	1.1557	1.1805

Appendix 2.12: Data used to plot Figures 2.4 and 2.5.

	T_j	T_m	r_A	r_P	LAR
HH	2	3	0.9343	0.7967	-0.40547
HH	2	4	0.8544	0.6869	-0.69315
HH	2	5	0.8431	0.6869	-0.91629
HH	2	6	0.7890	0.6197	-1.09861
HH	2	8	0.7048	0.4951	-1.38629
HH	2	10	0.6314	0.4410	-1.60944
HH	2	11	0.6053	0.4236	-1.70475
HH	3	7	0.8179	0.6746	-0.84730
HH	3	11	0.6694	0.5421	-1.29928
HH	4	5	0.9754	0.8916	-0.22314
HH	4	6	0.9303	0.8329	-0.40547
HH	4	8	0.8514	0.6841	-0.69315
HH	4	11	0.7477	0.6127	-1.01160
HH	5	6	0.9731	0.9506	-0.18232
HH	5	8	0.9157	0.7620	-0.47000
HH	5	9	0.8804	0.7354	-0.58779
HH	5	11	0.8408	0.6977	-0.78846
HH	6	8	0.9476	0.8203	-0.28768
HH	6	10	0.9114	0.7725	-0.51083
HH	6	11	0.8952	0.7552	-0.60614
HH	7	11	0.9343	0.8158	-0.45199
HH	8	11	0.9454	0.8632	-0.31845
DD	10	17	0.8730	0.9079	-0.53063
DD	10	19	0.8398	0.8896	-0.64185
DD	10	23	0.9033	0.8383	-0.83291
DD	12	16	0.9420	0.9642	-0.28768
DD	12	17	0.9146	0.9514	-0.34831
DD	12	19	0.8909	0.9377	-0.45953
DD	12	23	0.9335	0.8872	-0.65059
DD	14	23	0.9460	0.9305	-0.49644
DD	16	23	0.9620	0.9629	-0.36291
DD	17	23	0.9630	0.9715	-0.30228

	T_j	T_m	r_A	r_P	LAR
HD	2	12	0.5802	0.5277	-1.79176
HD	2	14	0.5712	0.5024	-1.94591
HD	2	16	0.4652	0.4858	-2.07944
HD	2	17	0.4506	0.4700	-2.14007
HD	2	23	0.3810	0.4264	-2.44235
HD	3	12	0.6453	0.6292	-1.38629
HD	3	16	0.5301	0.5687	-1.67398
HD	3	19	0.5309	0.5205	-1.84583
HD	3	23	0.6204	0.4927	-2.03688
HD	4	12	0.7461	0.6906	-1.09861
HD	4	14	0.7241	0.6502	-1.25276
HD	4	16	0.6301	0.6188	-1.38629
HD	4	23	0.7048	0.5402	-1.74920
HD	5	10	0.8307	0.7889	-0.69315
HD	5	12	0.8093	0.7624	-0.87547
HD	5	16	0.6922	0.6898	-1.16315
HD	5	19	0.6606	0.6535	-1.33500
HD	5	23	0.7537	0.6127	-1.52606
HD	6	12	0.8450	0.8011	-0.69315
HD	6	16	0.7167	0.7247	-0.98083
HD	6	23	0.7611	0.7084	-1.34373
HD	6	17	0.6897	0.7084	-1.04145
HD	7	14	0.7896	0.7708	-0.69315
HD	7	19	0.6400	0.6971	-0.99853
HD	7	23	0.7400	0.6465	-1.18958
HD	8	10	0.90.7	0.8326	-0.22314
HD	8	12	0.8679	0.8101	-0.40547
HD	8	16	0.7068	0.7370	-0.69315
HD	8	23	0.7737	0.6518	-1.05605
HD	9	12	0.9249	0.8497	-0.28768
HD	9	17	0.7171	0.7643	-0.63599
HD	9	23	0.8497	0.7004	-0.93827
HD	10	14	0.8032	0.8000	-0.33647
HD	10	19	0.7032	0.7542	-0.64185
HD	10	23	0.8142	0.7139	-0.83291
HD	11	12	0.8642	0.8151	-0.08701
HD	11	16	0.7477	0.7806	-0.37469
HD	11	23	0.8264	0.7223	-0.73760

Note: 1. HH = $height_j$:$height_m$ correlations .
HD = $height_j$:$diameter_m$ correlations
DD = $diamter_j$:$diameter_m$ correlaitons

2. $LAR = \log_e \frac{T_j}{T_m}$

Appendix 2.13: Estimated $r_{A_{j,40}}$ and $r_{P_{j,40}}$ and Q_{year} for ages $T_j = 2$ to $T_j = 15$ assuming a fixed $T_m = 40$ years for the three regression options listed in Chapter 2.3.3.2.

1. <u>Genetic Correlation (r_A)</u>

i. Diameter: diameter correlations.

T_j	LAR	Calculated $r_{j,40}$	Q_{year}		
			d = variable	d = 5 years	d = 3 years
2	-2.9957	0.6174	2.32	3.97	5.31
3	-2.5903	0.6659	2.30	3.75	4.77
4	-2.3026	0.7003	2.25	3.50	4.30
5	-2.0794	0.7269	2.18	3.27	3.91
6	-1.8971	0.7487	2.11	3.06	3.58
7	-1.7430	0.7672	2.16	2.88	3.30
8	-1.6094	0.7831	2.07	2.71	3.06
9	-1.4917	0.7972	2.11	2.56	2.86
10	-1.3863	0.8098	2.02	2.43	2.68
11	-1.2910	0.8212	2.05	2.31	2.52
12	-1.2040	0.8316	1.97	2.20	2.38
13	-1.1239	0.8418	1.99	2.10	2.26
14	-1.0498	0.8500	1.91	2.01	2.15
15	-0.9808	0.8583	1.93	1.93	2.05

Note: $r_{A_{DD_{j,40}}} = 0.9756 + 0.1196\ (LAR)$.

ii. Height:height correlations.

T_j	LAR	Calculated $r_{j,40}$	Q_{year}		
			d = variable	d = 5 years	d = 3 years
2	-2.9957	0.2896	1.09	1.86	2.49
3	-2.5903	0.3900	1.35	2.19	2.79
4	-2.3026	0.4612	1.48	2.31	2.83
5	-2.0794	0.5164	1.55	2.32	2.78
6	-1.8971	0.5615	1.58	2.30	2.68
7	-1.7430	0.5996	1.69	2.25	2.58
8	-1.6094	0.6327	1.67	2.19	2.47
9	-1.4917	0.6618	1.75	2.13	2.37
10	-1.3863	0.6879	1.72	2.06	2.28
11	-1.2910	0.7115	1.78	2.00	2.19
12	-1.2040	0.7330	1.74	1.94	2.10
13	-1.1239	0.7528	1.78	1.88	2.02
14	-1.0498	0.7712	1.74	1.83	1.95
15	-0.9808	0.7882	1.77	1.77	1.88

Note: $r_{A_{HH_{j,40}}} = 1.0309 + 0.2475\ (LAR)$

iii. Height: diameter correlations.

T_j	LAR	Calculated $r_{j,\,40}$	Q_{year}		
			d = variable	*d* = 5 years	*d* = 3 years
2	-2.9957	0.3602	1.35	2.32	3.10
3	-2.5903	0.4361	1.51	2.45	3.13
4	-2.3026	0.4899	1.57	2.45	3.01
5	-2.0794	0.5317	1.59	2.39	2.86
6	-1.8971	0.5658	1.59	2.31	2.70
7	-1.7430	0.5946	1.67	2.23	2.56
8	-1.6094	0.6196	1.64	2.14	2.42
9	-1.4917	0.6416	1.70	2.06	2.30
10	-1.3863	0.6613	1.65	1.98	2.19
11	-1.2910	0.6792	1.70	1.91	2.09
12	-1.2040	0.6955	1.65	1.84	1.99
13	-1.1239	0.7104	1.68	1.78	1.91
14	-1.0498	0.7243	1.63	1.72	1.83
15	-0.9808	0.73720	1.66	1.66	1.76

Note: $r_{A_{HD_{j,\,40}}} = 0.9207 + 0.1871\ (LAR)$

2. Phenotypic Correlations (r_P)

i. Diameter: diameter correlations.

T_j	LAR	Calculated $r_{j,\,40}$	Q_{year}		
			d = variable	*d* = 5 years	*d* = 3 years
2	-2.9957	0.3210	1.20	2.06	2.76
3	-2.5903	0.4186	1.45	2.35	3.00
4	-2.3026	0.4879	1.57	2.44	3.00
5	-2.0794	0.5416	1.62	2.44	2.91
6	-1.8971	0.5855	1.65	2.40	2.80
7	-1.7430	0.6226	1.75	2.33	2.68
8	-1.6094	0.6548	1.73	2.27	2.56
9	-1.4917	0.6831	1.81	2.20	2.45
10	-1.3863	0.7085	1.77	2.13	2.34
11	-1.2910	0.7315	1.83	2.06	2.25
12	-1.2040	0.7524	1.78	1.99	2.16
13	-1.1239	0.7717	1.83	1.93	2.07
14	-1.0498	0.7895	1.78	1.87	2.00
15	-0.9808	0.8062	1.81	1.81	1.93

Note: $r_{P_{DD_{j,\,40}}} = 1.0423 + 0.2408\ (LAR)$

ii. Height: height correlation.

T_j	LAR	Calculated $r_{j,\,40}$	Q_{year}		
			d = variable	d = 5 years	d = 3 years
2	-2.9957	0.0054	0.02	0.03	0.05
3	-2.5903	0.1323	0.46	0.74	0.95
4	-2.3026	0.2224	0.71	1.11	1.37
5	-2.0794	0.2922	0.88	1.31	1.57
6	-1.8971	0.3493	0.98	1.43	1.67
7	-1.7430	0.3975	1.12	1.49	1.71
8	-1.6094	0.4393	1.16	1.52	1.72
9	-1.4917	0.4762	1.26	1.53	1.71
10	-1.3863	0.5091	1.27	1.53	1.68
11	-1.2910	0.5390	1.35	1.52	1.66
12	-1.2040	0.5662	1.34	1.50	1.62
13	-1.1239	0.5912	1.40	1.48	1.59
14	-1.0498	0.6144	1.38	1.46	1.55
15	-0.9808	0.6360	1.43	1.43	1.52

Note: $r_{P_{HH_{j,\,40}}} = 0.9430 + 0.3143\ (LAR)$

iii. Height: diameter correlation.

T_j	LAR	Calculated $r_{j,\,40}$	Q_{year}		
			d = variable	d = 5 years	d = 3 years
2	-2.9957	0.3234	1.21	2.08	2.78
3	-2.5903	0.3993	1.38	2.25	2.86
4	-2.3026	0.4531	1.46	2.27	2.78
5	-2.0794	0.4949	1.48	2.23	2.66
6	-1.8971	0.5290	1.49	2.16	2.53
7	-1.7430	0.5579	1.57	2.09	2.40
8	-1.6094	0.5829	1.54	2.02	2.28
9	-1.4917	0.6049	1.60	1.94	2.17
10	-1.3863	0.6246	1.56	1.87	2.07
11	-1.2910	0.6425	1.61	1.81	1.97
12	-1.2040	0.6587	1.56	1.74	1.89
13	-1.1239	0.6737	1.60	1.68	1.81
14	-1.0498	0.6876	1.55	1.63	1.74
15	-0.9808	0.7005	1.58	1.58	1.67

Note: 1. $r_{P_{HD_{j,\,40}}} = 0.8841 + 0.1872\ (LAR)$

2. In all cases, estimated $r_{j,\,40}$ follows from substitution of LAR in the relevant regression equation. The estimated $r_{j,40}$ is then substituted in $Q_{year} = r_{j,\,40} \dfrac{(T_m + d)}{(T_j + d)}$ where d varies as stated.

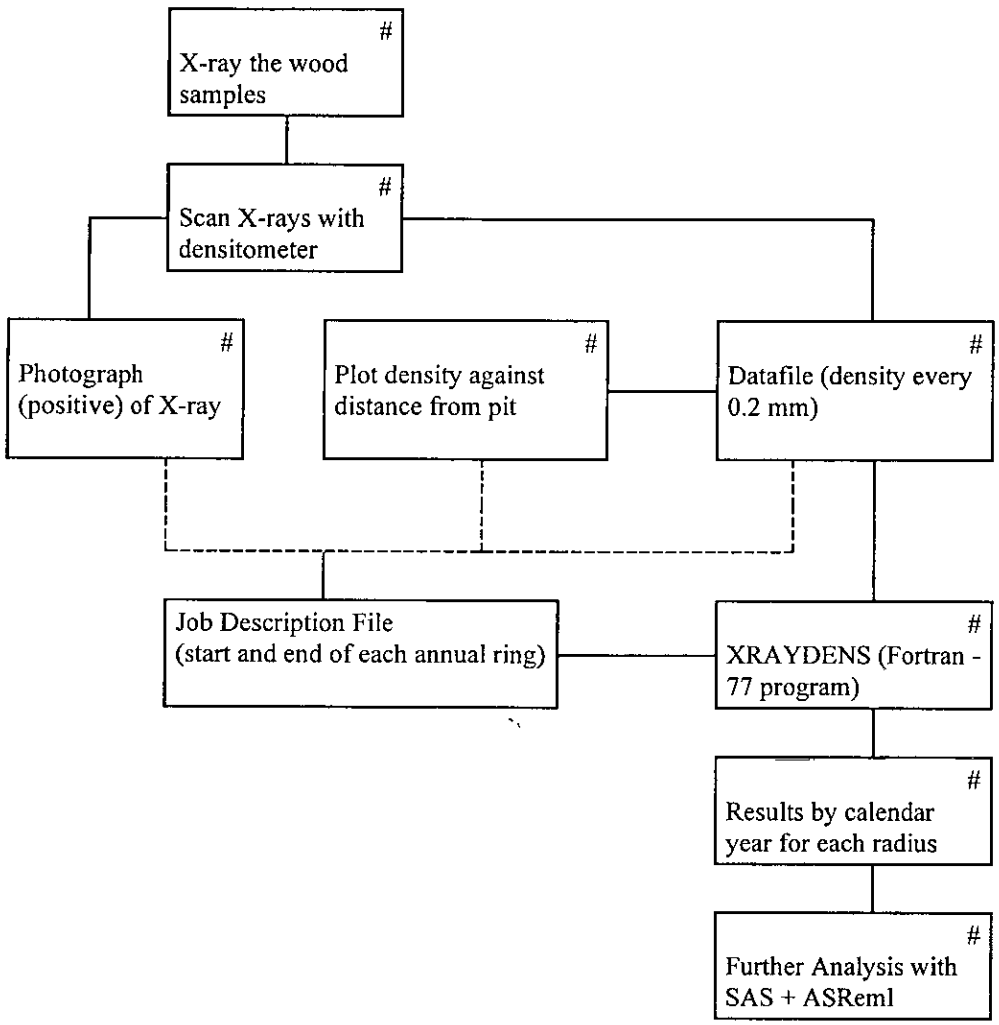
Appendix 3.1: Data used to plot Figure 3.1. Standardised values of DM16 and DN17, and value of w by family following substitution in Equation 3.2.

Family	w	DM16 (t_1)	DN17 (t_2)	Family	w	DM16 (t_1)	DN17 (t_2)
4063	26.0021	-2.70255	0.24282	4117	4.9241	-1.25855	-1.51026
4010	14.5241	-0.15958	2.03429	4054	4.9075	1.50166	0.56273
4016	13.7353	2.30672	2.39258	4149	4.4954	0.64548	-0.67851
4103	12.4587	-1.84638	0.20443	4079	4.2276	-1.43746	-1.04959
4142	11.5188	0.95217	-1.16476	4093	4.1540	0.63270	-0.64012
4008	11.0034	2.16615	2.03429	4098	4.0586	-1.28411	-0.29462
4092	10.8345	-2.16584	-1.99651	4104	4.0201	-0.83685	0.39637
4005	10.2920	2.16615	1.85514	4075	3.9527	0.70937	1.39448
4007	9.7965	0.72215	2.09827	4012	3.8374	-0.67073	-1.36950
4029	9.7236	0.38991	1.95751	4064	3.8273	-1.07965	-1.34391
4050	9.6928	-1.14354	0.79306	4091	3.8089	1.28442	0.38358
4030	9.5605	0.12155	1.80396	4148	3.6487	1.19497	0.23002
4044	9.2958	-1.07965	-2.13727	4124	3.5172	1.23330	1.13855
4043	9.0128	0.84994	2.05988	4118	3.4700	1.00329	-0.06429
4022	8.9484	-1.60358	0.11486	4114	3.3566	-0.55572	0.58832
4042	8.8930	0.86272	-0.99841	4133	3.2583	0.69660	-0.42258
4051	8.8196	-1.83360	-0.30742	4080	3.2088	1.19497	1.06178
4121	8.7303	-1.80804	-1.93253	4122	3.2011	-1.25855	-0.66571
4026	8.5994	1.25886	-0.53775	4073	3.1144	-0.00624	0.98500
4035	8.5930	1.96169	1.72718	4120	3.0889	0.73493	-0.34580
4116	7.9304	-0.84963	-1.94533	4119	3.0610	1.2775	0.52434
4017	7.6067	1.48888	1.90632	4112	3.0410	1.20775	0.93381
4068	7.4141	-1.70581	-0.33301	4025	3.0045	-0.61962	-1.21594
4069	7.2747	1.32275	-0.28182	4067	2.8973	-1.19466	-0.84486
4136	7.0860	-1.19466	-1.88135	4041	2.8359	1.13107	0.98500
4052	6.5548	-0.88797	-1.79177	4130	2.7376	-0.07013	0.88263
4053	6.2478	1.33553	-0.10268	4028	2.6931	0.76049	-0.23064
4057	6.1504	-1.09243	-1.75338	4071	2.5843	0.32601	1.06178
4140	5.9322	-0.50461	-1.61263	4027	2.5487	0.68382	-0.29462
4033	5.6791	0.59437	1.61201	4048	2.5450	-0.92631	-1.07519
4037	5.5195	1.65500	0.89543	4018	2.5179	1.11829	0.75467
4147	5.4032	-1.53969	-1.39509	4132	2.4932	-0.86241	-1.08798
4058	5.2238	-0.10847	-1.34391	4009	2.4879	-1.00298	-0.99841

Appendix 3.1 (continued)

Family	w	DM16 (t_1)	DN17 (t_2)	Family	w	DM16 (t_1)	DN17 (t_2)
4034	2.4161	0.90106	0.05088	4138	1.2755	-0.23625	0.46036
4060	2.3903	-1.04131	-0.37140	4011	1.2262	0.54325	-0.11547
4113	2.3361	-1.05409	-0.83206	4036	1.1959	0.54325	0.76746
4090	2.2711	-0.96464	-0.94723	4143	1.0476	0.12155	0.63950
4134	2.2664	-1.02854	-0.84486	4045	1.0073	-0.24903	-0.67851
4004	2.2625	1.04162	0.80585	4137	0.9885	-0.03179	0.53713
4084	2.2365	-1.05409	-0.57614	4055	0.9710	-0.17236	-0.64012
4006	2.2038	-1.01576	-0.40979	4107	0.9175	0.23656	-0.35860
4144	2.1396	0.65826	-0.23064	4015	0.9150	0.63270	0.57552
4066	2.1273	-0.72185	-1.02400	4141	0.9002	-0.07013	0.48595
4078	2.0862	0.86272	0.95941	4128	0.8594	-0.55572	-0.61452
4083	2.0585	-0.32570	-0.96002	4046	0.8059	0.63270	0.34519
4023	2.0514	0.86272	0.94661	4056	0.8057	-0.24903	-0.61452
4105	1.9639	-0.96464	-0.76808	4021	0.7649	0.53047	0.57552
4139	1.9388	0.74771	-0.05149	4001	0.7514	-0.37682	0.15325
4047	1.9377	0.96495	0.43476	4072	0.7334	-0.56850	-0.51215
4135	1.8780	0.13433	-0.67851	4020	0.6477	-0.46627	-0.02590
4115	1.8763	0.70937	-0.08988	4087	0.4860	0.47936	0.38358
4049	1.8421	-0.93908	-0.72969	4096	0.4438	-0.23625	0.17884
4085	1.7976	-0.40238	0.43476	4062	0.4388	-0.07013	-0.40979
4040	1.7674	0.93939	0.60111	4038	0.4145	-0.42793	-0.38419
4086	1.7646	-0.93908	-0.58893	4088	0.3905	-0.44071	-0.24343
4031	1.7513	-0.18514	0.61391	4074	0.3369	-0.15958	-0.39699
4019	1.6619	0.49214	0.90822	4059	0.2601	-0.31293	-0.33301
4146	1.6471	0.10877	0.78026	4032	0.2491	-0.23625	0.06367
4003	1.6141	0.67104	0.88263	4061	0.1942	-0.04457	0.21723
4131	1.5008	0.86272	0.58832	4002	0.1552	-0.27459	-0.20505
4014	1.4502	0.76049	0.76746	4100	0.0386	0.12155	0.12765
4106	1.3783	-0.72185	-0.11547	4024	0.0126	-0.03179	-0.07708
4129	1.3730	-0.12124	0.57552				

Appendix 3.2: The sequence of events involved from X-raying of the prepared wood samples to analysis of data at the calendar year level



Note: # denotes work carried out under contract by OFI.

