Genetic parameters and selection indices for a population of *Pinus elliottii* Engelm. var *elliottii*.

by

Idah Zviripayi Pswarayi

A thesis submitted for the degree of
Doctor of Philosophy at Oxford Univerity

Trinity Term
1993

Linacre College
Oxford

Genetic parameters and selection indices for a population of *Pinus elliottii* Engelm. var. *elliottii*.

A thesis submitted for the degree of Doctor of Philosophy at Oxford University
Trinity Term 1993

I.Z. Pswarayi
Linacre College

Abstract

P. elliottii Engelm. var. *elliottii* is an important exotic plantation species in Zimbabwe, where it is grown for saw-timber and resin production. Three progeny tests, originating from factorial matings between parents selected in plantations, were assessed at five, eight and 15 years. The objectives of the study were to characterise quantitative genetic variation in the population through the estimation of genetic parameters, and to use these parameters in combined indices to select for specified breeding objectives for *P. elliottii* in Zimbabwe.

All traits of interest were under a reasonable degree of additive genetic control, and the magnitudes of non-additive genetic variances were almost invariably much less than those of additive genetic variances. Narrow-sense heritabilities for growth traits, wood density and resin yield were moderate to high, ranging from 0.3 - 0.42; those for stem straightness and branching traits were lower, ranging between 0.10 and 0.25. Genetic correlations at each of the assessment ages were more variable; of most consequence for this study were the slight negative correlations between wood density and both stem diameter and volume, and the slight positive correlation between density and height. Age-age correlations for growth traits were high, indicating potential for early selection. Age-age correlations for other traits ranged from moderately negative to highly positive. Although statistically significant for many traits, genotype-environment interaction was judged by a number of criteria to be of little practical importance. No one site was the most efficient for selection across the range of traits for establishment at other sites; rather, a set of pooled parameters was estimated for application on sites typical of those on which commercial plantations of *P. elliottii* are established.

Selection indices were constructed for four breeding objectives, representing differing assumptions about the relative importance of saw-timber and resin production. Indices for both direct and indirect selection were compared in terms of genetic gain, efficiency and accuracy, which were influenced by the differential weighting of traits in the breeding objective. The highest gains, efficiency and accuracies were for the breeding objective of saw-timber only; increasing the emphasis on resin production reduced each of these parameters, and also had a more adverse impact on wood density. For a breeding objective corresponding to or emphasizing saw-timber production, selection based on diameter or height at five years was best; selection on the latter has the advantage of maintaining wood density at around its present level. Should resin production also be important, resin yield or a correlated trait must be included in the index. Efficiencies of indirect selection were highest at five years, regardless of the breeding objective or selection criteria considered. The lack of economic information was a considerable hinderance in conducting these analyses.

The construction of more complete indices, incorporating information from all siblings represented in the factorial mating design, was also investigated for the breeding objective of saw-timber production. These indices were compared in terms of gain and accuracy, and their effect on population structure in the subsequent generation. Selection based on the most complete index resulted in the greatest gain and accuracy, but also in the greatest reduction in additive genetic variance in the next generation. These results highlight the dilemma facing breeders charged both with achieving gains in the short term and maintaining diversity over the longer term. Breeding strategies which facilitate differential intensities of selection and breeding, and the maintenance of a large effective population size, are seen as the best means to resolve these conflicting demands; some implications for the breeding population of *P. elliottii* in Zimbabwe are discussed.

Acknowledgements

This work was made possible through funding from the UK Overseas Development Agency and the British Council, for which I am grateful. The Zimbabwe Forestry Commission allowed use of data for this study; I gratefully acknowledge the work of many Commission staff in establishing, maintaining and assessing the progeny tests, in particular, Richard Barnes, Lyn Mullin, Caleb Mhongwe and Gideon Mafodya.

I would also like to express my gratitude to the following persons at OFI:

- My supervisors, Peter Kanowski, Jackie Birks and Richard Barnes for their support and guidance. I would especially like to thank Peter for his patient review of my work which was vital for the completion of this thesis. *Thanks, Peter.*

- A very special special thanks to Nuno Borralho, for his help with statistical work and reviwing of the work.

- Andrew Dunsdon, for his help with statistical work.

- Guy Riddihough, whose constant support and reviewing was greatly appreciated.

- Cheryl Howse, Julie Smith, Peter Franklin, Kit Bailey and the library staff for their help with the computing and library facilities.

- All the horse-box members and other colleagues for their encouragement and friendship.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES

LIST OF TABLES

LIST OF TABLES

LIST OF TABLES

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1 -

1 - Introduction

Quantitative genetics is concerned with the inheritance of those differences between individuals that are of degree rather than of kind, quantitative rather than qualitative.

D.S. Falconer

1.1 - Taxonomy, natural distribution and exotic establishment

Pinus elliottii, like many species, has suffered a confused nomenclature (Little and Dorman 1954). The species now known as *P. elliottii* was known by many different names prior to the 1950's; for example, as *P. caribaea* Morelet as in the West Indies, *P. cubensis* Griseb., *P. heterophylla* (Elliot) Sudw. and many others. Little and Dorman (1954) recognised *P. caribaea* as a different species from *P. elliottii*, which they split into two varieties, *P. elliottii* Engelm. var. *elliottii* (typical slash pine) and *P. elliottii* Engelm. var. *densa* (South Florida slash pine) Little and Dorman. Gaussen (1960 in Nikles 1966) provisionally elevated *P. elliottii* var. *densa* to specific level, indicating that the taxonomic treatment of *P. elliottii* may not yet be complete.

The distribution of variety *elliottii* (typical slash pine) is confined to the coastal plains of the south-eastern United States, occurring in the southern parts of South Carolina, Georgia and Alabama, south-eastern Mississippi and Louisiana, and over much of Florida. The variety *densa* has a more restricted range along the east and west coast of south Florida (Little and Dorman 1954). However, Langdon (1963) reported the occurrence of the variety *densa* further inland in south-central Florida than reported by Little and Dorman in 1954. An area of overlap between the two varieties was recognised by Langdon (1963) in Polk County, Florida, where the two varieties are indistinguishable. It has been suggested that the highly fluctuating and more severe environmental conditions in the southern margins of distribution of the two taxa result in the maintenance of high heterozygosity in these populations (Squillace 1966).

In the subsequent discussion here, *P. elliottii* var. *elliottii* will be referred to as slash pine, and *P. elliottii* var. *densa* as South Florida slash pine. The two varieties differ quite markedly in several botanical and adaptational features. Slash pine has normal erect, slender, pencil-like-stemmed seedlings, while the South Florida slash pine is more grasslike. The needles of the former are in fascicles of two and three, whereas the latter has its needles in fascicles of two and rarely three. Slash pine is generally a large tree whereas the South Florida slash is medium sized to small. Oleoresin will flow easily and is tapped from living trees in slash pine, but this is not possible with South Florida slash pine. Although slash pine tolerates drier sites, it is normally found on moist swamp

soils. South Florida slash pine inhabits drier sites on sandy flatlands and limestone outcrops. Slash pine occurs naturally in latitudinal ranges from about 33^0 30'N in South Carolina to about 27^0N in Florida; the natural longitudinal limits are from about 79^0 45'W in South Carolina to about 91^0W in Louisiana. The altitudinal range is from sea level to about 150 m. The latitudinal range of South Florida slash pine is from about 29^0 15'N to about 24^0 40'N, and the longitudinal range from about 80 to 83^0W. South Florida slash pine will occur at altitudes of about 15 m, but more usually at less than