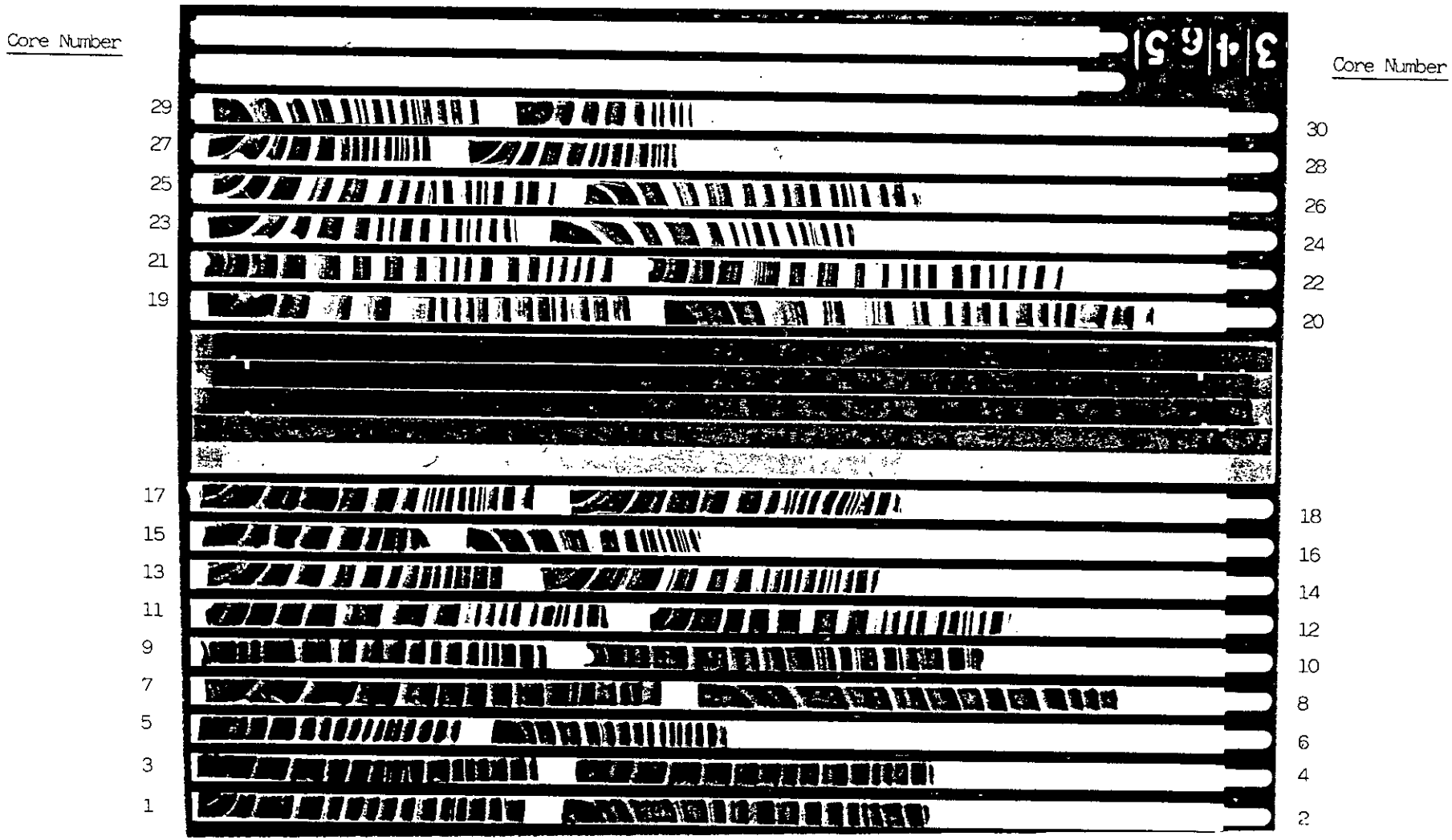
Appendix 3.3: Example of the data relating to just one of the thirty radii contained within the rawdata file F3465

Optical density is calculated every 0.2mm as the densitometer passes from the pith to the cambium. The start and finish of the sample together with the point where each ring starts and finishes is entered into the Job Discription File (JDF) and indicated here with a '/'.

Plot 8, Family 4010, tree 9, North radius:

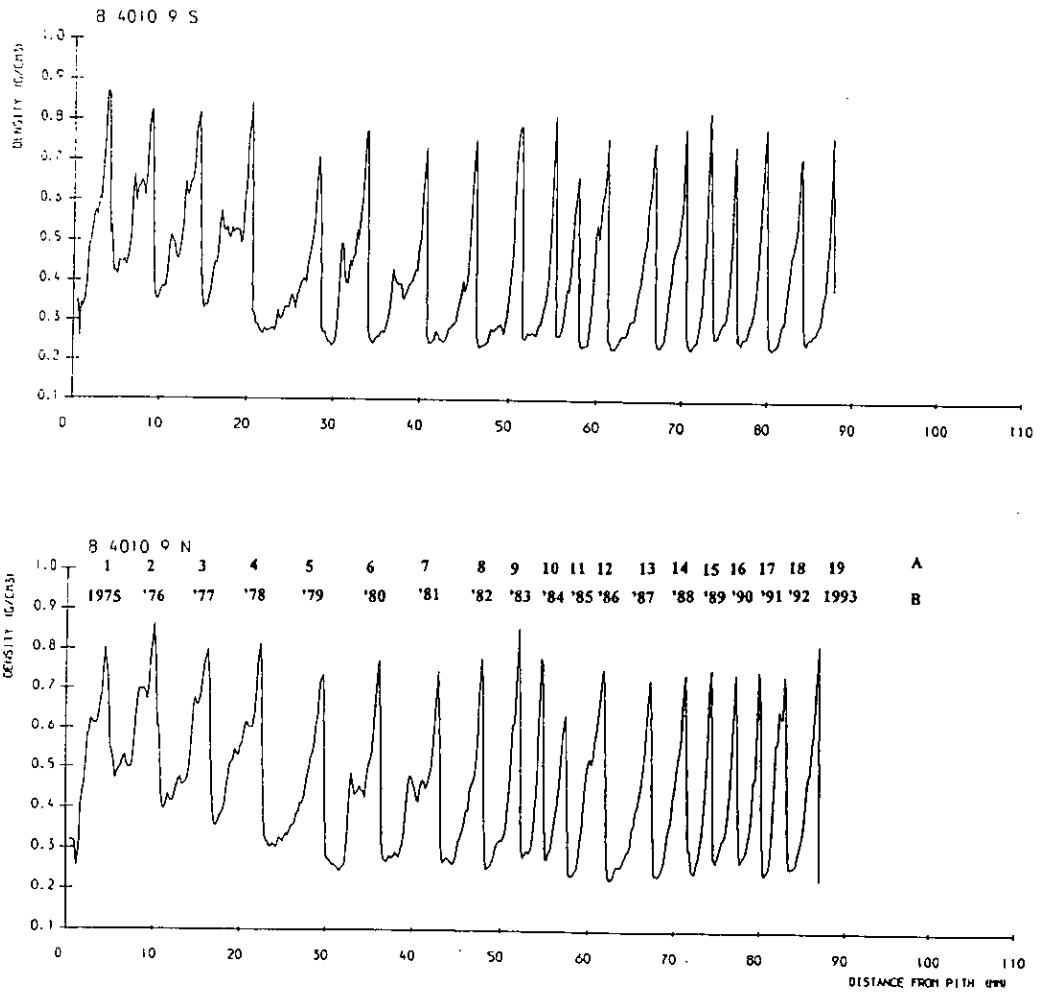
	1	2	3	4	5	6	7	8	9	0
0	2460	2472	2460	2457	2256	/1422	1176	1110	1074	981
1	882	879	828	840	846	846	825	783	744	675
2	612	/657	720	927	951	978	1056	1029	1011	1005
3	975	957	990	1008	1011	1002	945	876	804	741
4	729	735	729	738	768	732	651	591	546	/648
5	855	855	1119	1188	1188	1164	1119	1146	1152	1152
6	1107	1083	1053	1044	1080	1077	1068	1050	1011	957
7	855	777	759	786	777	747	699	660	636	615/
8	717	951	1170	1272	1278	1260	1224	1218	1191	1155
9	1092	1044	993	984	975	933	957	963	924	912
10	882	840	840	861	855	861	810	735	639	/600
11	690	978	1314	1362	1374	1404	1404	1380	1392	1407
12	1383	1341	1353	1371	1344	1320	1332	1302	1275	1278
13	1254	1212	1200	1161	1164	1137	1089	1044	1011	966
14	945	915	849	813	720	702	/687	1023	1461	1491
15	1506	1527	1551	1545	1566	1587	1620	1575	1563	1518
16	1362	1134	1026	1056	1122	1116	1101	1080	1101	1104
17	1134	1062	1002	978	942	870	783	690	645/	873
18	1368	1494	1509	1524	1467	1476	1491	1461	1440	1467
19	1482	1422	1374	1308	1182	1074	1038	1038	1074	1092
20	1146	1152	1089	1056	1056	1092	1074	1041	1014	942
21	840	744	675/	912	1380	1533	1506	1479	1497	1503
22	1533	1536	1497	1443	1356	1338	1296	1254	1191	1197
23	1098	1068	1056	1017	915	750	639/	696	1185	1578
24	1587	1563	1548	1512	1452	1401	1374	1353	1362	1344
25	1308	1245	1101	1017	843	840	681	555/	780	1404
26	1479	1455	1422	1440	1437	1392	1317	1188	1053	846
27	636	/654	1083	1488	1491	1437	1407	1311	1224	1173
28	1104	1005	897	828	810/	1164	1632	1662	1659	1626
29	1596	1566	1452	1353	1251	1128	1029	990	966	987
30	957	897	861	804	738	669	669/	966	1488	1674
31	1716	1704	1662	1584	1542	1560	1557	1539	1497	1473
32	1428	1428	1377	1281	1269	1185	1176	1125	1074	1023
33	939	849	774	699/	801	1197	1638	1647	1656	1647
34	1608	1539	1500	1395	1314	1275	1236	1137	1083	1017
35	975	930	885	753	681/	951	1407	1410	1587	1623
36	1617	1521	1473	1389	1308	1200	1101	933	726	666/
37	978	1470	1515	1476	1422	1383	1344	1332	1293	1221
38	1107	972	795	681/	810	1236	1509	1500	1467	1449
39	1410	1344	1305	1194	1056	1038	852	672/	768	1296
40	1635	1635	1605	1554	1452	1311	1110	906	906	792
41	816	819	684/	720	1281	1560	1563	1545	1551	1527
42	1458	1401	1362	1323	1236	1119	1029	1029	933	873
43	786	681	597/	1710	2600	2600	2600	2600	2600	2600/

Appendix 3.4: Photo-reduced positive from X-ray of the 30 cores which make up plate 3465. The photograph is used in combination with the graphs of density against distance from pith (Appendix 3.5) to help decide the location of annual rings within the raw-data file (Appendix 3.3)



Appendix 3.5: Graph of density (g cm^{-3}) against distance from pith. The radius-specific graph is used in conjunction with the positive of the X-ray (Appendix 3.4) to determine the start and finish of each annual ring within the raw-data file (Appendix 3.3)

Sitka spruce - Northern Research Station, Roslin



Note: S = South side, N = North side
A = measurable ring number from the pith
B = calendar year

Appendix 3.6: Specification of the Fortran-77 Program XRAYDENS and a sample Job Description File.

This computer program was written by Dr C I Goodwin-Bailey at the OFI. The program combines instruction from the Job Description File (JDF) with the raw data (F file) to generate various variables relating to ring density and width which are listed to the results (RES) file. (Appendix 3.7.)

Description

The program is written in Fortran V and uses output from the Joyce Lobel MDM6 to compute:

a. The density of the standards used for calibration.
b. The gravimetric density of the sample at 12% moisture content.
c. The mean unweighed density and mean weighted (by area) gravimetric density of each ring.
d. The width and area of each ring.
e. The percentage and width of each ring in specified density classes.
f. The linear transformation equation: $Y = mx + c$
   where: Y = Gravimetric density (g/cm^3); X = Optical density;
   Y = 1.000806 x -0.00183869 (from Wood, 1986)
g. The standard deviation, coefficient of variation, the maximum, minimum and range of density for each ring and density class.
h. The mean weighted and unweighed density of each radius.
i. The mean weighted and unweighed density of each level.
j. The mean gravimetric density of all levels within a tree - TREEMEAN.

Limits

a. The step interval of the MDM6 (200 microns).
b. The moisture content of the sample (12%).
c. The coefficient of volumetric shrinkage, coefficient of radial shrinkage and fibre saturation point, assuming a moisture content of 12%
d. A maximum error between optical and gravimetric density of 0.05%.
e. Assumes the number of radii/tree and the number of radii/level for all trees samples to be constant.

Method

a. Mean ring density.
   Measurements of density are made at a specified interval (200 microns) across each radius from pith to bark. The density of each ring within the radius is determined from the series of point measurements defined by successive values of NPOS (end of ring position).
   The unweighed ring density is obtained as the mean of these measurements expressed as gravimetric density.
   The weighted ring density is obtained as a summation of the product of step area by step density divided by ring area.
b. Weighted mean/radius density.
   Summation of the product of step area by steps from pith to bark divided by summation of all steps.
c. Weighted mean disc (level) density.
   Summation of the product of step density by step area for all steps in all radii in the disc, divided by summation of all step areas for all radii in the disc.
d. Whole tree weighted mean density.
   Summation of the product of step density by step area for all steps of all radii in all discs, divided by the summation of step areas for all areas for all radii in all discs. The assumption is made that the sampling interval between levels is equal.

Control Variables

Control variables are input as separate Job Description File (JDFfilmnumber) as follows:

1.	JDF	:	Job Description file number (eg JDF3465).
2.	NRAD	:	Number of samples per film (always 30).
3.	SD	:	Constant term of the regression gravimetric on X-ray density (-0.001838696).
4.	SLD	:	Slope of the regression (1.000806).
5.	NL	:	Number of levels/tree times number of rads/level (fixed at 1).
6.	NR	:	Number of rads/disc (fixed at 1).
7.	NRR	:	Max number of rings/radius + start position + end position (usually 19+2=21).
8.	TITLE	:	To identify each sample (max 40 chars) (eg 8 4010 9 N).
9.	NYEARS	:	Year of first ring from pith.
10.	NRINGS	:	Total number of rings (+2).
11.	TKNESS	:	The average thickness of each sample in cms (0.515 mm).
12.	DIAM	:	Diameter of pith, or diam of pith plus twice the widths of each subsequent missing ring (mm).
13.	NPOS	:	The number of the position of the last value in each ring in the formatted data. (Total number of counts in ring not to exceed 600).

Control variables 1 to 7 relate to the complete X-ray film; these are only entered once at the start of the JDF. Control variables 8-14 are repeated for each of the 30 samples on each X-ray film.

Example of a Job Description File (JDF):

1	JDF3456	
2	30	
3	-0.001838696	
4	1.000806	
5	1	
6	1	
7	21	
8	8 4010 9 N	# Plot 8, family 4010, tree 9, north radius
9	1975	
10	21	
11	0.515	
12	8	
13	6	
Ring 1	21	
Ring 2	49	
Ring 3	80	
Ring 4	109	
Ring 5	147	
Ring 6	179	
Ring 7	213	
Ring 8	237	
Ring 9	258	
Ring 10	271	
Ring 11	285	
Ring 12	307	
Ring 13	334	
Ring 14	355	
Ring 15	370	
Ring 16	384	
Ring 17	398	
Ring 18	413	
Ring 19	433	
14	440	

This is the actual JDF for the raw-data, photograph and graph given in Appendices 3.3, 3.4 and 3.5.

Appendix 3.7: Typical output (RES file) from the XRAYDENS program following interpretation of the rawdata file using information contained with the JDF.

A calendar year has been attached to each annual ring. Unweighted and weighted (by area) ring density, ring width and associated statistics of variation have been calculated. All subsequent analysis was using the weighted density values. Data are presented for just one radius although each X-ray film (46 in total) would contain similar information for a total of 30 cores; 15 trees x 2 positions (north and south).

ANALYSIS OF RADIUS NUMBER 8 4010 9 N (tree 21)

UNWEIGHTED RING DENSITY

YEAR	WIDTH	MEAN	SD	CV	MAXIM	MINIM	RNGDENS	AREA
1975	3.00	.5912	.1082	18.30	.7935	.3987	.3948	103.6727
1976	5.60	.6064	.1142	18.83	.8540	.4645	.3895	344.8167
1977	6.20	.5434	.1319	24.27	.7909	.3927	.3981	611.5928
1978	5.80	.5190	.1117	21.52	.7697	.3506	.4190	790.7842
1979	7.60	.4360	.1485	34.05	.8043	.3000	.5043	1356.1304
1980	6.40	.4082	.1449	35.49	.7644	.2414	.5230	1423.4814
1981	6.80	.4096	.1253	30.58	.7386	.2640	.4746	1794.4333
1982	4.80	.3865	.1402	36.27	.7697	.2608	.5089	1441.5767
1983	4.20	.4130	.1821	44.09	.8456	.2484	.5971	1380.1284
1984	2.60	.4048	.1672	41.30	.7723	.2767	.4956	909.9072
1985	2.80	.4429	.1521	34.34	.7566	.2732	.4834	1027.3984
1986	4.40	.4431	.1732	39.09	.7437	.2335	.5102	1714.0093
1987	5.40	.3634	.1414	38.91	.7184	.2251	.4933	2269.8032
1988	4.20	.4049	.1584	39.13	.7335	.2346	.4990	1892.0681
1989	3.00	.3905	.1657	42.42	.7463	.2408	.5055	1419.3345
1990	2.80	.4027	.1463	36.34	.7335	.2664	.4671	1375.7292
1991	2.80	.4097	.1518	37.06	.7412	.2681	.4731	1424.9890
1992	3.00	.4522	.1828	40.43	.7310	.2384	.4925	1581.4336
1993	4.00	.4323	.1801	41.66	.8070	.2540	.5530	2196.5427

WEIGHTED RING DENSITY

YEAR	WIDTH	MEAN	SD	CV	MAXIM	MINIM	RNGDENS	AREA
1975	3.00	.6068	.1032	17.01	.7935	.3987	.3948	103.6727
1976	5.60	.6178	.1144	18.52	.8540	.4645	.3895	344.8167
1977	6.20	.5524	.1314	23.78	.7909	.3927	.3981	611.5928
1978	5.80	.5250	.1093	20.82	.7697	.3506	.4190	790.7842
1979	7.60	.4408	.1462	33.17	.8043	.3000	.5043	1356.1304
1980	6.40	.4144	.1441	34.78	.7644	.2414	.5230	1423.4814
1981	6.80	.4140	.1242	29.99	.7386	.2640	.4746	1794.4333
1982	4.80	.3892	.1385	35.58	.7697	.2608	.5089	1441.5767
1983	4.20	.4153	.1786	43.00	.8456	.2484	.5971	1380.1284
1984	2.60	.4058	.1611	39.71	.7723	.2767	.4956	909.9072
1985	2.80	.4436	.1462	32.96	.7566	.2732	.4834	1027.3984
1986	4.40	.4464	.1697	38.01	.7437	.2335	.5102	1714.0093
1987	5.40	.3659	.1397	38.20	.7184	.2251	.4933	2269.8032
1988	4.20	.4066	.1550	38.11	.7335	.2346	.4990	1892.0681
1989	3.00	.3917	.1607	41.04	.7463	.2408	.5055	1419.3345
1990	2.80	.4037	.1416	35.06	.7335	.2664	.4671	1375.7292
1991	2.80	.4104	.1466	35.72	.7412	.2681	.4731	1424.9890
1992	3.00	.4534	.1767	38.98	.7310	.2384	.4925	1581.4336
1993	4.00	.4338	.1759	40.55	.8070	.2540	.5530	2196.5427

MEAN UNWEIGHTED DENSITY: = 0.4483 OVERALL LENGTH = 85.40 OVERALL AREA = 25057.82
MEAN WEIGHTED RADIUS DENSITY: DENSITY =0.4250 SD =0.1587 CV = 37.3315

Appendix 3.8. Comparison of family-mean (1) ring-width and (2) weighted density between north and south site.

Family	1. Ring-width (mm)			2. Weighted density (kg m^{-3})		
	North	South	Difference	North	South	Difference
4005	4.360	4.378	-0.01852	0.4747	0.4755	-0.000838
4007	4.588	4.499	0.08869	0.4897	0.4850	0.004766
4008	4.822	4.842	-0.02012	0.4956	0.5029	-0.007323
4010	4.122	4.141	-0.01816	0.4771	0.4766	0.000500
4016	4.276	4.186	0.09039	0.4842	0.4905	-0.006328
4017	4.782	4.765	0.01647	0.4921	0.4941	-0.001948
4022	4.380	4.349	0.03103	0.5341	0.5368	-0.002646
4026	4.197	4.090	0.10730	0.5492	0.5456	0.003535
4029	4.312	4.330	-0.01785	0.4594	0.4632	-0.003828
4030	4.263	4.198	0.06480	0.4832	0.4888	-0.005554
4033	4.840	4.882	-0.04249	0.4609	0.4634	-0.002522
4037	4.000	4.044	-0.04480	0.5029	0.5003	0.002531
4042	4.414	4.493	-0.07898	0.5308	0.5318	-0.000934
4043	4.245	4.220	0.02515	0.4758	0.4739	0.001899
4044	3.919	3.875	0.04389	0.5470	0.5465	0.000461
4050	3.954	3.948	0.00665	0.5215	0.5184	0.003128
4051	3.899	3.894	0.00492	0.5178	0.5115	0.006338
4052	3.778	3.671	0.10696	0.5542	0.5419	0.012324
4054	5.130	5.113	0.01681	0.4622	0.4631	-0.000880
4057	3.863	3.854	0.00903	0.5359	0.5347	0.001190
4058	4.311	4.220	0.09140	0.5506	0.5593	-0.008696
4064	3.957	3.953	0.00364	0.5540	0.5524	0.001589
4069	4.887	4.920	-0.03296	0.4885	0.4902	-0.001735
4075	4.194	4.171	0.02290	0.4739	0.4753	-0.001335
4079	3.705	3.718	-0.01291	0.5221	0.5179	0.004177
4080	4.031	3.911	0.11973	0.4834	0.4867	-0.003231
4091	4.208	4.145	0.06318	0.4819	0.4777	0.004179
4092	3.729	3.700	0.02894	0.5176	0.5149	0.002708
4093	4.489	4.527	-0.03802	0.4865	0.4826	0.003949
4098	3.804	3.708	0.09543	0.5386	0.5463	-0.007695
4103	4.241	4.218	0.02343	0.5053	0.5025	0.002874
4104	4.023	3.993	0.02955	0.5238	0.5275	-0.003638
4116	3.702	3.620	0.08200	0.5533	0.5482	0.005058
4117	4.041	3.956	0.08424	0.5468	0.5480	-0.001162
4118	4.690	4.682	0.00862	0.4775	0.4815	-0.003951
4121	4.131	4.152	-0.02048	0.5149	0.5093	0.005633
4133	4.271	4.294	-0.02342	0.5111	0.5128	-0.001718
4136	3.769	3.818	-0.04925	0.5223	0.5186	0.003713
4140	4.067	4.005	0.06198	0.5261	0.5260	0.000030
4142	3.990	4.057	-0.06668	0.5385	0.5303	0.008119
4144	4.304	4.245	0.05905	0.5153	0.5160	-0.000764
4147	3.256	3.251	0.00501	0.5696	0.5686	0.001021
4148	4.103	4.076	0.02751	0.4948	0.4987	-0.003911
4149	4.476	4.356	0.11973	0.5198	0.5216	-0.001738

Appendix 3.9. Comparison of (1) mean ring width and (2) mean weighted density by year between the north and south radii.

Calender Year	1. Ring-width (mm)			2. Weighted density (kg m^{-3})		
	North	South	Difference	North	South	Difference
1975	1.825	1.795	0.02962	0.5421	0.5855	-0.043414
1976	2.718	2.630	0.08823	0.5912	0.5894	0.001796
1977	3.908	3.795	0.11375	0.6192	0.6285	-0.009354
1978	5.540	5.416	0.12376	0.5941	0.5940	0.000143
1979	6.477	6.443	0.03425	0.5457	0.5511	-0.005351
1980	7.288	7.298	-0.00955	0.4983	0.5030	-0.004684
1981	7.328	7.367	-0.03866	0.4728	0.4757	-0.002846
1982	6.015	6.059	-0.04409	0.4662	0.4657	0.000428
1983	4.801	4.885	-0.08385	0.4694	0.4649	0.004492
1984	3.870	3.985	-0.11458	0.4918	0.4840	0.007783
1985	3.384	3.403	-0.01951	0.4792	0.4741	0.005179
1986	3.397	3.363	0.03434	0.4892	0.4873	0.001896
1987	3.982	3.935	0.04722	0.4622	0.4650	-0.002863
1988	3.200	3.186	0.01400	0.4850	0.4840	0.001020
1989	2.288	2.215	0.07293	0.5138	0.5195	-0.005709
1990	2.922	2.807	0.11474	0.4922	0.4903	0.001920
1991	3.520	3.432	0.08823	0.4612	0.4684	-0.007188
1992	3.567	3.494	0.07239	0.4934	0.4832	0.010209
1993	3.723	3.598	0.12514	0.4682	0.4544	0.013775

Appendix 3.10: Example of an *.as* file used in the analysis of variance components for density of ring-groupings using trivariate analysis including DM16 and DN17 as covariates.

```
Analysis of garcrogo 3 height, diameter and density data
1   id       1     -1  0
2   sire     1      0  150  # coded 1 to 150
3   dam      1      0  9375 # open pollinated
4   rep      1      3  # coded 1 to 3
5   plot     1    375  # coded 1 to 375
6   tree     1     25  # coded 1 to 25
7   DN19-22  1      1  !M-9 !P-9   #Trait A
8   DM16     1      1  !M-9         #Trait B
9   DN17     1      1  !M-9         #Trait C
10  Trait    0      1
trees.ped
den19-22.dat
7 1 1 0 19             # analyse, normal distr, link, filter maxit
-9
10.4 10/1 10/5
0 .1 .1 .1 .1 .1 .1
1 2 2 !STEP 0.1
9375 0 0
3 0 9 .58 .0001 .83 0.001 0.001 0.55 !GP              #σ²e - A, AxB, B, AxC, BxC, C
12 2
3 0 9 0.32 .00001 0.13 0.00001 0.00001 0.32 !GP       #σ²f - A, AxB, B, AxC, BxC, C
9375 1 0
15 2
3 0 9 0.1 .000001 0.028 0.014 0.031 0.095 !GP         #σ²fr - A, AxB, B, AxC, BxC, C
375 0 0
```

Note:
1. 18 different components of variance and covariance are estimated by this model.
2. A predigree file ('trees.ped') was used.
3. Data held in file den19-22.dat.
4. Trait A is the primary trait of interest, traits B and C are covariates.

Appendix 3.11: Example of an (edited) *.asr* output file giving calculated variance components following trivariate analysis of ring-groupings including DM16 and DN17 as covariates.

```
 ASREML Sat Jul 27 15:37:07 1996 analysis of garcrogo 3 height, diameter
den16-19.asr
 A-inverse retrieved from ainverse.bin
 PEDIGREE [trees.ped ] has 11400 animals, 22650 Non zero elements
 Multivariate analysis of DN19-22      to DN17
  Data being read from den19-22.dat
  Model term      Size Type      COL  Minimum      Mean         Maximum    # zero
   1 id          11400 Direct      1  151.00       5459.4       11325.          0.
   2 sire            1 Covariate   2  1.0000       71.288       149.00          0.
   3 dam             1 Covariate   3 0.10000E+25 0.00000E+00-0.10000E+25 9375.
   4 rep             3 Factor      4  1.0000       2.0000       3.0000          0.
   5 plot          375 Factor      5  1.0000       188.00       375.00          0.
   6 tree           25 Factor      6  1.0000       13.000       25.000          0.
   7 DN19-22         1 Variate     7 -2.4032      0.36926E-07  4.1150       8783.
   8 DM16            1 Covariate   8 -3.4627      0.52930E-06  3.6694        169.
   9 DN17            1 Covariate   9 -3.0092     -0.57258E-05  3.9484        609.
  10 Trait           3 Traits/Variat
  11 Tra.rep         9 Interaction 10 Trait :     3    4 rep        :     3
  12 Tr_1.id     11400 Conditional 10 Trait :     1    1 id         :11400
  13 Tr_2.id     11400 Conditional 10 Trait :     2    1 id         :11400
  14 Tr_3.id     11400 Conditional 10 Trait :     3    1 id         :11400
  15 Tr_1.plot     375 Conditional 10 Trait :     1    5 plot       :  375
  16 Tr_2.plot     375 Conditional 10 Trait :     2    5 plot       :  375
  17 Tr_3.plot     375 Conditional 10 Trait :     3    5 plot       :  375
       9375 records read,        9375 records retained
  9375  identity
     3  Unstruct    0.58    0.00    0.83    0.00    0.00    0.55
     3  Unstruct    0.32    0.00    0.13    0.00    0.00    0.32
  9375  identity
 Structure of Tr_1.id      has 34200 levels defined
     3  Unstruct    0.10    0.00    0.03    0.01    0.03    0.10
   375  identity
 Structure of Tr_1.plot    has  1125 levels defined
  Forming        35335 equations:            10 dense
 Initial updates will be shrunk by factor    0.100
 LogL=-13128.1     S2=  1.000     28116 df   1.00000   0.58000   0.00010
     0.83000   0.00100   0.00100   0.55000   0.32000   0.00001   0.13000
   0.00001   0.00001   0.32000   0.10000   0.00000   0.02800   0.01400
   0.03100   0.09500
```

(16 iteration edited out)

```
 Final parameter values                          1.00000   0.58250  -0.27986
     0.82991  -0.05971   0.40722   0.55239   0.32337  -0.16380   0.13067
  -0.48911   0.16234   0.40045   0.05712  -0.00221   0.02860   0.01040
   0.02894   0.09455

   Source       Model  terms     Gamma      Component    Stnd error
   Residual   Unstruct      3  0.582497      0.582497      0.104566
   Residual   Unstruct      3 -0.279863     -0.279863      0.535429E-01
   Residual   Unstruct      3  0.829908      0.829908      0.258426E-01
   Residual   Unstruct      3 -0.597071E-01 -0.597071E-01  0.645961E-01
   Residual   Unstruct      3  0.407223      0.407223      0.313667E-01
   Residual   Unstruct      3  0.552386      0.552386      0.568889E-01
   Residual   Unstruct      3  0.323371      0.323371      0.119073
   Residual   Unstruct      3 -0.163797     -0.163797      0.497887E-01
   Residual   Unstruct      3  0.130673      0.130673      0.289919E-01
   Residual   Unstruct      3 -0.489106     -0.489106      0.737420E-01
   Residual   Unstruct      3  0.162339      0.162339      0.388847E-01
   Residual   Unstruct      3  0.400450      0.400450      0.736677E-01
  Tr_1.plot   Unstruct      3  0.571159E-01  0.571159E-01  0.332425E-01
  Tr_1.plot   Unstruct      3 -0.220645E-02 -0.220645E-02  0.124314E-01
  Tr_1.plot   Unstruct      3  0.285969E-01  0.285969E-01  0.599726E-02
  Tr_1.plot   Unstruct      3  0.103988E-01  0.103988E-01  0.169758E-01
```

Appendix 3.11 (continued)

```
 Tr_1.plot    Unstruct      3  0.289368E-01  0.289368E-01  0.674419E-02
 Tr_1.plot    Unstruct      3  0.945534E-01  0.945534E-01  0.117284E-01
Variance of Variance components
 0.109340E-01
-0.313902E-02  0.286684E-02
 0.338573E-03 -0.455271E-03  0.667842E-03
-0.281146E-02  0.208646E-02 -0.436860E-03  0.417266E-02
 0.465195E-03 -0.503958E-03  0.596161E-03 -0.828776E-03  0.983867E-03
 0.788885E-03 -0.606079E-03  0.562814E-03 -0.147354E-02  0.135025E-02  0.323635E-02
-0.106708E-01  0.249856E-02 -0.402407E-03  0.270088E-02 -0.589734E-03 -0.102855E-02
 0.141784E-01
 0.249176E-02 -0.186794E-02  0.494006E-03 -0.168044E-02  0.603928E-03  0.764850E-03
-0.330267E-02  0.247892E-02
-0.402409E-03  0.494114E-03 -0.630422E-03  0.518077E-03 -0.646564E-03 -0.665813E-03
 0.536497E-03 -0.658599E-03  0.840528E-03
 0.279397E-02 -0.171343E-02  0.517510E-03 -0.405479E-02  0.102246E-02  0.188286E-02
-0.372433E-02  0.228378E-02 -0.689930E-03  0.543788E-02
-0.590297E-03  0.604713E-03 -0.646648E-03  0.102579E-02 -0.113409E-02 -0.164591E-02
 0.786856E-03 -0.805151E-03  0.862077E-03 -0.136301E-02  0.151202E-02
-0.103112E-02  0.767629E-03 -0.665924E-03  0.188941E-02 -0.164587E-02 -0.407011E-02
 0.137055E-02 -0.101918E-02  0.887762E-03 -0.250986E-02  0.219452E-02  0.542693E-02
 0.571493E-03 -0.363850E-04  0.121362E-05  0.454784E-04 -0.189761E-06 -0.142860E-05
-0.136473E-02  0.110592E-03 -0.364458E-05 -0.444071E-06 -0.104438E-05  0.124703E-05
 0.110506E-02
-0.733586E-04  0.105899E-03 -0.619775E-05  0.693364E-04 -0.166767E-05  0.135946E-05
 0.151528E-03 -0.204673E-03  0.128989E-04 -0.135585E-03  0.502702E-05 -0.196482E-06
-0.931750E-04  0.154540E-03
 0.104341E-05 -0.620242E-05  0.277203E-04 -0.539738E-05  0.225142E-04  0.179422E-04
-0.344386E-05  0.129357E-04 -0.475808E-04  0.984869E-05 -0.360797E-04 -0.273818E-04
 0.271149E-05 -0.987090E-05  0.359671E-04
 0.498465E-05  0.819166E-04 -0.542278E-05  0.248453E-03 -0.705208E-05  0.175751E-05
 0.178340E-04 -0.136328E-03  0.987158E-05 -0.383180E-03  0.127667E-04  0.923833E-06
 0.473302E-05  0.100034E-03 -0.750700E-05  0.288178E-03
-0.949350E-06 -0.187311E-05  0.226368E-04 -0.756680E-05  0.402416E-04  0.488495E-04
-0.929685E-08  0.527707E-05 -0.362422E-04  0.131129E-04 -0.604870E-04 -0.709506E-04
 0.118729E-06 -0.397115E-05  0.272851E-04 -0.983086E-05  0.454841E-04
-0.701590E-06  0.886652E-06  0.180907E-04  0.140320E-05  0.488928E-04  0.130167E-03
 0.143656E-07  0.547013E-06 -0.275786E-04  0.111286E-05 -0.710836E-04 -0.183269E-03
 0.133946E-06 -0.440168E-06  0.207081E-04 -0.895443E-06  0.533416E-04  0.137555E-03
            Solution       Standard Error    T-value     T-prev
 11 Tra.rep         9        31.25
           1   0.164676       0.736339E-01      2.24
           2   0.628949E-01   0.756113E-01      0.83     -1.07
           3   0.855541E-01   0.752068E-01      1.14      0.23
           4   0.572778E-01   0.281533E-01      2.03     -0.34
           5   0.971924E-01   0.281558E-01      3.45      1.22
           6  -0.150222       0.281583E-01     -5.33     -7.59
           7   0.820008E-02   0.429078E-01      0.19      3.56
           8  -0.277327       0.429511E-01     -6.46     -6.25
           9   0.789291E-01   0.429841E-01      1.84      7.79
Finished: Sat Jul 27 16:08:14 1996   LogL Converged
```

Note:
1. Variance components calculated for RG19-22.
2. This model required 17 iterations to converge.

Appendix 3.12: **Example of *.pin* file used in the calculation of (1) single-tree and (2) family-mean heritability following trivariate analysis including DM16 and DN17 as covariates.**

1. Single tree heritabilities:

```
#           Residual                  Dam                   Plot
#          A AB B AC BC C   A AB B AC BC C   A AB B AC BC C
P phenA    1 0 0 0 0 0      1 0 0 0 0 0      1 0 0 0 0 0
P phenAB   0 1 0 0 0 0      0 1 0 0 0 0      0 1 0 0 0 0 0
P phenB    0 0 1 0 0 0      0 0 1 0 0 0      0 0 1 0 0 0 0 0
P phenAC   0 0 0 1 0 0      0 0 0 1 0 0      0 0 0 1 0 0 0 0 0
P phenBC   0 0 0 0 1 0      0 0 0 0 1 0      0 0 0 0 1 0 0 0 0 0
P phenC    0 0 0 0 0 1      0 0 0 0 0 1      0 0 0 0 0 1 0 0 0 0

P damA     0 0 0 0 0 0      1 0 0 0 0 0      0 0 0 0 0 0 0 0 0 0 0
P damAB    0 0 0 0 0 0      0 1 0 0 0 0      0 0 0 0 0 0 0 0 0 0 0 0
P damB     0 0 0 0 0 0      0 0 1 0 0 0      0 0 0 0 0 0 0 0 0 0 0 0 0
P damAC    0 0 0 0 0 0      0 0 0 1 0 0      0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damBC    0 0 0 0 0 0      0 0 0 0 1 0      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damC     0 0 0 0 0 0      0 0 0 0 0 1      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

H direct_herit_A  25 19
H direct_herit_B  27 21
H direct_herit_C  30 24
H plot_csqA       13 19
H plot_csqB       15 21
H plot_csqC       18 24

R direct_corr_AB     25 26 27
R direct_corr_AC     25 28 30
R direct_corr_BC     27 29 30
R plot_corr_A        13 14 15
R plot_corr_B        15 17 18
R plot_corr_C        13 16 18
R Phen_corr_AB       19 20 21
R Phen_corr_AC       19 22 24
R Phen_corr_BC       21 23 24
```

2. Family heritabilities:

```
#           Residual                  Dam                   Plot
#          A AB B AC BC C   A AB B AC BC C   A AB B AC BC C
P phenA    0.3333 0 0 0 0 0     1 0 0 0 0 0      0.06667 0 0 0 0 0
P phenAB   0 0.3333 0 0 0 0     0 1 0 0 0 0      0 0.06667 0 0 0 0 0
P phenB    0 0 0.3333 0 0 0     0 0 1 0 0 0      0 0 0.06667 0 0 0 0 0
P phenAC   0 0 0 0.3333 0 0     0 0 0 1 0 0      0 0 0 0.06667 0 0 0 0 0
P phenBC   0 0 0 0 0.3333 0     0 0 0 0 1 0      0 0 0 0 0.06667 0 0 0 0 0
P phenC    0 0 0 0 0 0.3333     0 0 0 0 0 1      0 0 0 0 0 0.06667 0 0 0 0 0

P damA     0 0 0 0 0 0      1 0 0 0 0 0      0 0 0 0 0 0 0 0 0 0 0
P damAB    0 0 0 0 0 0      0 1 0 0 0 0      0 0 0 0 0 0 0 0 0 0 0 0
P damB     0 0 0 0 0 0      0 0 1 0 0 0      0 0 0 0 0 0 0 0 0 0 0 0 0
P damAC    0 0 0 0 0 0      0 0 0 1 0 0      0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damBC    0 0 0 0 0 0      0 0 0 0 1 0      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damC     0 0 0 0 0 0      0 0 0 0 0 1      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

H direct_herit_A  25 19
H direct_herit_B  27 21
H direct_herit_C  30 24
H plot_csqA       13 19
H plot_csqB       15 21
H plot_csqC       18 24

R direct_corr_AB     25 26 27
R direct_corr_AC     25 28 30
R direct_corr_BC     27 29 30
R plot_corr_A        13 14 15
R plot_corr_B        15 17 18
R plot_corr_C        13 16 18
R Phen_corr_AB       19 20 21
R Phen_corr_AC       19 22 24
R Phen_corr_BC       21 23 24
```

Note: 1. As well as heritability, this file calculates the phenotypic (Phen.corr) and genetic correlations (direct_corr) between the primary trait (ring-grouping) and the DM16 and DN17 covariates.

Appendix 3.13: Example of *.pvs* output file generated in the calculation of heritabilities using trivariate analysis including DM16 and DN17 as covariates.

```
 19 phenA         0.9630      0.8347E-03 -0.6768E-03 -0.6262E-04 -0.6510E-04
                 -0.1247E-03 -0.2411E-03  0.2143E-02 -0.7003E-03  0.1304E-03
                 -0.9308E-03  0.1955E-03  0.3407E-03  0.3118E-03 -0.1501E-04
                  0.3110E-06  0.2755E-04 -0.8399E-06 -0.5533E-06  0.3289E-02
 20 phenAB       -0.4459     -0.7206E-03  0.1105E-02  0.3254E-04  0.4754E-03
                  0.9830E-04  0.1601E-03 -0.6526E-03  0.4063E-03 -0.1516E-03
                  0.4348E-03 -0.1954E-03 -0.2517E-03 -0.1897E-04  0.5577E-04
                 -0.3138E-05  0.4562E-04 -0.5672E-06  0.9935E-06 -0.1392E-02
                  0.1567E-02
 21 phenB         0.9892     -0.6279E-04  0.3264E-04  0.6514E-04  0.7582E-04
                 -0.2789E-04 -0.8506E-04  0.1306E-03 -0.1517E-03  0.1625E-03
                 -0.1626E-03  0.1793E-03  0.1945E-03  0.2805E-06 -0.3170E-05
                  0.1611E-04 -0.3058E-05  0.1368E-04  0.1122E-04  0.6813E-04
                 -0.1222E-03  0.2438E-03
 22 phenAC       -0.5384     -0.1251E-04  0.4549E-03  0.7523E-04  0.3663E-03
                  0.1866E-03  0.4111E-03 -0.1006E-02  0.4670E-03 -0.1620E-03
                  0.9999E-03 -0.3245E-03 -0.6195E-03  0.4977E-04  0.3379E-04
                 -0.3056E-05  0.1535E-03 -0.4285E-05  0.1621E-05 -0.9684E-03
                  0.9557E-03 -0.8981E-04  0.1520E-02
 23 phenBC        0.5985     -0.1261E-03  0.9888E-04 -0.2785E-04  0.1894E-03
                 -0.1100E-03 -0.2468E-03  0.1971E-03 -0.1959E-03  0.1793E-03
                 -0.3274E-03  0.3174E-03  0.4777E-03 -0.1115E-05 -0.6118E-06
                  0.1372E-04 -0.4116E-05  0.2524E-04  0.3115E-04  0.6995E-04
                 -0.9768E-04  0.1651E-03 -0.1421E-03  0.2327E-03
 24 phenC         1.047      -0.2429E-03  0.1624E-03 -0.8502E-04  0.4173E-03
                 -0.2467E-03 -0.7036E-03  0.3420E-03 -0.2538E-03  0.1944E-03
                 -0.6259E-03  0.4775E-03  0.1174E-02 -0.4762E-07  0.7228E-06
                  0.1127E-04  0.1786E-05  0.3124E-04  0.8445E-04  0.9903E-04
                 -0.9062E-04  0.1206E-03 -0.2068E-03  0.2620E-03  0.5544E-03
 25 damA          0.3234     -0.1067E-01  0.2499E-02 -0.4024E-03  0.2701E-02
                 -0.5897E-03 -0.1029E-02  0.1418E-01 -0.3303E-02  0.5365E-03
                 -0.3724E-02  0.7869E-03  0.1371E-02 -0.1365E-02  0.1515E-03
                 -0.3444E-05  0.1783E-04 -0.9297E-08  0.1437E-07  0.2143E-02
                 -0.6526E-03  0.1306E-03 -0.1006E-02  0.1971E-03  0.3420E-03
                  0.1418E-01
 26 damAB        -0.1638      0.2492E-02 -0.1868E-02  0.4940E-03 -0.1680E-02
                  0.6039E-03  0.7649E-03 -0.3303E-02  0.2479E-02 -0.6586E-03
                  0.2284E-02 -0.8052E-03 -0.1019E-02  0.1106E-03 -0.2047E-03
                  0.1294E-04 -0.1363E-03  0.5277E-05  0.5470E-06 -0.7003E-03
                  0.4063E-03 -0.1517E-03  0.4670E-03 -0.1959E-03 -0.2538E-03
                 -0.3303E-02  0.2479E-02
 27 damB          0.1307     -0.4024E-03  0.4941E-03 -0.6304E-03  0.5181E-03
                 -0.6466E-03 -0.6658E-03  0.5365E-03 -0.6586E-03  0.8405E-03
                 -0.6899E-03  0.8621E-03  0.8878E-03 -0.3645E-05  0.1290E-04
                 -0.4758E-04  0.9872E-05 -0.3624E-04 -0.2758E-04  0.1304E-03
                 -0.1516E-03  0.1625E-03 -0.1620E-03  0.1793E-03  0.1944E-03
                  0.5365E-03 -0.6586E-03  0.8405E-03
 28 damAC        -0.4891      0.2794E-02 -0.1713E-02  0.5175E-03 -0.4055E-02
                  0.1022E-02  0.1883E-02 -0.3724E-02  0.2284E-02 -0.6899E-03
                  0.5438E-02 -0.1363E-02 -0.2510E-02 -0.4441E-06 -0.1356E-03
                  0.9849E-05 -0.3832E-03  0.1311E-04  0.1113E-05 -0.9308E-03
                  0.4348E-03 -0.1626E-03  0.9999E-03 -0.3274E-03 -0.6259E-03
                 -0.3724E-02  0.2284E-02 -0.6899E-03  0.5438E-02
 29 damBC         0.1623     -0.5903E-03  0.6047E-03 -0.6466E-03  0.1026E-02
                 -0.1134E-02 -0.1646E-02  0.7869E-03 -0.8052E-03  0.8621E-03
                 -0.1363E-02  0.1512E-02  0.2195E-02 -0.1044E-05  0.5027E-05
                 -0.3608E-04  0.1277E-04 -0.6049E-04 -0.7108E-04  0.1955E-03
                 -0.1954E-03  0.1793E-03 -0.3245E-03  0.3174E-03  0.4775E-03
                  0.7869E-03 -0.8052E-03  0.8621E-03 -0.1363E-02  0.1512E-02
 30 damC          0.4004     -0.1031E-02  0.7676E-03 -0.6659E-03  0.1889E-02
                 -0.1646E-02 -0.4070E-02  0.1371E-02 -0.1019E-02  0.8878E-03
                 -0.2510E-02  0.2195E-02  0.5427E-02  0.1247E-05 -0.1965E-06
                 -0.2738E-04  0.9238E-06 -0.7095E-04 -0.1833E-03  0.3407E-03
                 -0.2517E-03  0.1945E-03 -0.6195E-03  0.4777E-03  0.1174E-02
                  0.1371E-02 -0.1019E-02  0.8878E-03 -0.2510E-02  0.2195E-02
                  0.5427E-02
   direct_herit = damA        /phenA       =        0.3358  0.1189
   direct_herit = damB        /phenB       =        0.1321  0.0286
   direct_herit = damC        /phenC       =        0.3823  0.0648
   plot_csqA    = Tr_1.plot   /phenA       =        0.0593  0.0341
   plot_csqB    = Tr_1.plot   /phenB       =        0.0289  0.0060
   plot_csqC    = Tr_1.plot   /phenC       =        0.0903  0.0108
   direct_corr_ = damAB   /SQR[damA    *damB    ]= -0.7968  0.1814
   direct_corr_ = damAC   /SQR[damA    *damC    ]= -0.9500  0.2507
   direct_corr_ = damBC   /SQR[damB    *damC    ]=  0.7097  0.0785
   plot_corr_A  = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]= -0.0546  0.3037
   plot_corr_B  = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.5565  0.0797
   plot_corr_C  = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.1415  0.2345
   Phen_corr_AB = phenAB  /SQR[phenA   *phenB   ]= -0.4568  0.0334
   Phen_corr_AC = phenAC  /SQR[phenA   *phenC   ]= -0.5361  0.0342
   Phen_corr_BC = phenBC  /SQR[phenB   *phenC   ]=  0.5880  0.0083
```

Note: 1. In this example h_i^2 for trait A = 0.3358 SE 0.1189, $r_{A_{AB}}$ = -0.7968 SE 0.1814; $r_{P_{AB}}$ = -0.4568 SE 0.0334.

Appendix 3.14: A sample of the pedigree file (trees.*ped*) used by the ASReml software package to assist in the estimation of variance and covariance components.

```
  1     0     0     4001
  2     0     0     4002
  3     0     0     4003
  4     0     0     4004
  5     0     0     4005
  6     0     0     4006
  7     0     0     4007
  8     0     0     4008
  9     0     0     4009
 10     0     0     4010
(lines 11-144 edited out)
145     0     0     4145
146     0     0     4146
147     0     0     4147
148     0     0     4148
149     0     0     4149
150     0     0     4150

151     1     0     4001     1      1
152     1     0     4001     1      2
153     1     0     4001     1      3
154     1     0     4001     1      4
155     1     0     4001     1      5
156     1     0     4001     1      6
157     1     0     4001     1      7
158     1     0     4001     1      8
159     1     0     4001     1      9
160     1     0     4001     1     10
161     1     0     4001     1     11
162     1     0     4001     1     12
163     1     0     4001     1     13
164     1     0     4001     1     14
165     1     0     4001     1     15
166     1     0     4001     1     16
167     1     0     4001     1     17
168     1     0     4001     1     18
169     1     0     4001     1     19
170     1     0     4001     1     20
171     1     0     4001     1     21
172     1     0     4001     1     22
173     1     0     4001     1     23
174     1     0     4001     1     24
175     1     0     4001     1     25
176     1     0     4001     2      1
177     1     0     4001     2      2
178     1     0     4001     2      3
179     1     0     4001     2      4
180     1     0     4001     2      5
181     1     0     4001     2      6
182     1     0     4001     2      7
183     1     0     4001     2      8
184     1     0     4001     2      9
185     1     0     4001     2     10
186     1     0     4001     2     11
187     1     0     4001     2     12
188     1     0     4001     2     13
189     1     0     4001     2     14
190     1     0     4001     2     15
191     1     0     4001     2     16
192     1     0     4001     2     17
193     1     0     4001     2     18
```

Appendix 3.14 (continued)

194	1	0	4001	2	19
195	1	0	4001	2	20
196	1	0	4001	2	21
197	1	0	4001	2	22
198	1	0	4001	2	23
199	1	0	4001	2	24
200	1	0	4001	2	25

(lines 201-11375 edited out)

11376	150	0	4150	3	1
11377	150	0	4150	3	2
11378	150	0	4150	3	3
11379	150	0	4150	3	4
11380	150	0	4150	3	5
11381	150	0	4150	3	6
11382	150	0	4150	3	7
11383	150	0	4150	3	8
11384	150	0	4150	3	9
11385	150	0	4150	3	10
11386	150	0	4150	3	11
11387	150	0	4150	3	12
11388	150	0	4150	3	13
11389	150	0	4150	3	14
11390	150	0	4150	3	15
11391	150	0	4150	3	16
11392	150	0	4150	3	17
11393	150	0	4150	3	18
11394	150	0	4150	3	19
11395	150	0	4150	3	20
11396	150	0	4150	3	21
11397	150	0	4150	3	22
11398	150	0	4150	3	23
11399	150	0	4150	3	24
11400	150	0	4150	3	25

Note:
1. The actual file consists of 11400 lines.
2. Many lines have been edited out here.
3. Each tree has an identification number (1-11,400).
4. The description of each column (reading left to right) is as follows:
   - i.d. number
   - female parent (0 is unknown, 1-150 if known)
   - male parent (0 if unknown)
   - description of genetic unit in the data set
   - replicate number
   - tree number
5. The first 150 lines relate to the ortets at South Stome. In all cases female and male parents were unknown and there was no plot structure.
6. Line 151-11400 relate to the trees in the 'Main Study' at Garcrogo. Here, female parent was known, but male parent was not. There were 3 replicates and 25 trees/plot.

Appendix 3.15. List of starting values used in trivariate analysis including DM16 and DN17 as covariates.

```
RG6-9

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG7-10

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG8-11

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG10-13

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG12-15

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG16-19

3 0 9 0.73394  -0.48318  0.829905 -0.194675 0.408455 0.572605 !GP
3 0 9 0.254515  0.120095 0.130675  0.29231  0.160805 0.372195 !GP
3 0 9 0.025795 -0.01448  0.0286  -0.00184  0.02892  0.09453  !GP

RG18-21

3 0 9 0.58 .0001  .83  0.001  0.001  0.55  !GP
3 0 9 0.32 .00001  0.13  0.00001  0.000001  0.32  !GP
3 0 9 0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG19-22

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.013  0.095  !GP

RG8-15

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP

RG8-22

3  0  9  .58  .0001  .83  0.001  0.001  0.55  !GP
3  0  9  0.32  .00001  0.13  0.00001  0.00001  0.32  !GP
3  0  9  0.1  .000001  0.028  0.014  0.031  0.095  !GP
```

Appendix 3.16: Example of *.as* input file used in the calculation of genetic and phenotypic correlations using quadrivariate analysis of density across ring-groupings involving DM16 and DN17 as covariates.

```
Analysis of garcrogo 3 height data
1   id       1     -1   0
2   sire     1      0 150  # coded 1 to 150
3   dam      1      0 9375 # open pollinated
4   rep      1      3  # coded 1 to 3
5   plot     1    375  # coded 1 to 375
6   tree     1     25  # coded 1 to 25
7   RG12-15  1      1  !M-9 !P-10      #Trait A
8   RG19-22  1      1  !M-9            #Trait B
9   DM16     1      1  !M-9            #Trait C
10  DN17     1      1  !M-9            #Trait D
11  Trait    0      1
trees.ped
~/den9121619.dat
7 1 1 0 19            # analyse HT01, normal distr, link, filter maxit
 -9
11.4 11/1 11/5
0 .1 .1 .1 .1 .1 .1 .1 .1
1 2 2 !STEP 0.1
9375 0 0
4 0 9 0.6703 0.29895 0.61317 -0.43312 -0.27674 0.82991 -0.22011 -0.05981 0.40811
0.5711 !GP
13 2
4 0 9 0.31149 0.27584 0.27066 -0.14337 -0.15789 0.13068 -0.32454 -0.30253 0.16119
0.37468 !GP
9375 1 0
17 2
4 0 9 0.05721 0.0354 0.05809 -0.02719 -0.00401 0.02857 -0.03426 0.0122 0.02891
0.09454 !GP
375 0 0
```

Note:
1. Genetic and phenotypic correlations are estimated for RG12-15 with the breeding goal of RG19-22.
2. A pedigree file (trees.*ped*) will be used (see Appendix 3.14).
3. Data held in file ~/den9121619.dat.
4. 30 different components of variance and covariance are estimated by this model:

   A, AxB, B, AxC, BxC, C, AxD, BxD, CxD, D for σ^2_e, σ^2_f and σ^2_{fr}.

Appendix 3.17: Example of *.asr* output file following quadrivariate analysis to generate variance and covariances involved in the estimation of genetic and phenotypic correlations. DM16 and DN17 have been used as covariates.

```
ASREML Thu Aug  8 12:50:18 1996 analysis of garcrogo 3 height data quadcollped.asr

A-inverse retrieved from ainverse.bin
PEDIGREE [trees.ped ] has 11400 animals, 22650 Non zero elements
Multivariate analysis of RG12-15        to DN17
 Data being read from ~/den9121619.dat
 Model term      Size Type      COL  Minimum      Mean         Maximum    # zero
  1 id          11400 Direct      1  151.00       5459.4       11325.         0.
  2 sire            1 Covariate   2  1.0000       71.288       149.00         0.
  3 dam             1 Covariate   3 0.10000E+25 0.00000E+00-0.10000E+25 9375.
  4 rep             3 Factor      4  1.0000       2.0000       3.0000         0.
  5 plot          375 Factor      5  1.0000       188.00       375.00         0.
  6 tree           25 Factor      6  1.0000       13.000       25.000         0.
  7 RG12-15         1 Variate     7 -2.4962      0.14644E-06  3.2856      8689.
  8 RG19-22         1 Covariate   8 -2.4032      0.36926E-07  4.1150      8783.
  9 DM16            1 Covariate   9 -3.4627      0.52930E-06  3.6694       169.
 10 DN17            1 Covariate  10 -3.0092     -0.57258E-05  3.9484       609.
 11 Trait           4 Traits/Variat
 12 Tra.rep        12 Interaction 11 Trait :     4     4 rep        :     3
 13 Tr_1.id     11400 Conditional 11 Trait :     1     1 id         :11400
 14 Tr_2.id     11400 Conditional 11 Trait :     2     1 id         :11400
 15 Tr_3.id     11400 Conditional 11 Trait :     3     1 id         :11400
 16 Tr_4.id     11400 Conditional 11 Trait :     4     1 id         :11400
 17 Tr_1.plot     375 Conditional 11 Trait :     1     5 plot       :  375
 18 Tr_2.plot     375 Conditional 11 Trait :     2     5 plot       :  375
 19 Tr_3.plot     375 Conditional 11 Trait :     3     5 plot       :  375
 20 Tr_4.plot     375 Conditional 11 Trait :     4     5 plot       :  375
      9375 records read,        9375 records retained
 9375  identity
    4  Unstruct    0.67    0.30    0.61   -0.43   -0.28    0.83   -0.22   -0.06
  0.41    0.57
    4  Unstruct    0.31    0.28    0.27   -0.14   -0.16    0.13   -0.32   -0.30
  0.16    0.37
 9375  identity
Structure of Tr_1.id      has 45600 levels defined
    4  Unstruct    0.06    0.04    0.06   -0.03    0.00    0.03   -0.03    0.01
  0.03    0.09
  375  identity
Structure of Tr_1.plot    has  1500 levels defined
 Forming        47113 equations:           13 dense
Initial updates will be shrunk by factor    0.100
LogL=-13296.9     S2=  1.000     37488 df   1.00000   0.67030   0.29895
    0.61317  -0.43312  -0.27674   0.82991  -0.22011  -0.05981   0.40811
  0.57110   0.31149   0.27584   0.27066  -0.14337  -0.15789   0.13068
 -0.32454  -0.30253   0.16119   0.37468   0.05721   0.03540   0.05809
 -0.02719  -0.00401   0.02857  -0.03426   0.01220   0.02891   0.09454
```

(10 iterations have been edited out)

```
Final parameter values                          1.00000   0.66927   0.29757
    0.61029  -0.43314  -0.27698   0.82991  -0.21853  -0.05767   0.40805
  0.56903   0.31294   0.32262   0.27492  -0.14334  -0.15751   0.13068
 -0.38424  -0.48446   0.16128   0.37746   0.05721   0.03536   0.05800
 -0.02719  -0.00398   0.02857  -0.03426   0.01221   0.02891   0.09454
  Source       Model  terms     Gamma      Component     Stnd error
  Residual   Unstruct      4  0.669267      0.669267      0.913702E-01
  Residual   Unstruct      4  0.297574      0.297574      0.781421E-01
  Residual   Unstruct      4  0.610295      0.610295      0.970435E-01
  Residual   Unstruct      4 -0.433135     -0.433135      0.482840E-01
  Residual   Unstruct      4 -0.276976     -0.276976      0.516655E-01
  Residual   Unstruct      4  0.829915      0.829915      0.258438E-01
```

Appendix 3.17 (continued)

```
   Residual    Unstruct      4 -0.218531      -0.218531       0.599491E-01
   Residual    Unstruct      4 -0.576689E-01 -0.576689E-01   0.605667E-01
   Residual    Unstruct      4  0.408048       0.408048       0.308990E-01
   Residual    Unstruct      4  0.569031       0.569031       0.543859E-01
   Dams        Unstruct      4  0.312940       0.312940       0.101268
   Dams        Unstruct      4  0.322616       0.322616       0.875855E-01
   Dams        Unstruct      4  0.274923       0.274923       0.108248
   Dams        Unstruct      4 -0.143340      -0.143340       0.462950E-01
   Dams        Unstruct      4 -0.157506      -0.157506       0.472885E-01
   Dams        Unstruct      4  0.130679       0.130679       0.289935E-01
   Dams        Unstruct      4 -0.384244      -0.384244       0.697644E-01
   Dams        Unstruct      4 -0.484464      -0.484464       0.679489E-01
   Dams        Unstruct      4  0.161280       0.161280       0.382152E-01
   Dams        Unstruct      4  0.377460       0.377460       0.702331E-01
 Tr_1.plot     Unstruct      4  0.572090E-01   0.572090E-01   0.272466E-01
 Tr_1.plot     Unstruct      4  0.353586E-01   0.353586E-01   0.234992E-01
 Tr_1.plot     Unstruct      4  0.580047E-01   0.580047E-01   0.324925E-01
 Tr_1.plot     Unstruct      4 -0.271877E-01  -0.271877E-01   0.110036E-01
 Tr_1.plot     Unstruct      4 -0.397682E-02  -0.397682E-02   0.121965E-01
 Tr_1.plot     Unstruct      4  0.285689E-01   0.285689E-01   0.599456E-02
 Tr_1.plot     Unstruct      4 -0.342577E-01  -0.342577E-01   0.150543E-01
 Tr_1.plot     Unstruct      4  0.122113E-01   0.122113E-01   0.166916E-01
 Tr_1.plot     Unstruct      4  0.289065E-01   0.289065E-01   0.674116E-02
 Tr_1.plot     Unstruct      4  0.945407E-01   0.945407E-01   0.117243E-01
Variance of Variance components
 0.834851E-02
 0.514432E-02  0.610618E-02
 0.319986E-02  0.556681E-02  0.941745E-02
-0.294185E-02 -0.206761E-02 -0.143104E-02  0.233134E-02
-0.172191E-02 -0.244324E-02 -0.283814E-02  0.137700E-02  0.266932E-02
 0.471389E-03  0.384470E-03  0.316094E-03 -0.549834E-03 -0.441550E-03  0.667901E-03
-0.356504E-02 -0.199473E-02 -0.112779E-02  0.184982E-02  0.107577E-02 -0.513432E-03
```

(The balance of 'Variance of variance components' have been edited out to simplify presentation)

```
            Solution        Standard Error     T-value      T-prev
 12 Tra.rep         12        24.06
          1    0.146884        0.652283E-01       2.25
          2    0.931775E-01    0.651652E-01       1.43       -0.65
          3    0.162744        0.651645E-01       2.50        0.84
          4    0.183684        0.721895E-01       2.54        0.23
          5    0.491103E-01    0.737745E-01       0.67       -1.42
          6    0.713488E-01    0.734500E-01       0.97        0.23
          7    0.572810E-01    0.281498E-01       2.03       -0.17
          8    0.972164E-01    0.281523E-01       3.45        1.23
          9   -0.150214        0.281547E-01      -5.34       -7.59
         10    0.815706E-02    0.423697E-01       0.19        3.59
         11   -0.277335        0.424134E-01      -6.54       -6.25
         12    0.789087E-01    0.424469E-01       1.86        7.79
Finished: Thu Aug  8 13:21:52 1996   LogL Converged
```

Appendix 3.18: Example of *.pin* file used to estimate genetic and phenotypic correlations following quadrivariate analysis including DM16 and DN17 as covariates.

```
#         Residual                          Dam
#       A AB B AC AB C AD BD CD D
P phenA  1 0 0 0 0 0 0 0 0 0  1 0 0 0 0 0 0 0 0 0  1 0 0 0 0 0 0 0 0 0
P phenAB 0 1 0 0 0 0 0 0 0 0  0 1 0 0 0 0 0 0 0 0  0 1 0 0 0 0 0 0 0 0 0
P phenB  0 0 1 0 0 0 0 0 0 0  0 0 1 0 0 0 0 0 0 0  0 0 1 0 0 0 0 0 0 0 0 0
P phenAC 0 0 0 1 0 0 0 0 0 0  0 0 0 1 0 0 0 0 0 0  0 0 0 1 0 0 0 0 0 0 0 0 0
P phenBC 0 0 0 0 1 0 0 0 0 0  0 0 0 0 1 0 0 0 0 0  0 0 0 0 1 0 0 0 0 0 0 0 0 0
P phenC  0 0 0 0 0 1 0 0 0 0  0 0 0 0 0 1 0 0 0 0  0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
P phenAD 0 0 0 0 0 0 1 0 0 0  0 0 0 0 0 0 1 0 0 0  0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
P phenBD 0 0 0 0 0 0 0 1 0 0  0 0 0 0 0 0 0 1 0 0  0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
P phenCD 0 0 0 0 0 0 0 0 1 0  0 0 0 0 0 0 0 0 1 0  0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
P phenD  0 0 0 0 0 0 0 0 0 1  0 0 0 0 0 0 0 0 0 1  0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
P damA   0 0 0 0 0 0 0 0 0 0  1 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damAB  0 0 0 0 0 0 0 0 0 0  0 1 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damB   0 0 0 0 0 0 0 0 0 0  0 0 1 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damAC  0 0 0 0 0 0 0 0 0 0  0 0 0 1 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damBC  0 0 0 0 0 0 0 0 0 0  0 0 0 0 1 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damC   0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 1 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damAD  0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 1 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damBD  0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 1 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damCD  0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 1 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P damD   0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 1  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

H direct_herit_A  41 31     R direct_corr_AB  41 42 43     R Phen_corr_AB   31 32 33
H direct_herit_B  43 33     R direct_corr_AC  41 44 46     R Phen_corr_AC   31 34 36
H direct_herit_C  46 36     R direct_corr_BC  43 45 46     R Phen_corr_BC   33 35 36
H direct_herit_D  50 40     R direct_corr_AD  41 47 50     R Phen_corr_AD   31 37 40
H plot_csqA       21 31     R direct_corr_BD  43 48 50     R Phen_corr_BD   33 38 40
H plot_csqB       23 33     R direct_corr_CD  46 49 50     R Phen_corr_CD   36 39 40
H plot_csqC       26 36     R plot_corr_AB    21 22 23
H plot_csqD       30 40     R plot_corr_AC    21 24 26
                            R plot_corr_BC    23 25 26
                            R plot_corr_AD    21 27 30
                            R plot_corr_BD    23 28 30
                            R plot_corr_CD    26 29 30
```

Appendix 3.19: Example of *.pvs* output file from quadrivariate analysis including DM16 and DN17 as covariates.

```
31 phenA          1.039       0.1135E-02  0.3861E-03  0.5004E-04 -0.8047E-03
                 -0.3084E-03 -0.5232E-04 -0.1993E-03  0.5148E-04 -0.1595E-03
                 -0.3490E-03  0.1670E-02  0.1203E-02  0.8522E-03 -0.5474E-03
                 -0.3805E-03  0.1542E-03 -0.9762E-03 -0.6754E-03  0.2850E-03
                  0.5259E-03  0.2551E-03  0.1359E-03  0.7241E-04 -0.6787E-04
                 -0.4037E-04  0.1032E-04 -0.7896E-04 -0.4561E-04  0.1167E-04
                  0.1303E-04  0.3060E-02
32 phenAB         0.6555      0.3953E-03  0.6730E-03  0.4951E-03 -0.3877E-03
                 -0.6406E-03 -0.5799E-04 -0.9175E-06 -0.1738E-03 -0.1285E-03
                 -0.2283E-03  0.1179E-02  0.1243E-02  0.1197E-02 -0.4689E-03
                 -0.4644E-03  0.1391E-03 -0.6326E-03 -0.7206E-03  0.2133E-03
                  0.3323E-03  0.1505E-03  0.1835E-03  0.1521E-03 -0.2989E-04
                 -0.5040E-04  0.3167E-05 -0.1089E-04 -0.4400E-04  0.1036E-05
                 -0.1644E-05  0.1725E-02  0.2099E-02
33 phenB          0.9432      0.5889E-04  0.4842E-03  0.1145E-02 -0.1471E-03
                 -0.6818E-03 -0.5679E-04  0.6522E-04 -0.1525E-03 -0.9314E-04
                 -0.1695E-03  0.8292E-03  0.1191E-02  0.1599E-02 -0.3808E-03
                 -0.5930E-03  0.1209E-03 -0.4096E-03 -0.6407E-03  0.1469E-03
                  0.2386E-03  0.8654E-04  0.1688E-03  0.3080E-03 -0.1247E-04
                 -0.2389E-04  0.5766E-06  0.1292E-04  0.3408E-04 -0.1060E-05
                 -0.2892E-06  0.9746E-03  0.1844E-02  0.3051E-02
34 phenAC        -0.6037     -0.7788E-03 -0.3763E-03 -0.1435E-03  0.7973E-03
                  0.3278E-03  0.1032E-04  0.2947E-03  0.6249E-04  0.9779E-04
                  0.1859E-03 -0.5559E-03 -0.4810E-03 -0.3890E-03  0.3640E-03
                  0.2718E-03 -0.1589E-03  0.4279E-03  0.3246E-03 -0.2339E-03
                 -0.3189E-03 -0.8518E-04 -0.2918E-04 -0.7944E-05  0.4735E-04
                  0.2713E-04 -0.1304E-04  0.4053E-04  0.2184E-04 -0.1288E-04
                 -0.1212E-04 -0.1420E-02 -0.8864E-03 -0.5404E-03  0.1209E-02
35 phenBC        -0.4385     -0.2997E-03 -0.6206E-03 -0.6865E-03  0.3277E-03
                  0.1085E-02  0.2941E-04  0.8753E-04  0.4928E-03  0.8190E-04
                  0.1253E-03 -0.3811E-03 -0.4735E-03 -0.5911E-03  0.2718E-03
                  0.3527E-03 -0.1453E-03  0.2827E-03  0.3634E-03 -0.1660E-03
                 -0.1974E-03 -0.4847E-04 -0.6131E-04 -0.2099E-04  0.2713E-04
                  0.5439E-04 -0.3604E-05  0.1910E-04  0.4428E-04 -0.2672E-06
                  0.1770E-05 -0.7292E-03 -0.1155E-02 -0.1299E-02  0.6266E-03
                  0.1492E-02
36 phenC          0.9892     -0.5236E-04 -0.5811E-04 -0.5680E-04  0.1029E-04
                  0.2959E-04  0.6509E-04  0.6750E-04  0.7171E-04 -0.2729E-04
                 -0.8367E-04  0.1543E-03  0.1392E-03  0.1209E-03 -0.1589E-03
                 -0.1454E-03  0.1626E-03 -0.1727E-03 -0.1558E-03  0.1786E-03
                  0.1926E-03  0.1025E-04  0.3136E-05  0.5437E-06 -0.1298E-04
                 -0.3654E-05  0.1608E-04 -0.1074E-04 -0.3430E-05  0.1366E-04
                  0.1120E-04  0.1122E-03  0.8424E-04  0.6464E-04 -0.1616E-03
                 -0.1195E-03  0.2438E-03
37 phenAD        -0.6370     -0.1350E-03  0.5062E-04  0.1006E-03  0.2758E-03
                  0.7300E-04  0.6741E-04  0.1518E-03 -0.6004E-04  0.1870E-03
                  0.4673E-03 -0.1038E-02 -0.6931E-03 -0.4542E-03  0.4545E-03
                  0.3006E-03 -0.1726E-03  0.9325E-03  0.6362E-03 -0.3606E-03
                 -0.7455E-03 -0.8200E-04 -0.1854E-05  0.2222E-04  0.3288E-04
                  0.1571E-04 -0.1080E-04  0.1180E-03  0.6366E-04 -0.2112E-04
                 -0.3320E-04 -0.1254E-02 -0.6444E-03 -0.3314E-03  0.7631E-03
                  0.3893E-03 -0.1160E-03  0.1202E-02
38 phenBD        -0.5299      0.7821E-04 -0.1304E-03 -0.9416E-04  0.5533E-04
                  0.4727E-03  0.7093E-04 -0.5406E-04  0.4674E-03  0.1568E-03
                  0.2998E-03 -0.7005E-03 -0.7662E-03 -0.7211E-03  0.3352E-03
                  0.3946E-03 -0.1550E-03  0.6304E-03  0.8077E-03 -0.2795E-03
                 -0.4596E-03 -0.4720E-04 -0.4188E-04  0.5614E-04  0.1843E-04
                  0.3321E-04 -0.3414E-05  0.6351E-04  0.1482E-03 -0.4345E-05
                  0.3861E-05 -0.6695E-03 -0.9384E-03 -0.7591E-03  0.4089E-03
                  0.9005E-03 -0.8753E-04  0.6398E-03  0.1423E-02
39 phenCD         0.5982     -0.1596E-03 -0.1289E-03 -0.9328E-04  0.9761E-04
                  0.8272E-04 -0.2726E-04  0.1878E-03  0.1607E-03 -0.1004E-03
                 -0.2259E-03  0.2853E-03  0.2139E-03  0.1474E-03 -0.2338E-03
```

Appendix 3.19 (continued)

```
                -0.1667E-03  0.1785E-03 -0.3616E-03 -0.2836E-03  0.3046E-03
                 0.4497E-03  0.1147E-04  0.7059E-06 -0.1399E-05 -0.1284E-04
                -0.3229E-06  0.1370E-04 -0.2090E-04 -0.4251E-05  0.2521E-04
                 0.3112E-04  0.1372E-03  0.8577E-04  0.5269E-04 -0.1490E-03
                -0.8433E-04  0.1649E-03 -0.1947E-03 -0.1271E-03  0.2294E-03
40 phenD          1.041     -0.3491E-03 -0.2318E-03 -0.1716E-03  0.1859E-03
                 0.1287E-03 -0.8363E-04  0.4680E-03  0.3092E-03 -0.2258E-03
                -0.6114E-03  0.5262E-03  0.3361E-03  0.2403E-03 -0.3188E-03
                -0.2005E-03  0.1925E-03 -0.7464E-03 -0.4691E-03  0.4495E-03
                 0.1050E-02  0.1283E-04 -0.1915E-05  0.5091E-07 -0.1214E-04
                 0.1494E-05  0.1125E-04 -0.3297E-04  0.3955E-05  0.3121E-04
                 0.8440E-04  0.1900E-03  0.1024E-03  0.6875E-04 -0.1451E-03
                -0.7029E-04  0.1201E-03 -0.3113E-03 -0.1559E-03  0.2549E-03
                 0.5233E-03
41 damA           0.3129     -0.7656E-02 -0.5012E-02 -0.3292E-02  0.2274E-02
                 0.1491E-02 -0.5405E-03  0.3500E-02  0.2349E-02 -0.9394E-03
                -0.1669E-02  0.1026E-01  0.6694E-02  0.4392E-02 -0.3041E-02
                -0.1989E-02  0.7205E-03 -0.4752E-02 -0.3169E-02  0.1252E-02
                 0.2225E-02 -0.9296E-03 -0.5026E-03 -0.2706E-03  0.2116E-03
                 0.1170E-03 -0.2570E-04  0.2154E-03  0.1192E-03 -0.2758E-04
                -0.2952E-04  0.1670E-02  0.1179E-02  0.8292E-03 -0.5559E-03
                -0.3811E-03  0.1543E-03 -0.1038E-02 -0.7005E-03  0.2853E-03
                 0.5262E-03  0.1026E-01
42 damAB          0.3226     -0.4990E-02 -0.5746E-02 -0.5373E-02  0.1734E-02
                 0.1900E-02 -0.4483E-03  0.2008E-02  0.2484E-02 -0.6569E-03
                -0.1007E-02  0.6694E-02  0.7671E-02  0.7144E-02 -0.2319E-02
                -0.2542E-02  0.5976E-03 -0.2750E-02 -0.3385E-02  0.8755E-03
                 0.1342E-02 -0.5002E-03 -0.6818E-03 -0.5803E-03  0.1042E-03
                 0.1685E-03 -0.1014E-04  0.4888E-04  0.1347E-03 -0.4656E-05
                 0.1612E-05  0.1203E-02  0.1243E-02  0.1191E-02 -0.4810E-03
                -0.4735E-03  0.1392E-03 -0.6931E-03 -0.7662E-03  0.2139E-03
                 0.3361E-03  0.6694E-02  0.7671E-02
43 damB           0.2749     -0.3272E-02 -0.5342E-02 -0.8822E-02  0.1303E-02
                 0.2197E-02 -0.3746E-03  0.1169E-02  0.1755E-02 -0.4392E-03
                -0.7253E-03  0.4392E-02  0.7144E-02  0.1172E-01 -0.1742E-02
                -0.2932E-02  0.4995E-03 -0.1610E-02 -0.2464E-02  0.5858E-03
                 0.9657E-03 -0.2674E-03 -0.6056E-03 -0.1297E-02  0.4995E-04
                 0.1440E-03 -0.3944E-05 -0.1337E-04 -0.1219E-04  0.7642E-06
                -0.1259E-06  0.8522E-03  0.1197E-02  0.1599E-02 -0.3890E-03
                -0.5911E-03  0.1209E-03 -0.4542E-03 -0.7211E-03  0.1474E-03
                 0.2403E-03  0.4392E-02  0.7144E-02  0.1172E-01
44 damAC         -0.1433      0.2283E-02  0.1746E-02  0.1311E-02 -0.1620E-02
                -0.1097E-02  0.5819E-03 -0.1615E-02 -0.1150E-02  0.7983E-03
                 0.1043E-02 -0.3041E-02 -0.2319E-02 -0.1742E-02  0.2143E-02
                 0.1456E-02 -0.7757E-03  0.2180E-02  0.1544E-02 -0.1064E-02
                -0.1391E-02  0.2110E-03  0.1045E-03  0.5038E-04 -0.1594E-03
                -0.8667E-04  0.3491E-04 -0.1112E-03 -0.5921E-04  0.3205E-04
                 0.2852E-04 -0.5474E-03 -0.4689E-03 -0.3808E-03  0.3640E-03
                 0.2718E-03 -0.1589E-03  0.4545E-03  0.3352E-03 -0.2338E-03
                -0.3188E-03 -0.3041E-02 -0.2319E-02 -0.1742E-02  0.2143E-02
45 damBC         -0.1575      0.1490E-02  0.1916E-02  0.2223E-02 -0.1097E-02
                -0.1687E-02  0.4779E-03 -0.1015E-02 -0.1455E-02  0.5133E-03
                 0.5994E-03 -0.1989E-02 -0.2542E-02 -0.2932E-02  0.1456E-02
                 0.2236E-02 -0.6372E-03  0.1369E-02  0.1979E-02 -0.6843E-03
                -0.7984E-03  0.1181E-03  0.1607E-03  0.1158E-03 -0.8715E-04
                -0.1967E-03  0.1381E-04 -0.5338E-04 -0.1299E-03  0.4287E-05
                -0.1417E-05 -0.3805E-03 -0.4644E-03 -0.5930E-03  0.2718E-03
                 0.3527E-03 -0.1454E-03  0.3006E-03  0.3946E-03 -0.1667E-03
                -0.2005E-03 -0.1989E-02 -0.2542E-02 -0.2932E-02  0.1456E-02
                 0.2236E-02
46 damC          0.1307     -0.5404E-03 -0.4482E-03 -0.3744E-03  0.5817E-03
                 0.4780E-03 -0.6305E-03  0.5982E-03  0.5000E-03 -0.6441E-03
                -0.6602E-03  0.7205E-03  0.5976E-03  0.4995E-03 -0.7757E-03
```

Appendix 3.19 (continued)

```
                -0.6372E-03  0.8406E-03 -0.7975E-03 -0.6656E-03  0.8588E-03
                 0.8802E-03 -0.2591E-04 -0.1037E-04 -0.4259E-05  0.3511E-04
                 0.1382E-04 -0.4754E-04  0.2669E-04  0.1054E-04 -0.3620E-04
                -0.2754E-04  0.1542E-03  0.1391E-03  0.1209E-03 -0.1589E-03
                -0.1453E-03  0.1626E-03 -0.1726E-03 -0.1550E-03  0.1785E-03
                 0.1925E-03  0.7205E-03  0.5976E-03  0.4995E-03 -0.7757E-03
                -0.6372E-03  0.8406E-03
47 damAD        -0.3842      0.3564E-02  0.2069E-02  0.1212E-02 -0.1642E-02
                -0.1035E-02  0.5982E-03 -0.3634E-02 -0.2361E-02  0.1230E-02
                 0.2459E-02 -0.4752E-02 -0.2750E-02 -0.1610E-02  0.2180E-02
                 0.1369E-02 -0.7975E-03  0.4867E-02  0.3149E-02 -0.1640E-02
                -0.3279E-02  0.2125E-03  0.4863E-04 -0.1204E-04 -0.1104E-03
                -0.5169E-04  0.2654E-04 -0.3006E-03 -0.1583E-03  0.4866E-04
                 0.7354E-04 -0.9762E-03 -0.6326E-03 -0.4096E-03  0.4279E-03
                 0.2827E-03 -0.1727E-03  0.9325E-03  0.6304E-03 -0.3616E-03
                -0.7464E-03 -0.4752E-02 -0.2750E-02 -0.1610E-02  0.2180E-02
                 0.1369E-02 -0.7975E-03  0.4867E-02
48 damBD        -0.4845      0.2375E-02  0.2534E-02  0.1851E-02 -0.1160E-02
                -0.1488E-02  0.4993E-03 -0.2354E-02 -0.3440E-02  0.8907E-03
                 0.1398E-02 -0.3169E-02 -0.3385E-02 -0.2464E-02  0.1544E-02
                 0.1979E-02 -0.6656E-03  0.3149E-02  0.4617E-02 -0.1187E-02
                -0.1863E-02  0.1187E-03  0.1301E-03 -0.2759E-04 -0.5930E-04
                -0.1283E-03  0.1053E-04 -0.1591E-03 -0.3694E-03  0.1298E-04
                -0.4039E-05 -0.6754E-03 -0.7206E-03 -0.6407E-03  0.3246E-03
                 0.3634E-03 -0.1558E-03  0.6362E-03  0.8077E-03 -0.2836E-03
                -0.4691E-03 -0.3169E-02 -0.3385E-02 -0.2464E-02  0.1544E-02
                 0.1979E-02 -0.6656E-03  0.3149E-02  0.4617E-02
49 damCD         0.1613     -0.9395E-03 -0.6568E-03 -0.4381E-03  0.7980E-03
                 0.5143E-03 -0.6442E-03  0.1231E-02  0.8952E-03 -0.1095E-02
                -0.1562E-02  0.1252E-02  0.8755E-03  0.5858E-03 -0.1064E-02
                -0.6843E-03  0.8588E-03 -0.1640E-02 -0.1187E-02  0.1460E-02
                 0.2082E-02 -0.2781E-04 -0.5518E-05 -0.8340E-06  0.3218E-04
                 0.4071E-05 -0.3605E-04  0.4874E-04  0.1256E-04 -0.6043E-04
                -0.7101E-04  0.2850E-03  0.2133E-03  0.1469E-03 -0.2339E-03
                -0.1660E-03  0.1786E-03 -0.3606E-03 -0.2795E-03  0.3046E-03
                 0.4495E-03  0.1252E-02  0.8755E-03  0.5858E-03 -0.1064E-02
                -0.6843E-03  0.8588E-03 -0.1640E-02 -0.1187E-02  0.1460E-02

50 damD          0.3775     -0.1669E-02 -0.1010E-02 -0.7271E-03  0.1043E-02
                 0.6031E-03 -0.6603E-03  0.2459E-02  0.1407E-02 -0.1561E-02
                -0.3699E-02  0.2225E-02  0.1342E-02  0.9657E-03 -0.1391E-02
                -0.7984E-03  0.8802E-03 -0.3279E-02 -0.1863E-02  0.2082E-02
                 0.4933E-02 -0.2993E-04  0.6405E-06  0.9980E-08  0.2870E-04
                -0.2059E-05 -0.2735E-04  0.7383E-04 -0.4250E-05 -0.7088E-04
                -0.1831E-03  0.5259E-03  0.3323E-03  0.2386E-03 -0.3189E-03
                -0.1974E-03  0.1926E-03 -0.7455E-03 -0.4596E-03  0.4497E-03
                 0.1050E-02  0.2225E-02  0.1342E-02  0.9657E-03 -0.1391E-02
                -0.7984E-03  0.8802E-03 -0.3279E-02 -0.1863E-02  0.2082E-02
   direct_herit = damA        /phenA       =        0.3011  0.0939
   direct_herit = damB        /phenB       =        0.2915  0.1114
   direct_herit = damC        /phenC       =        0.1321  0.0286
   direct_herit = damD        /phenD       =        0.3626  0.0625
   plot_csqA    = Tr_1.plot   /phenA       =        0.0550  0.0259
   plot_csqB    = Tr_1.plot   /phenB       =        0.0615  0.0340
   plot_csqC    = Tr_1.plot   /phenC       =        0.0289  0.0060
   plot_csqD    = Tr_1.plot   /phenD       =        0.0908  0.0108
   direct_corr_ = damAB   /SQR[damA    *damB    ]=  0.9500  0.1447
   direct_corr_ = damAC   /SQR[damA    *damC    ]= -0.7088  0.1460
   direct_corr_ = damBC   /SQR[damB    *damC    ]= -0.8310  0.1849
   direct_corr_ = damAD   /SQR[damA    *damD    ]= -0.9500  0.1373
   direct_corr_ = damBD   /SQR[damB    *damD    ]= -0.9500  0.3120
   direct_corr_ = damCD   /SQR[damC    *damD    ]=  0.7262  0.0764
   plot_corr_AB = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.6138  0.2616
```

Appendix 3.19 (continued)

```
plot_corr_AC = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]= -0.6725  0.2135
plot_corr_BC = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]= -0.0977  0.2928
plot_corr_AD = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]= -0.4658  0.1844
plot_corr_BD = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.1649  0.2284
plot_corr_CD = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.5562  0.0798
Phen_corr_AB = phenAB  /SQR[phenA   *phenB   ]=  0.6621  0.0251
Phen_corr_AC = phenAC  /SQR[phenA   *phenC   ]= -0.5953  0.0239
Phen_corr_BC = phenBC  /SQR[phenB   *phenC   ]= -0.4539  0.0330
Phen_corr_AD = phenAD  /SQR[phenA   *phenD   ]= -0.6124  0.0238
Phen_corr_BD = phenBD  /SQR[phenB   *phenD   ]= -0.5348  0.0350
Phen_corr_CD = phenCD  /SQR[phenC   *phenD   ]=  0.5895  0.0082
```

Note: 1. Genetic correlaiton of traits A and B (direct_corr) was 0.95 SE 0.1447, phenotypic correlation (Phen_corr) for A and B was 0.6621 SE 0.0251.

Appendix 3.20: Starting values used in various quadrivariate analyses.

```
RG14-17
RG19-22

4 0 9 0.66927 0.29757 0.61029 -0.43314 -0.27698 0.82991 -0.21853 -0.05767 0.40805
0.56903 !GP
4 0 9 0.31294 0.32262 0.27492 -0.14334 -0.15751 0.13068 -0.38424 -0.48446 0.16128
0.37746 !GP
4 0 9 0.05721 0.03536 0.058 -0.0271 -0.00398 0.02857 -0.03426 0.01221 0.02891 0.09454
!GP

RG16-19
RG19-22

4 0 9 0.9497 0.55 0.93 -0.48015 -0.27104 0.529 -0.21778 -0.08327 0.40963 0.59624 !GP
4 0 9 0.05 0.45 0.020704 -0.12159 -0.16392 0.43077 -0.43689 -0.44902 0.15922 0.34022
!GP
4 0 9 0.02579 0.02728 0.0452728 -0.01451 -0.0068 0.02861 -0.00189 0.00607 0.02891
0.094533 !GP

RG18-21
RG19-22

4 0 9 0.635 0.586 0.627 -0.3476 -0.295 0.8295 -0.153 -0.086 0.408 0.5745 !GP
4 0 9 0.311 0.285 0.29 -0.12735 -0.155 0.13045 -0.322 -0.311 0.160 0.369 !GP
4 0 9 0.04514 0.04112 0.04675 -0.01144 -0.00294 0.02862 -0.00192 0.00259 0.02895
0.09457 !GP

RG6-9
RG19-22

4 0 9 0.17 0.041 0.618 -0.284 -0.257 0.8303 -0.02256 -0.09125 0.4005 0.576 !GP
4 0 9 0.674 0.408 0.2741 -0.18525 -0.1835 0.1302 -0.4835 -0.30225 0.16933 0.37 !GP
4 0 9 0.067 0.01654 0.06009 -0.03996 -0.00477 0.02641 -0.04512 0.00992 0.02883
0.09448 !GP

RG7-10
RG19-22

4 0 9 0.17 0.041 0.618 -0.284 -0.257 0.8303 -0.02256 -0.09125 0.4005 0.576 !GP
4 0 9 0.674 0.408 0.2741 -0.18525 -0.1835 0.1302 -0.4835 -0.30225 0.16933 0.37 !GP
4 0 9 0.067 0.01654 0.06009 -0.03996 -0.00477 0.02641 -0.04512 0.00992 0.02883
0.09448 !GP

RG8-22
RG19-22

4 0 9 0.45143 0.20258 0.6104 -0.39951 -0.2754 0.82986 -0.18205 -0.07045 0.40667
0.58184 !GP
4 0 9 0.52062 0.44058 0.26582 -0.19599 -0.15978 0.13078 -0.4203 -0.46167 016318
0.36048 !GP
4 0 9 0.05994 0.02518 0.0620319 -0.04702 -0.00484 0.02833 -0.0523 0.01111 0.02891
0.094547 !GP

RG8-22
RG19-22

4 0 9 0.45143 0.20258 0.6104 -0.39951 -0.2754 0.82986 -0.18205 -0.07045 0.40667
0.58184 !GP
4 0 9 0.52062 0.44058 0.26582 -0.19599 -0.15978 0.13078 -0.4203 -0.46167 016318
0.36048 !GP
4 0 9 0.05994 0.02518 0.062032 -0.04702 -0.00484 0.02833 -0.05298 0.0111 0.02891
0.0945468 !GP
```

```
RG8-11
RG19-22

4 0 9 0.86 0.001 0.78 0.001 0.001 0.77 0.001 0.001 0.001 0.95 !GP
4 0 9 0.025 0.00001 0.07 0.00001 0.00001 0.07 0.00001 0.00001 0.00001 0.025 !GP
4 0 9 0.09 0.000001 0.15 0.000001 0.000001 0.16 0.000001 0.000001 0.00001 0.025 !GP

RG12-15
RG19-22

4 0 9 0.6703 0.29895 0.61317 -0.43312 -0.27674 0.82991 -0.22011 -0.05981 0.40811
0.5711 !GP
4 0 9 0.31149 0.27584 0.27066 -0.14337 -0.15789 0.13068 -0.32454 -0.30253 0.16119
0.37468 !GP
4 0 9 0.05721 0.0354 0.05809 -0.02719 -0.00401 0.02857 -0.03426 0.0122 0.02891
0.09454 !GP
```

Appendix 3.21: Q_{gen} and Q_{year} of early selection for wood density against direct selection for RG19-22 years from planting.

					Q_{gen}		Q_{year}				
							Individual			Family	
Ring-Grouping (years from planting)	T_j	h_i^2	h_f^2	$r_{A_j, 19-22}$	Individual	Family	d = variable (value of d in years)	d = 5 years	d = 3 years	d = 5 years	d = 3 years
8-15	15	0.5260	0.7847	0.95	1.1890	1.0685	1.6051 (5)	1.6051	1.6514	1.4425	1.4840
8-22	22	0.5384	0.7877	0.95	1.2029	1.0705	1.2029 (5)	1.2029	1.2029	1.0705	1.0705
6-9	9	0.8504	0.9612	0.95	1.5118	1.1826	2.4011 (8)	2.9156	3.1496	2.2807	2.4637
7-10	10	0.5938	0.8407	0.95	1.2633	1.1060	1.8949 (8)	2.2739	2.4294	1.9907	2.1269
8-11	11	0.5916	0.8308	0.95	1.2609	1.0994	1.8914 (7)	2.1279	2.2517	1.8553	1.9633
10-13	13	0.4677	0.7354	0.95	1.1212	1.0344	1.5932 (6)	1.6817	1.7518	1.5516	1.6162
12-15	15	0.3149	0.5956	0.95	0.9200	0.9309	1.2419 (5)	1.2419	1.2777	1.2567	1.2929
14-17	17	0.3191	0.5995	0.95	0.9261	0.9339	1.1365 (5)	1.1365	1.1576	1.1462	1.1674
16-19	19	0.2789	0.7459	0.95	0.8658	1.0417	0.9740 (5)	0.9740	0.9838	1.1720	1.1838
18-21	21	0.3343	0.6142	0.95	0.9479	0.9453	0.9843 (5)	0.9843	0.9874	0.9817	0.9847
19-22	22	0.3358	0.6203	1.00	1.0000	1.0000	1.0000 (5)	1.0000	1.0000	1.0000	1.0000

Appendix 4.1: Calculation of variate/covariate genetic correlations and accuracy of estimated breeding values.

The genetic correlation given in Table 4.7 were calculated as follows: reduction in variance components = (accuracy)^2 x (r_g)^2.

$$\therefore r_{g_{BV}} = \sqrt{\frac{\text{reduction in variance components}}{\text{accuracy}^2}}$$

Where accuracy of breeding value estimation is calculated for (i) progeny data (ii) ortet data as follows:

i) $$\text{progeny} = \frac{0.5}{\sqrt{0.25 + \frac{(\frac{1}{h^2} - 0.25)}{n}}}$$

where n = 40 trees/site#.

ii) ortet = $\sqrt{h_i^2}$ and where h_i^2 is (a) diameter = 0.15# (b) density = 0.41#.

(i) and (ii) from Mrode (1996); # from Lee (1994).

The calculated values of accuracy are:

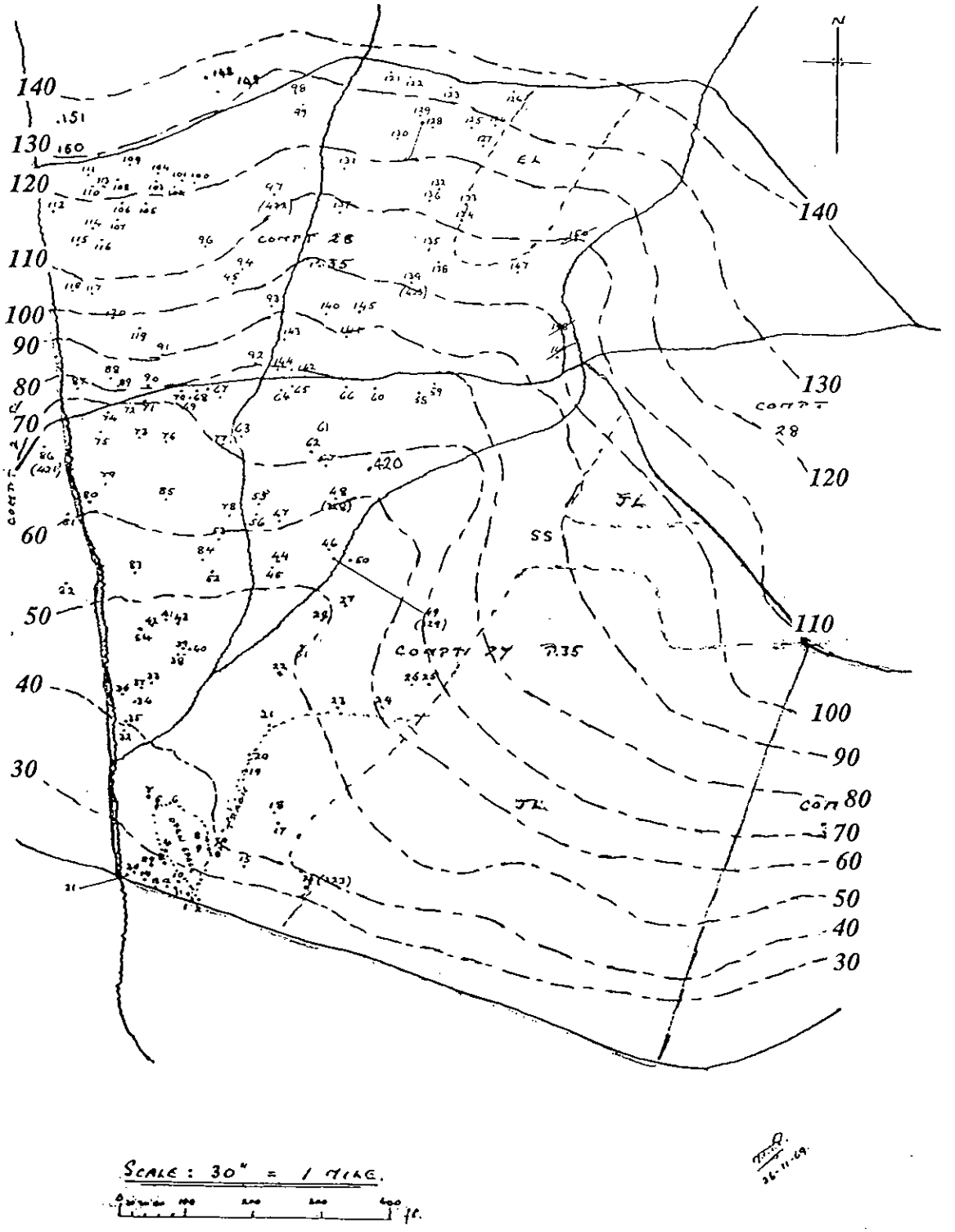
	15-year diameter	15-year density
progeny	0.78	0.91
ortet	0.39	0.64

Appendix 5.1: Original and adjusted ortet total tree heights, height above sea level (h.a.s.l.) and dominance class.

1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
4001	C	21.29	30	18.46	4051	C	25.68	50	24.09	4101	C	19.43	120	22.18
4002	C	19.08	30	16.25	4052	C	22.50	50	20.91	4102	S	18.27	120	21.02
4003	D	24.13	35	21.61	4053	D	26.52	55	25.24	4103	D	20.57	120	23.32
4004	C	22.56	35	20.04	4054	C	25.49	45	23.59	4104	C	18.06	120	20.81
4005	D	25.72	40	23.51	4055	S	21.91	60	20.94	4105	S	16.45	115	18.89
4006	C	24.84	40	22.63	4056	S	21.05	60	20.08	4106	S	17.08	115	19.52
4007	C	25.92	40	23.71	4057	C	24.15	60	23.18	4107	D	21.95	115	24.39
4008	C	23.70	40	21.49	4058	D	23.29	75	23.25	4108	D	23.49	120	26.24
4009	S	20.61	40	18.40	4059	S	17.40	75	17.36	4109	C	20.25	120	23.00
4010	S	21.20	30	18.37	4060	D	23.60	75	23.56	4110	C	20.83	120	23.58
4011	S	22.72	30	19.89	4061	S	20.38	70	20.03	4111	C	18.31	120	21.06
4012	S	23.97	30	21.14	4062	D	24.73	70	24.38	4112	C	17.11	115	19.55
4013	C	23.22	30	20.39	4063	D	25.20	70	24.85	4113	S	18.28	120	21.03
4014	C	21.35	30	18.52	4064	C	24.77	75	24.73	4114	D	19.58	115	22.02
4015	D	25.58	40	23.37	4065	D	25.61	75	25.57	4115	C	19.73	110	21.86
4016	D	32.04	40	29.83	4066	S	21.05	75	21.01	4116	S	18.43	110	20.56
4017	D	32.04	45	30.14	4067	S	18.82	75	18.88	4117	S	16.14	100	17.65
4018	D	27.64	45	25.74	4068	D	22.89	75	22.85	4118	C	20.05	100	21.56
4019	D	25.12	45	23.22	4069	C	23.31	70	22.96	4119	D	22.07	90	22.96
4020	C	27.60	45	25.70	4070	S	19.26	70	18.91	4120	D	20.14	90	21.03
4021	D	22.98	50	21.39	4071	S	21.02	70	20.67	4121	D	20.88	130	24.25
4022	C	26.05	50	24.46	4072	S	20.51	70	20.16	4122	C	19.25	130	22.62
4023	C	28.91	60	27.94	4073	D	24.93	65	24.27	4123	C	18.35	130	21.72
4024	C	27.00	70	26.65	4074	S	20.04	70	19.69	4124	D	21.94	125	25.00
4025	C	27.49	70	27.14	4075	D	27.47	65	26.81	4125	S	18.36	120	21.11
4026	C	29.30	70	28.95	4076	C	23.95	70	23.60	4126	D	21.06	120	23.81
4027	C	24.13	60	23.16	4077	C	23.12	70	22.77	4127	C	21.60	115	24.04
4028	S	23.83	55	22.55	4078	C	27.48	60	26.51	4128	S	18.50	120	21.25
4029	C	23.82	30	20.99	4079	S	21.12	60	20.15	4129	D	22.10	120	24.85
4030	C	23.30	30	20.47	4080	D	29.87	60	28.90	4130	C	22.00	115	24.44
4031	D	22.06	30	19.23	4081	S	20.61	55	19.33	4131	D	22.62	110	24.75
4032	D	28.82	35	26.30	4082	D	27.61	50	26.02	4132	S	20.00	110	22.13
4033	D	29.75	40	27.54	4083	C	24.87	50	23.28	4133	C	21.48	110	23.61
4034	C	29.78	40	27.57	4084	D	24.35	55	23.07	4134	D	22.08	105	23.90
4035	C	29.16	40	26.95	4085	C	24.58	60	23.61	4135	S	20.63	100	22.14
4036	D	28.99	40	26.78	4086	D	21.89	65	21.23	4136	D	22.30	110	24.43
4037	C	28.88	40	26.67	4087	D	25.85	70	25.50	4137	C	19.17	105	20.99
4038	C	26.45	45	24.55	4088	D	21.68	80	21.95	4138	D	23.50	100	25.01
4039	S	24.21	45	22.31	4089	S	15.45	70	15.10	4139	D	25.30	95	26.50
4040	C	27.17	45	25.27	4090	D	22.53	70	22.18	4140	C	22.50	85	23.08
4041	C	25.01	45	23.11	4091	C	17.55	85	18.13	4141	C	24.30	80	24.57
4042	C	25.67	45	23.77	4092	C	20.88	80	21.15	4142	S	19.50	75	19.46
4043	D	26.17	45	24.27	4093	C	22.34	90	23.23	4143	C	24.60	80	24.87
4044	D	23.52	50	21.93	4094	D	21.32	100	22.83	4144	C	23.50	75	23.46
4045	S	21.27	50	19.68	4095	D	22.46	95	23.66	4145	D	25.60	85	26.18
4046	C	24.20	55	22.92	4096	D	20.21	105	22.03	4146	C	19.91	120	22.66
4047	D	25.72	55	24.44	4097	D	22.15	105	23.97	4147	D	25.57	100	27.08
4048	D	24.02	60	23.05	4098	S	19.73	125	22.79	4148	C	19.63	125	22.69
4049	D	25.08	55	23.80	4099	S	17.35	125	20.41	4149	C	18.49	125	21.55
4050	C	22.01	55	20.73	4100	S	19.30	120	22.05	4150	S	18.98	120	21.73

Note: 1 = ortet number, 2 = dominance class (D = dominant, C = co-dominant, S = sub-dominant), 3 = original total tree height, 4 = h.a.s.l., 5 = adjusted total tree height.

Appendix 5.2: Location of the 150 ortets at the South Strome site



Note: This is a photo-reduced copy of the original tracing used to mark the location of ortets superimposed with 10 m contour lines. The original tracing was copied from the forest compartment stock map by M T T Phillips (Head Forester, Genetics Branch, Newton Field Station, Elgin, North Scotland) on 26 November 1969. Ten-meter contours were added by S J Lee (see Chapter 5.3). The figure 4000 was subsequently added to the identity of each tree e.g. 1 became 4001 and 150 became 4150.

Appendix 5.3: Pedigree information and individual grafted-ramet values for wood density, Pilodyn and diameter.

Clone	M	F	Site	Rep	Plot Number	Ramet	Density g cm^{-3}	Pilodyn (mm)	Diameter (mm)
4005	0	0	5	13	757	3	0.28571	23.5	260
4005	0	0	5	13	757	2	0.32847	20.5	185
4005	0	0	5	13	757	1	0.33068	22.0	275
4007	0	0	5	13	757	3	0.34211	21.5	220
4007	0	0	5	13	757	2	0.32044	19.0	245
4007	0	0	5	13	757	1	0.29048	20.0	210
4008	0	0	5	13	757	3	-9	-9	165
4008	0	0	5	13	757	2	-9	-9	150
4008	0	0	5	13	757	1	-9	-9	135
4010	0	0	5	13	757	3	0.33824	21.5	185
4010	0	0	5	13	757	2	-9	-9	95
4010	0	0	5	13	757	1	-9	-9	90
4012	0	0	5	13	757	3	0.39157	12.0	125
4012	0	0	5	13	757	2	0.35319	15.5	220
4012	0	0	5	13	757	1	0.33544	15.5	130
4016	0	0	5	13	757	3	0.26633	23.0	250
4016	0	0	5	13	757	2	-9	-9	-9
4016	0	0	5	13	757	1	0.26897	22.5	205
4017	0	0	5	13	757	3	0.31217	20.5	240
4017	0	0	5	13	757	2	0.30457	21.0	225
4017	0	0	5	13	757	1	0.28636	18.5	245
4022	0	0	5	13	757	3	-9	-9	90
4022	0	0	5	13	757	2	0.32584	18.5	160
4022	0	0	5	13	757	1	0.31905	21.5	195
4026	0	0	5	13	757	3	0.35762	16.0	170
4026	0	0	5	13	757	2	-9	-9	150
4026	0	0	5	13	757	1	0.43258	11.0	120
4029	0	0	5	13	757	3	0.30899	22.5	170
4029	0	0	5	13	757	2	-9	-9	130
4029	0	0	5	13	757	1	0.29530	21.5	180
4030	0	0	5	13	757	3	0.31646	20.5	190
4030	0	0	5	13	757	2	0.30137	19.5	155
4030	0	0	5	13	757	1	0.30726	24.5	205
4033	0	0	5	13	757	3	0.31638	18.0	200
4033	0	0	5	13	757	2	0.34000	18.5	165
4033	0	0	5	13	757	1	0.33333	18.0	165
4035	0	0	5	13	757	3	0.34031	20.0	215
4035	0	0	5	13	757	2	0.33005	20.0	210
4035	0	0	5	13	757	1	-9	-9	-9
4037	0	0	5	13	757	3	0.27074	21.0	235
4037	0	0	5	13	757	2	0.28342	22.0	225
4037	0	0	5	13	757	1	0.26016	23.5	230
4042	0	0	5	13	757	3	0.41317	15.0	150
4042	0	0	5	13	757	2	-9	-9	110
4042	0	0	5	13	757	1	0.40351	15.5	155
4043	0	0	5	13	757	3	0.32836	15.0	145
4043	0	0	5	13	757	2	-9	-9	120
4043	0	0	5	13	757	1	0.32727	19.0	155
4044	0	0	5	13	757	3	0.40972	18.5	205
4044	0	0	5	13	757	2	0.33099	18.5	230
4044	0	0	5	13	757	1	0.32948	18.5	205
4050	0	0	5	13	757	3	0.33824	18.0	130
4050	0	0	5	13	757	2	-9	18.5	180
4050	0	0	5	13	757	1	0.33645	14.5	155
4051	0	0	5	13	757	3	0.31757	21.5	150
4051	0	0	5	13	757	2	0.43049	16.0	205
4051	0	0	5	13	757	1	-9	18.0	185
4052	0	0	5	13	757	3	0.35172	17.5	140
4052	0	0	5	13	757	2	0.31469	16.5	185
4052	0	0	5	13	757	1	0.35714	15.5	120
4054	0	0	5	13	757	3	0.32039	19.5	205
4054	0	0	5	13	757	2	-9	-9	170
4054	0	0	5	13	757	1	0.38235	19.0	170
4057	0	0	5	13	757	3	0.35948	16.0	175
4057	0	0	5	13	757	2	0.42143	12.5	140
4057	0	0	5	13	757	1	0.38346	12.5	125
4058	0	0	5	13	757	3	-9	-9	90
4058	0	0	5	13	757	2	-9	-9	65
4058	0	0	5	13	757	1	-9	-9	-9
4064	0	0	5	13	757	3	0.37241	18.5	150
4064	0	0	5	13	757	2	0.33880	17.0	190
4064	0	0	5	13	757	1	0.38621	14.5	120

4069	0	0	5	13	757	3	0.40110	13.5	195
4069	0	0	5	13	757	2	0.41618	12.0	185
4069	0	0	5	13	757	1	0.39063	14.5	190
4075	0	0	5	13	757	3	0.34132	19.0	160
4075	0	0	5	13	757	2	0.36301	16.5	125
4075	0	0	5	13	757	1	0.33333	21.0	160
4079	0	0	5	13	757	3	0.34545	16.5	220
4079	0	0	5	13	757	2	-9	-9	165
4079	0	0	5	13	757	1	0.33125	17.5	205
4080	0	0	5	13	757	3	0.33523	22.0	255
4080	0	0	5	13	757	2	0.26957	22.0	235
4080	0	0	5	13	757	1	0.32558	19.5	245
4091	0	0	5	13	757	3	0.31481	20.0	210
4091	0	0	5	13	757	2	0.33750	13.5	180
4091	0	0	5	13	757	1	0.31677	20.5	220
4092	0	0	5	13	757	3	0.34000	21.5	205
4092	0	0	5	13	757	2	0.37805	18.5	205
4092	0	0	5	13	757	1	0.33140	19.0	170
4093	0	0	5	13	757	3	-9	-9	115
4093	0	0	5	13	757	2	0.35961	17.5	160
4093	0	0	5	13	757	1	-9	-9	100
4098	0	0	5	13	757	3	0.35862	18.5	155
4098	0	0	5	13	757	2	0.36943	19.5	225
4098	0	0	5	13	757	1	-9	-9	105
4103	0	0	5	13	757	3	0.32195	21.5	195
4103	0	0	5	13	757	2	-9	23.5	190
4103	0	0	5	13	757	1	0.29756	22.5	190
4104	0	0	5	13	757	3	-9	-9	-9
4104	0	0	5	13	757	2	0.35294	17.0	145
4104	0	0	5	13	757	1	0.34899	18.0	185
4114	0	0	5	13	757	3	0.33146	17.5	200
4114	0	0	5	13	757	2	0.32500	20.5	205
4114	0	0	5	13	757	1	0.30961	20.5	260
4116	0	0	5	13	757	3	0.36420	16.5	145
4116	0	0	5	13	757	2	0.38462	16.5	165
4116	0	0	5	13	757	1	0.35366	17.0	160
4117	0	0	5	13	757	3	-9	-9	-9
4117	0	0	5	13	757	2	0.31609	18.5	210
4117	0	0	5	13	757	1	0.34483	18.0	185
4118	0	0	5	13	757	3	-9	-9	-9
4118	0	0	5	13	757	2	-9	-9	-9
4118	0	0	5	13	757	1	-9	-9	140
4121	0	0	5	13	757	3	0.38235	15.5	160
4121	0	0	5	13	757	2	0.39344	16.5	160
4121	0	0	5	13	757	1	0.36257	16.5	200
4133	0	0	5	13	757	3	-9	-9	150
4133	0	0	5	13	757	2	0.30994	21.0	210
4133	0	0	5	13	757	1	-9	-9	110
4136	0	0	5	13	757	3	0.34091	19.0	195
4136	0	0	5	13	757	2	0.38288	17.5	170
4136	0	0	5	13	757	1	0.32258	20.5	220
4140	0	0	5	13	757	3	-9	-9	-9
4140	0	0	5	13	757	2	-9	-9	140
4140	0	0	5	13	757	1	-9	-9	-9
4142	0	0	5	13	757	3	0.35341	17.5	180
4142	0	0	5	13	757	2	0.34742	16.5	170
4142	0	0	5	13	757	1	0.33486	18.5	170
4147	0	0	5	13	757	3	0.37607	18.0	205
4147	0	0	5	13	757	2	0.36478	18.5	190
4147	0	0	5	13	757	1	0.37705	16.5	150
4148	0	0	5	13	757	3	0.35268	18.5	120
4148	0	0	5	13	757	2	-9	-9	115
4148	0	0	5	13	757	1	0.34574	18.5	140
4149	0	0	5	13	757	3	0.34375	17.5	165
4149	0	0	5	13	757	2	0.31855	21.0	225
4149	0	0	5	13	757	1	0.35983	17.0	210

Note:
1. M = Male parent, F = female parent; 0 = parent unknown.
2. All grafted-ramets were considered to be within the same plot and replication.
3. -9 is recognised as a missing value by ASReml
4. 46 clones with up to 3 ramets per clone. Actual number of observations are: Diameter 129, Pilodyn 107, Density 104.

Appendix 5.4 : Example of ASReml *.as* file used in bivariate analysis involving ortet height (Trait X) and progeny data (Trait Y).

```
Analysis of garcrogo 3 height, diameter and density data
1   id    1    -1  0
2   sire  1     0  150  # coded 1 to 150
3   dam   1     0  9375 # open pollinated
4   site  1     2  2
5   rep   1    27 !A # coded 1 to 27
6   plot  1   800  # coded 1 to 800
7   tree  1    25  # coded 1 to 25
8   DM23  1     1  !M-9 !P9   #Trait Y
9   Ort   1     1  !M-9       #Trait X
10  Trait 0     1
../trees.ped
../../coll.dat
8 1 1 0 19            # analyse DM23 + ort, normal distr, link, filter maxit
-9
4 5 10/1 10/6
0 0 .1 .1 .1 .1
1 2 2
9525 0 0
2 0 9 .6788 * .68668 !GP
11 2
2 0 9 0.24722 0.4 0.4 !GP
9525 1 0
13 2
2 0 9 0.00599 * 0.01039 !GP
800 0 0
```

Note: 1. On this occasion the bivariate analysis involves DM23 (Trait Y).

2. An '*' is substituted for all phenotypic covariances since this can not be estimated by the model.

Appendix 5.5: Example of ASReml.*pin* file used to generate functions of variance components in bivariate analysis involving ortet height (Trait X) and progeny vigour traits (Trait Y).

```
#           Residual Genetic Plot
#           A AB B  A AB B  A AB B
P phenA     1 0 0   1 0 0   1 0 0
P phenAB    0 1 0   0 1 0   0 0 0 0
P phenB     0 0 1   0 0 1   0 0 0 0 0

P GenA      0 0 0   1 0 0   0 0 0 0 0 0
P GenAB     0 0 0   0 1 0   0 0 0 0 0 0 0
P GenB      0 0 0   0 0 1   0 0 0 0 0 0 0 0

P ProgOrt_Cov 0 0 0   0 0.5 0   0 0 0 0 0 0 0 0 0
P ProgAvg     0.01333 0 0   0.26 0 0   0.3333 0 0 0 0 0 0 0 0 0

H dirct_herit_A       13 10
H g_r_of_BonA         14 13
H resp_AonB           14 12
R Correlation         12 16 17
R Cor_G_BV            13 14 12
```

Notes:
1. Residual progeny mean (ProgAvg) = $1/n$ where n = 75; genetic variance = 0.25 + 0.01 (where 0.25 = additive genetic variance between family means and 0.01 = additive genetic variance within families/n; 0.75/75 = 0.01); plots = 0.3333 ($1/r$ where r = number of replicates);
2. Progeny/Ortet genetic covariance (ProgOrt_Cov) is 0.5.
3. Traits X and Y from Equations 5.4, 5.5 and 5.6 are presented within ASReml as B and A respectively.

Appendix 5.6: Example of ASReml *.pvs* file used to estimate functions of variance components in bivariate analysis involving ortet height (Trait X) and progeny vigour traits (Trait Y).

```
10 phenA      0.9778       0.2391E-03   0.0000E+00   0.2559E-04   0.2104E-03
              0.1373E-03   0.2559E-04   0.3154E-05   0.0000E+00   0.0000E+00
              0.4527E-03
11 phenAB     0.1412      -0.4095E-03   0.0000E+00   0.7301E-03   0.5471E-03
              0.2071E-02   0.7301E-03  -0.3395E-06   0.0000E+00   0.0000E+00
              0.1373E-03   0.2071E-02
12 phenB      0.9999      -0.1535E-03   0.0000E+00   0.5207E-02   0.2047E-03
              0.1460E-02   0.5207E-02  -0.1809E-11   0.0000E+00   0.0000E+00
              0.5118E-04   0.1460E-02   0.1041E-01
13 GenA       0.1435      -0.8557E-03   0.0000E+00   0.1024E-03   0.1141E-02
              0.5471E-03   0.1024E-03  -0.7455E-04   0.0000E+00   0.0000E+00
              0.2104E-03   0.5471E-03   0.2047E-03   0.1141E-02
14 GenAB      0.1402      -0.4095E-03   0.0000E+00   0.7301E-03   0.5471E-03
              0.2071E-02   0.7301E-03  -0.3395E-06   0.0000E+00   0.0000E+00
              0.1373E-03   0.2071E-02   0.1460E-02   0.5471E-03   0.2071E-02
15 GenB       0.3566      -0.7677E-04   0.0000E+00  -0.9082E-02   0.1024E-03
              0.7301E-03   0.1429E-01  -0.9046E-12   0.0000E+00   0.0000E+00
              0.2559E-04   0.7301E-03   0.5207E-02   0.1024E-03   0.7301E-03
              0.1429E-01
16 ProgOrt_Cov   0.7009E-01  -0.2048E-03   0.0000E+00   0.3650E-03   0.2736E-03
                 0.1036E-02   0.3650E-03  -0.1697E-06   0.0000E+00   0.0000E+00
                 0.6864E-04   0.1036E-02   0.7301E-03   0.2736E-03   0.1036E-02
                 0.3650E-03   0.5178E-03
17 ProgAvg       0.4953E-01  -0.2015E-03   0.0000E+00   0.2559E-04   0.2603E-03
                 0.1367E-03   0.2559E-04   0.1269E-06   0.0000E+00   0.0000E+00
                 0.5895E-04   0.1367E-03   0.5118E-04   0.2603E-03   0.1367E-03
                 0.2559E-04   0.6834E-04   0.6504E-04
     dirct_herit_ = GenA        /phenA        =          0.1468   0.0337
     g_r_of_BonA  = GenAB       /GenA         =          0.9766   0.3185
     resp_AonB    = GenAB       /phenB        =          0.1402   0.0432
     Correlation  = ProgOrt_/SQR[phenB    *ProgAvg ]=    0.3150   0.0919
     Cor_G_BV     = GenAB    /SQR[GenA     *phenB   ]=    0.3700   0.1078
```

Note: Traits X and Y from Equations 5.4, 5.5 and 5.6 are presented within ASReml as B and A respectively.

Appendix 5.7 : Example of ASReml.*as* file used in bivariate analysis involving grafted-ramet traits (Trait X) and progeny traits for vigour (Trait Y).

```
Analysis of garcrogo 3 height, diameter and density data
1   id       1    -1   0
2   sire     1     0  150  # coded 1 to 150
3   dam      1     0  11400 # open pollinated
4   site     1     2  2
5   rep      1    27  !A # coded 1 to 27
6   plot     1   800  # coded 1 to 800
7   tree     1    25  # coded 1 to 25
8   DM23     1     1  !M-9 !P9   #Trait Y
9   gden     1     1  !M-9       #Trait X
10   Trait   0     1
../trees.ped
../../coll.dat
8 1 1 0 19      #  analyse DM23 + graft, normal distr, link, filter maxit
-9
4 5 10/1 10/6
0 0 .1 .1 .1 .1
1 2 2
9514 0 0
2 0 9 .6788 * .68668 !GP
11 2
2 0 9 0.247 0.1 0.2 !GP
11400 1 0
13 2
2 0 9 0.00599 * 0.01039 !GP
800 0 0
```

Note: 1. In this example grafted-ramet density is involved in analysis with DM23 (Trait Y).

2. An '*' is introduced to represent phenotypic covariances between unrelated data sources.

Appendix 5.8: Example of ASReml *.pin* file used to generate functions of variance components in bivariate analysis involving grafted-ramet traits (Trait X) and progeny vigour traits (Trait Y).

```
#          Residual Genetic Plot
#          A AB B  A AB B  A AB B
P phenA    1 0 0   1 0 0   1 0 0
P phenAB   0 1 0   0 1 0   0 0 0 0
P phenB    0 0 1   0 0 1   0 0 0 0 0

P GenA     0 0 0   1 0 0   0 0 0 0 0 0
P GenAB    0 0 0   0 1 0   0 0 0 0 0 0 0
P GenB     0 0 0   0 0 1   0 0 0 0 0 0 0 0

P PgCl_Cov    0 0 0   0 0.5 0  0 0 0 0 0 0 0 0 0
P PgAvg       0.01333 0 0   0.26 0 0   0.3333 0 0 0 0 0 0 0 0
P Cl_mean     0 0 0.3333   0 0 1  0 0 0 0 0 0 0 0 0 0

H dirct_herit_A      13 10
H resp_AonB          14 18
H clone_herit_B      15 12

R Correlation        18 16 17
R Cor_G_BV           13 14 15
```

Notes:
1. Residual progeny mean (ProgAvg) = $1/n$ where n = 75; genetic variance = 0.25 + 0.01 (where 0.25 = additive genetic variance between family means and 0.05 = additive genetic variance within families/n; 0.75/75 = 0.01); plots = 0.3333 ($1/r$ where r = number off replicates).

2. Progeny/grafted-ramet genetic covariance (PgCl_Cov) is 0.5.

3. Traits X and Y from Equations 5.4, 5.5 and 5.6 are presented within ASReml as B and A respectively.

Appendix 5.9: Example of ASReml.*pvs* file giving estimated functions of variance components involving bivariate analysis of grafted-ramet traits (Trait X) and progeny vigour traits (Trait Y).

```
10 phenA    0.9741     0.2339E-03  0.0000E+00 -0.4546E-09  0.2130E-03
           -0.1290E-03  0.6394E-04  0.3042E-05  0.0000E+00  0.0000E+00
            0.4500E-03
11 phenAB -0.1242    0.3906E-03  0.0000E+00 -0.4043E-04 -0.5214E-03
            0.3277E-02 -0.3008E-02  0.1824E-05  0.0000E+00  0.0000E+00
           -0.1290E-03  0.3277E-02
12 phenB    0.9575  -0.1929E-03  0.0000E+00  0.3486E-02  0.2564E-03
           -0.3048E-02  0.2187E-01  0.4240E-06  0.0000E+00  0.0000E+00
            0.6393E-04 -0.3048E-02  0.2535E-01
13 GenA     0.1445 -0.8604E-03  0.0000E+00  0.9202E-07  0.1147E-02
           -0.5214E-03  0.2563E-03 -0.7373E-04  0.0000E+00  0.0000E+00
            0.2130E-03 -0.5214E-03  0.2564E-03  0.1147E-02
14 GenAB  -0.1252  0.3906E-03  0.0000E+00 -0.4043E-04 -0.5214E-03
            0.3277E-02 -0.3008E-02  0.1824E-05  0.0000E+00  0.0000E+00
           -0.1290E-03  0.3277E-02 -0.3048E-02 -0.5214E-03  0.3277E-02
15 GenB     0.5267 -0.1928E-03  0.0000E+00 -0.2486E-02  0.2563E-03
           -0.3008E-02  0.2435E-01  0.4751E-06  0.0000E+00  0.0000E+00
            0.6394E-04 -0.3008E-02  0.2187E-01  0.2563E-03 -0.3008E-02
            0.2435E-01
16 PgCl_Cov -0.6258E-01  0.1953E-03  0.0000E+00 -0.2021E-04 -0.2607E-03
             0.1639E-02 -0.1504E-02  0.9120E-06  0.0000E+00  0.0000E+00
            -0.6452E-04  0.1639E-02 -0.1524E-02 -0.2607E-03  0.1639E-02
            -0.1504E-02  0.8193E-03
17 PgAvg     0.4969E-01 -0.2028E-03  0.0000E+00  0.6372E-08  0.2622E-03
            -0.1298E-03  0.6423E-04  0.1411E-06  0.0000E+00  0.0000E+00
             0.5951E-04 -0.1298E-03  0.6423E-04  0.2622E-03 -0.1298E-03
             0.6423E-04 -0.6488E-04  0.6552E-04
18 Cl_mean   0.6703     -0.1929E-03  0.0000E+00 -0.4954E-03  0.2563E-03
            -0.3021E-02  0.2352E-01  0.4581E-06  0.0000E+00  0.0000E+00
             0.6393E-04 -0.3021E-02  0.2303E-01  0.2563E-03 -0.3021E-02
             0.2352E-01 -0.1511E-02  0.6423E-04  0.2336E-01

     dirct_herit_ = GenA        /phenA       =        0.1484  0.0340
     resp_AonB    = GenAB       /Cl_mean     =       -0.1867  0.0812
     clone_herit_ = GenB        /phenB       =        0.5501  0.0932
     Correlation  = PgCl_Cov/SQR[Cl_mean *PgAvg   ]= -0.3429  0.1426
     Cor_G_BV     = GenAB   /SQR[GenA    *GenB    ]= -0.4537  0.1882
```

Note: Traits X and Y from Equations 5.4, 5.5 and 5.6 are presented within ASReml as B and A respectively.

Appendix 5.10: Example of ASReml *.as* file used in quadrivariate analysis involving grafted-ramet traits (Trait X) and progeny wood density traits (Trait Y).

```
Analysis of garcrogo 3 height data
1   id       1    -1  0
2   sire     1     0  150  # coded 1 to 150
3   dam      1     0  9513 # open pollinated
4   site     1     2
5   rep      1    27  !A # coded 1 to 27
6   plot     1   800  # coded 1 to 800
7   tree     1    25  # coded 1 to 25
8   gden     1     1  !M-9 B!P-11   #Trait X
9   RG69     1     1  !M-9          #Trait Y
10  DM16     1     1  !M-9
11  DN17     1     1  !M-9
12  Trait    0     1
~/leesj/test/trees.ped
~/leesj/gden+RG69.dat
8 1 1 0 19            # analyse gden+RG69 (DM16+DN17)
 -9
4 5 12/1 12/6
0 0 .1 .1 .1 .1 .1 .1 .1 .1
1 2 2  !STEP 0.1
9513 0 0
4 0 9 0.4329 * 0.04675 * -0.23232 0.83191 * 0.11874 0.38048 0.561 !GP
13 2
4 0 9 0.41641 0.32836 0.77699 -0.12921 -0.20254 0.12524 -0.3242 -0.65583 0.19489 0.3875
!GP
11400 1 0
17 2
4 0 9 0.09 * 0.125 * -0.10004 0.03383 * 0.01988 0.0113 0.14301 !GP
800 0 0
```

Note: 1. In this example grafted-ramet density is involved in quadrivariate analysis with RG6-9 from the progeny data alonf with DM16 and DN17 as covariates.

2. An '*' is introduced to represent phenotypic covariances between traits from different genetic sources.

Appendix 5.11: Example of ASReml.*pin* file used to generate functions of variance components in quadrivariate analysis involving grafted-ramet density (Trait X) and progeny wood density (Trait Y) including covariates DN17 and DM16.

```
#          Residual                                  Genetic
#        A AB B AC AB C AD BD CD D
P phenA  1 0 0 0 0 0 0 0 0 0  1 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0
P phenAB 0 1 0 0 0 0 0 0 0 0  0 1 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0
P phenB  0 0 1 0 0 0 0 0 0 0  0 0 1 0 0 0 0 0 0 0  0 0 1 0 0 0 0 0 0 0 0 0
P phenAC 0 0 0 1 0 0 0 0 0 0  0 0 0 1 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0
P phenBC 0 0 0 0 1 0 0 0 0 0  0 0 0 0 1 0 0 0 0 0  0 0 0 0 1 0 0 0 0 0 0 0 0
P phenC  0 0 0 0 0 1 0 0 0 0  0 0 0 0 0 1 0 0 0 0  0 0 0 0 0 1 0 0 0 0 0 0 0 0
P phenAD 0 0 0 0 0 0 1 0 0 0  0 0 0 0 0 0 1 0 0 0  0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
P phenBD 0 0 0 0 0 0 0 1 0 0  0 0 0 0 0 0 0 1 0 0  0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
P phenCD 0 0 0 0 0 0 0 0 1 0  0 0 0 0 0 0 0 0 1 0  0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
P phenD  0 0 0 0 0 0 0 0 0 1  0 0 0 0 0 0 0 0 0 1  0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0

P GenA   0 0 0 0 0 0 0 0 0 0  1 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenAB  0 0 0 0 0 0 0 0 0 0  0 1 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenB   0 0 0 0 0 0 0 0 0 0  0 0 1 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenAC  0 0 0 0 0 0 0 0 0 0  0 0 0 1 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenBC  0 0 0 0 0 0 0 0 0 0  0 0 0 0 1 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenC   0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 1 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenAD  0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 1 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenBD  0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 1 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenCD  0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 1 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P GenD   0 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 1  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

P Cl_mean 0.3333 0 0 0 0 0 0 0 0 0  1 0 0 0 0 0 0 0 0 0  0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P Prog_mean 0 0 0.0667 0 0 0 0 0 0 0   0 0 0.3 0 0 0 0 0 0 0  0 0 0.3333 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
P ProgB_Cl_Cov 0 0 0 0 0 0 0 0 0 0   0 0.5 0 0 0 0 0 0 0 0   0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

H drct_herit_B  43 33                R direct_corr_AB  41 42 43          R Phen_corr_BC    33 35 36
H drct_herit_C  46 36                R direct_corr_AC  41 44 46          R Phen_corr_BD    33 38 40
H drct_herit_D  50 40                R direct_corr_BC  43 45 46          R Phen_corr_CD    36 39 40
                                     R direct_corr_AD  41 47 50          R Correlation     51 53 52
H plot_csqB       23 33              R direct_corr_BD  43 48 50          R Cor_G_BV        41 42 43
H plot_csqC       26 36              R direct_corr_CD  46 49 50
H plot_csqD       30 40              R plot_corr_BC    23 25 26
                                     R plot_corr_BD    23 28 30
H resp_AonB       42 51              R plot_corr_CD    26 29 30
```

Note: 1. Cl_mean residual = 0.333 ($1/n$ where n = 3).

2. Prog_mean residual = 0.0667 ($1/n$ where n = 15); genetic covariance = 0.3 equivalent to 0.25 (additive variation between family means) + 0.05 additive genetic variation within families/n where n= 15; 0.75/15 = 0.05); plot variance = 0.3333 ($1/r$ where r = number of replicates).

3. Prog_Cl genetic covariance between progeny and clonal mean = 0.5.

4. Traits X and Y from Equations 5.4, 5.5 and 5.6 are presented within ASReml as A and B respectively.

Appendix 5.12: Example of ASReml.*pvs* file used to estimate functions of variance componenets in quadrivariate analysis invloving grafted-ramet wood density traits (Trait X) and progeny wood density traits (Trait Y) including DN17 and DM16 as covariates.

```
31 phenA          0.8491       0.3531E-02   0.0000E+00  -0.1759E-02   0.0000E+00
                  0.6145E-03  -0.2085E-03   0.0000E+00   0.1514E-02  -0.5185E-03
                 -0.1289E-02   0.1285E-01   0.6499E-02   0.2368E-02  -0.2241E-02
                 -0.8545E-03   0.2779E-03  -0.5553E-02  -0.2047E-02   0.6924E-03
                  0.1719E-02   0.0000E+00   0.0000E+00   0.4134E-05   0.0000E+00
                 -0.2074E-06   0.7585E-08   0.0000E+00   0.9014E-06   0.1073E-06
                  0.9341E-07   0.1638E-01
32 phenAB         0.3310       0.1676E-04   0.0000E+00  -0.8096E-02   0.0000E+00
                  0.2049E-02  -0.4405E-03   0.0000E+00   0.4533E-02  -0.9041E-03
                 -0.1764E-02   0.6483E-02   0.1547E-01   0.1096E-01  -0.3073E-02
                 -0.3007E-02   0.5868E-03  -0.4883E-02  -0.6278E-02   0.1206E-02
                  0.2352E-02   0.0000E+00   0.0000E+00  -0.2148E-05   0.0000E+00
                  0.5666E-04   0.2017E-05   0.0000E+00   0.6976E-04   0.5766E-06
                 -0.1293E-05   0.6499E-02   0.1547E-01
33 phenB          0.9519       0.1162E-05   0.0000E+00  -0.5264E-02   0.0000E+00
                 -0.4225E-04  -0.2068E-03   0.0000E+00   0.1598E-02  -0.3639E-03
                 -0.5942E-03   0.6119E-03   0.2859E-02   0.1009E-01  -0.4652E-03
                 -0.1917E-02   0.3039E-03  -0.6954E-03  -0.3376E-02   0.5056E-03
                  0.8077E-03   0.0000E+00   0.0000E+00   0.1246E-02   0.0000E+00
                 -0.2170E-03   0.9204E-05   0.0000E+00   0.1441E-03   0.4981E-05
                  0.2574E-04   0.6130E-03   0.2859E-02   0.6071E-02
34 phenAC        -0.1282      -0.1934E-04   0.0000E+00   0.1347E-02   0.0000E+00
                 -0.8076E-03   0.3556E-03   0.0000E+00  -0.1127E-02   0.6380E-03
                  0.9618E-03  -0.2221E-02  -0.3073E-02  -0.1807E-02   0.2402E-02
                  0.1095E-02  -0.4741E-03   0.2380E-02   0.1515E-02  -0.8507E-03
                 -0.1282E-02   0.0000E+00   0.0000E+00  -0.5352E-05   0.0000E+00
                  0.2660E-05   0.3107E-06   0.0000E+00   0.2447E-05   0.1694E-06
                 -0.1844E-06  -0.2241E-02  -0.3073E-02  -0.4652E-03   0.2402E-02
35 phenBC        -0.5354      -0.1135E-05   0.0000E+00   0.3422E-03   0.0000E+00
                  0.1306E-02   0.1114E-03   0.0000E+00   0.2087E-03   0.2376E-03
                  0.3539E-03  -0.2390E-03  -0.9012E-03  -0.2097E-02   0.2900E-03
                  0.9069E-03  -0.2326E-03   0.3466E-03   0.1199E-02  -0.3705E-03
                 -0.5059E-03   0.0000E+00   0.0000E+00  -0.4210E-03   0.0000E+00
                  0.1355E-03  -0.2267E-04   0.0000E+00   0.4060E-04   0.1043E-05
                  0.1148E-04  -0.2402E-03  -0.9012E-03  -0.2176E-02   0.2900E-03
                  0.2348E-02
36 phenC          0.9910       0.5450E-07   0.0000E+00  -0.1924E-03   0.0000E+00
                  0.9767E-04   0.6736E-04   0.0000E+00   0.1468E-03  -0.4565E-04
                 -0.1167E-03   0.6935E-04   0.1483E-03   0.2888E-03  -0.1182E-03
                 -0.2184E-03   0.1584E-03  -0.1278E-03  -0.2459E-03   0.2020E-03
                  0.2359E-03   0.0000E+00   0.0000E+00   0.9922E-05   0.0000E+00
                 -0.2318E-04   0.2203E-04   0.0000E+00  -0.1886E-04   0.6027E-05
                 -0.3124E-05   0.6941E-04   0.1483E-03   0.1064E-03  -0.1182E-03
                 -0.1439E-03   0.2478E-03
37 phenAD        -0.3231      -0.1625E-04   0.0000E+00   0.2000E-02   0.0000E+00
                 -0.9293E-03   0.3844E-03   0.0000E+00  -0.2341E-02   0.9762E-03
                  0.2477E-02  -0.5537E-02  -0.4883E-02  -0.2687E-02   0.2380E-02
                  0.1271E-02  -0.5125E-03   0.6137E-02   0.3143E-02  -0.1304E-02
                 -0.3305E-02   0.0000E+00   0.0000E+00  -0.9163E-05   0.0000E+00
                  0.5355E-05   0.2632E-06   0.0000E+00   0.4661E-05   0.2121E-06
                  0.1245E-06  -0.5553E-02  -0.4883E-02  -0.6954E-03   0.2380E-02
                  0.3466E-03  -0.1278E-03   0.6137E-02
38 phenBD        -0.5185      -0.6468E-06   0.0000E+00   0.1515E-02   0.0000E+00
                  0.2864E-03   0.1558E-03   0.0000E+00  -0.2367E-03   0.3775E-03
                  0.8576E-03  -0.5305E-03  -0.1676E-02  -0.3187E-02   0.3904E-03
                  0.1127E-02  -0.2555E-03   0.8058E-03   0.2309E-02  -0.5658E-03
                 -0.1207E-02   0.0000E+00   0.0000E+00   0.3769E-04   0.0000E+00
                  0.3494E-04  -0.1823E-04   0.0000E+00   0.3358E-03  -0.1840E-04
                  0.3639E-04  -0.5312E-03  -0.1676E-02  -0.1634E-02   0.3904E-03
                  0.1449E-02  -0.1179E-03   0.8058E-03   0.2408E-02
39 phenCD        0.5866       0.8796E-07   0.0000E+00  -0.3479E-03   0.0000E+00
                 0.2094E-03  -0.4552E-04   0.0000E+00   0.3626E-03  -0.1331E-03
                -0.3121E-03   0.1739E-03   0.3026E-03   0.4901E-03  -0.2125E-03
                -0.3408E-03   0.2019E-03  -0.3276E-03  -0.5494E-03   0.3477E-03
                 0.5640E-03   0.0000E+00   0.0000E+00   0.4462E-05   0.0000E+00
                -0.4701E-06   0.6064E-05   0.0000E+00  -0.1991E-04   0.3427E-04
                 0.3333E-04   0.1740E-03   0.3026E-03   0.1467E-03  -0.2125E-03
                -0.1319E-03   0.1624E-03  -0.3276E-03  -0.2067E-03   0.2488E-03
40 phenD          1.091       0.7064E-07   0.0000E+00  -0.5809E-03   0.0000E+00
```

	0.3154E-03	-0.1165E-03	0.0000E+00	0.8349E-03	-0.3095E-03
	-0.8251E-03	0.4308E-03	0.5872E-03	0.7968E-03	-0.3208E-03
	-0.4641E-03	0.2356E-03	-0.8283E-03	-0.1182E-02	0.5612E-03
	0.1336E-02	0.0000E+00	0.0000E+00	0.2331E-04	0.0000E+00
	0.8216E-05	-0.3042E-05	0.0000E+00	0.3416E-04	0.3347E-04
	0.1817E-03	0.4309E-03	0.5872E-03	0.2393E-03	-0.3208E-03
	-0.1405E-03	0.1160E-03	-0.8283E-03	-0.3132E-03	0.2852E-03
	0.6924E-03				
41 GenA	0.4166	-0.2470E-02	0.0000E+00	-0.1758E-02	0.0000E+00
	0.6143E-03	-0.2084E-03	0.0000E+00	0.1513E-02	-0.5183E-03
	-0.1288E-02	0.1532E-01	0.6483E-02	0.2367E-02	-0.2221E-02
	-0.8529E-03	0.2777E-03	-0.5537E-02	-0.2044E-02	0.6921E-03
	0.1719E-02	0.0000E+00	0.0000E+00	0.3647E-05	0.0000E+00
	-0.3980E-06	-0.8016E-08	0.0000E+00	0.4020E-06	0.1099E-06
	0.1405E-06	0.1285E-01	0.6483E-02	0.6119E-03	-0.2221E-02
	-0.2390E-03	0.6935E-04	-0.5537E-02	-0.5305E-03	0.1739E-03
	0.4308E-03	0.1532E-01			
42 GenAB	0.3300	0.1676E-04	0.0000E+00	-0.8096E-02	0.0000E+00
	0.2049E-02	-0.4405E-03	0.0000E+00	0.4533E-02	-0.9041E-03
	-0.1764E-02	0.6483E-02	0.1547E-01	0.1096E-01	-0.3073E-02
	-0.3007E-02	0.5868E-03	-0.4883E-02	-0.6278E-02	0.1206E-02
	0.2352E-02	0.0000E+00	0.0000E+00	-0.2148E-05	0.0000E+00
	0.5666E-04	0.2017E-05	0.0000E+00	0.6976E-04	0.5766E-06
	-0.1293E-05	0.6499E-02	0.1547E-01	0.2859E-02	-0.3073E-02
	-0.9012E-03	0.1483E-03	-0.4883E-02	-0.1676E-02	0.3026E-03
	0.5872E-03	0.6483E-02	0.1547E-01		
43 GenB	0.7802	0.1412E-05	0.0000E+00	-0.4013E-01	0.0000E+00
	0.7142E-02	-0.9423E-03	0.0000E+00	0.9199E-02	-0.1467E-02
	-0.2460E-02	0.2367E-02	0.1096E-01	0.5381E-01	-0.1807E-02
	-0.9882E-02	0.1256E-02	-0.2687E-02	-0.1234E-01	0.1953E-02
	0.3278E-02	0.0000E+00	0.0000E+00	-0.3595E-02	0.0000E+00
	0.6438E-03	-0.2491E-04	0.0000E+00	-0.5045E-04	0.3569E-05
	-0.2108E-04	0.2368E-02	0.1096E-01	0.1009E-01	-0.1807E-02
	-0.2097E-02	0.2888E-03	-0.2687E-02	-0.3187E-02	0.4901E-03
	0.7968E-03	0.2367E-02	0.1096E-01	0.5381E-01	
44 GenAC	-0.1292	-0.1934E-04	0.0000E+00	0.1347E-02	0.0000E+00
	-0.8076E-03	0.3556E-03	0.0000E+00	-0.1127E-02	0.6380E-03
	0.9618E-03	-0.2221E-02	-0.3073E-02	-0.1807E-02	0.2402E-02
	0.1095E-02	-0.4741E-03	0.2380E-02	0.1515E-02	-0.8507E-03
	-0.1282E-02	0.0000E+00	0.0000E+00	-0.5352E-05	0.0000E+00
	0.2660E-05	0.3107E-06	0.0000E+00	0.2447E-05	0.1694E-06
	-0.1844E-06	-0.2241E-02	-0.3073E-02	-0.4652E-03	0.2402E-02
	0.2900E-03	-0.1182E-03	0.2380E-02	0.3904E-03	-0.2125E-03
	-0.3208E-03	-0.2221E-02	-0.3073E-02	-0.1807E-02	0.2402E-02
45 GenBC	-0.2027	-0.1559E-05	0.0000E+00	0.7409E-02	0.0000E+00
	-0.3845E-02	0.8079E-03	0.0000E+00	-0.3642E-02	0.1029E-02
	0.1338E-02	-0.8529E-03	-0.3007E-02	-0.9882E-02	0.1095E-02
	0.5114E-02	-0.1077E-02	0.1271E-02	0.4910E-02	-0.1372E-02
	-0.1784E-02	0.0000E+00	0.0000E+00	0.5566E-03	0.0000E+00
	-0.3619E-03	0.5077E-04	0.0000E+00	-0.1411E-03	0.1914E-05
	-0.1866E-04	-0.8545E-03	-0.3007E-02	-0.1917E-02	0.1095E-02
	0.9069E-03	-0.2184E-03	0.1271E-02	0.1127E-02	-0.3408E-03
	-0.4641E-03	-0.8529E-03	-0.3007E-02	-0.9882E-02	0.1095E-02
	0.5114E-02				
46 GenC	0.1253	0.1682E-06	0.0000E+00	-0.9346E-03	0.0000E+00
	0.7946E-03	-0.6536E-03	0.0000E+00	0.8529E-03	-0.6687E-03
	-0.7043E-03	0.2777E-03	0.5868E-03	0.1256E-02	-0.4741E-03
	-0.1077E-02	0.8713E-03	-0.5125E-03	-0.1147E-02	0.8916E-03
	0.9390E-03	0.0000E+00	0.0000E+00	-0.1756E-04	0.0000E+00
	0.4983E-04	-0.5935E-04	0.0000E+00	0.3828E-04	-0.2099E-04
	0.8619E-06	0.2779E-03	0.5868E-03	0.3039E-03	-0.4741E-03
	-0.2326E-03	0.1584E-03	-0.5125E-03	-0.2555E-03	0.2019E-03
	0.2356E-03	0.2777E-03	0.5868E-03	0.1256E-02	-0.4741E-03
	-0.1077E-02	0.8713E-03			
47 GenAD	-0.3241	-0.1625E-04	0.0000E+00	0.2000E-02	0.0000E+00
	-0.9293E-03	0.3844E-03	0.0000E+00	-0.2341E-02	0.9762E-03
	0.2477E-02	-0.5537E-02	-0.4883E-02	-0.2687E-02	0.2380E-02
	0.1271E-02	-0.5125E-03	0.6137E-02	0.3143E-02	-0.1304E-02
	-0.3305E-02	0.0000E+00	0.0000E+00	-0.9163E-05	0.0000E+00
	0.5355E-05	0.2632E-06	0.0000E+00	0.4661E-05	0.2121E-06
	0.1245E-06	-0.5553E-02	-0.4883E-02	-0.6954E-03	0.2380E-02
	0.3466E-03	-0.1278E-03	0.6137E-02	0.8058E-03	-0.3276E-03
	-0.8283E-03	-0.5537E-02	-0.4883E-02	-0.2687E-02	0.2380E-02
	0.1271E-02	-0.5125E-03	0.6137E-02		
48 GenBD	-0.6556	-0.2417E-05	0.0000E+00	0.9222E-02	0.0000E+00
	-0.3573E-02	0.8602E-03	0.0000E+00	-0.8968E-02	0.1764E-02
	0.3331E-02	-0.2044E-02	-0.6278E-02	-0.1234E-01	0.1515E-02

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                 0.4910E-02 -0.1147E-02  0.3143E-02  0.1206E-01 -0.2353E-02
                -0.4444E-02  0.0000E+00  0.0000E+00 -0.2627E-03  0.0000E+00
                -0.1379E-03  0.4052E-04  0.0000E+00 -0.7860E-03  0.4036E-04
                -0.6964E-04 -0.2047E-02 -0.6278E-02 -0.3376E-02  0.1515E-02
                 0.1199E-02 -0.2459E-03  0.3143E-02  0.2309E-02 -0.5494E-03
                -0.1182E-02 -0.2044E-02 -0.6278E-02 -0.1234E-01  0.1515E-02
                 0.4910E-02 -0.1147E-02  0.3143E-02  0.1206E-01
49 GenCD         0.1949      0.3211E-06  0.0000E+00 -0.1447E-02  0.0000E+00
                 0.1002E-02 -0.6688E-03  0.0000E+00  0.1750E-02 -0.1278E-02
                -0.1910E-02  0.6921E-03  0.1206E-02  0.1953E-02 -0.8507E-03
                -0.1372E-02  0.8916E-03 -0.1304E-02 -0.2353E-02  0.1705E-02
                 0.2547E-02  0.0000E+00  0.0000E+00 -0.3967E-06  0.0000E+00
                -0.8884E-06 -0.2070E-04  0.0000E+00  0.3765E-04 -0.7870E-04
                -0.7585E-04  0.6924E-03  0.1206E-02  0.5056E-03 -0.8507E-03
                -0.3705E-03  0.2020E-03 -0.1304E-02 -0.5658E-03  0.3477E-03
                 0.5612E-03  0.6921E-03  0.1206E-02  0.1953E-02 -0.8507E-03
                -0.1372E-02  0.8916E-03 -0.1304E-02 -0.2353E-02  0.1705E-02
50 GenD          0.3871      0.4059E-06  0.0000E+00 -0.2432E-02  0.0000E+00
                 0.1301E-02 -0.7045E-03  0.0000E+00  0.3310E-02 -0.1908E-02
                -0.5130E-02  0.1719E-02  0.2352E-02  0.3278E-02 -0.1282E-02
                -0.1784E-02  0.9390E-03 -0.3305E-02 -0.4444E-02  0.2547E-02
                 0.6845E-02  0.0000E+00  0.0000E+00 -0.3796E-04  0.0000E+00
                -0.2355E-04  0.1378E-05  0.0000E+00 -0.7293E-04 -0.7560E-04
                -0.3786E-03  0.1719E-02  0.2352E-02  0.8077E-03 -0.1282E-02
                -0.5059E-03  0.2359E-03 -0.3305E-02 -0.1207E-02  0.5640E-03
                 0.1336E-02  0.1719E-02  0.2352E-02  0.3278E-02 -0.1282E-02
                -0.1784E-02  0.9390E-03 -0.3305E-02 -0.4444E-02  0.2547E-02
                 0.6845E-02
51 Cl_mean       0.5608     -0.4699E-03  0.0000E+00 -0.1759E-02  0.0000E+00
                 0.6144E-03 -0.2084E-03  0.0000E+00  0.1514E-02 -0.5184E-03
                -0.1289E-02  0.1450E-01  0.6488E-02  0.2367E-02 -0.2228E-02
                -0.8534E-03  0.2778E-03 -0.5543E-02 -0.2045E-02  0.6922E-03
                 0.1719E-02  0.0000E+00  0.0000E+00  0.3809E-05  0.0000E+00
                -0.3345E-06 -0.2817E-08  0.0000E+00  0.5684E-06  0.1090E-06
                 0.1248E-06  0.1403E-01  0.6488E-02  0.6123E-03 -0.2228E-02
                -0.2394E-03  0.6937E-04 -0.5543E-02 -0.5307E-03  0.1740E-03
                 0.4308E-03  0.1450E-01  0.6488E-02  0.2367E-02 -0.2228E-02
                -0.8534E-03  0.2778E-03 -0.5543E-02 -0.2045E-02  0.6922E-03
                 0.1719E-02  0.1434E-01
52 Prog_mean     0.2795      0.5366E-06  0.0000E+00 -0.9191E-02  0.0000E+00
                 0.1514E-02 -0.2305E-03  0.0000E+00  0.2296E-02 -0.3666E-03
                -0.6060E-03  0.5939E-03  0.2747E-02  0.1227E-01 -0.4541E-03
                -0.2285E-02  0.3086E-03 -0.6756E-03 -0.3173E-02  0.4893E-03
                 0.8084E-03  0.0000E+00  0.0000E+00  0.1301E-04  0.0000E+00
                 0.2394E-04 -0.1017E-05  0.0000E+00  0.3450E-04  0.2578E-05
                 0.5610E-05  0.5945E-03  0.2747E-02  0.3091E-02 -0.4541E-03
                -0.7466E-03  0.7712E-04 -0.6756E-03 -0.8424E-03  0.1253E-03
                 0.2081E-03  0.5939E-03  0.2747E-02  0.1227E-01 -0.4541E-03
                -0.2285E-02  0.3086E-03 -0.6756E-03 -0.3173E-02  0.4893E-03
                 0.8084E-03  0.5941E-03  0.3072E-02
53 ProgB_Cl_Cov  0.1650      0.8381E-05  0.0000E+00 -0.4048E-02  0.0000E+00
                 0.1025E-02 -0.2203E-03  0.0000E+00  0.2266E-02 -0.4520E-03
                -0.8819E-03  0.3241E-02  0.7735E-02  0.5479E-02 -0.1536E-02
                -0.1504E-02  0.2934E-03 -0.2441E-02 -0.3139E-02  0.6031E-03
                 0.1176E-02  0.0000E+00  0.0000E+00 -0.1074E-05  0.0000E+00
                 0.2833E-04  0.1009E-05  0.0000E+00  0.3488E-04  0.2883E-06
                -0.6467E-06  0.3250E-02  0.7735E-02  0.1429E-02 -0.1536E-02
                -0.4506E-03  0.7416E-04 -0.2441E-02 -0.8381E-03  0.1513E-03
                 0.2936E-03  0.3241E-02  0.7735E-02  0.5479E-02 -0.1536E-02
                -0.1504E-02  0.2934E-03 -0.2441E-02 -0.3139E-02  0.6031E-03
                 0.1176E-02  0.3244E-02  0.1373E-02  0.3868E-02
   drct_herit_B = GenB         /phenB        =         0.8196  0.2136
   drct_herit_C = GenC         /phenC        =         0.1265  0.0292
   drct_herit_D = GenD         /phenD        =         0.3547  0.0709
   plot_csqB    = Tr_1.plot    /phenB        =         0.1342  0.0542
   plot_csqC    = Tr_1.plot    /phenC        =         0.0341  0.0067
   plot_csqD    = Tr_1.plot    /phenD        =         0.1310  0.0144
   resp_AonB    = GenAB        /Cl_mean      =         0.5884  0.2018
   direct_corr_ = GenAB    /SQR[GenA     *GenB     ]=  0.5788  0.1832
   direct_corr_ = GenAC    /SQR[GenA     *GenC     ]= -0.5654  0.1892
   direct_corr_ = GenBC    /SQR[GenB     *GenC     ]= -0.6483  0.1614
   direct_corr_ = GenAD    /SQR[GenA     *GenD     ]= -0.8071  0.1395
   direct_corr_ = GenBD    /SQR[GenB     *GenD     ]= -1.1930  0.1901
   direct_corr_ = GenCD    /SQR[GenC     *GenD     ]=  0.8849  0.0866
   plot_corr_BC = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]= -1.5210  0.2972
   plot_corr_BD = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.1427  0.1774
   plot_corr_CD = Tr_1.plo/SQR[Tr_1.plo*Tr_1.plo]=  0.1616  0.1027
```

```
Phen_corr_BC = phenBC   /SQR[phenB    *phenC    ]= -0.5513  0.0407
Phen_corr_BD = phenBD   /SQR[phenB    *phenD    ]= -0.5087  0.0427
Phen_corr_CD = phenCD   /SQR[phenC    *phenD    ]=  0.5641  0.0091
Correlation  = ProgB_Cl/SQR[Cl_mean  *Prog_mea]=  0.4167  0.1320
Cor_G_BV     = GenAB    /SQR[GenA     *GenB     ]=  0.5788  0.1832
```

Note: Traits X and Y from Equations 5.4, 5.5 and 5.6 are presented within ASReml as A and B respectively.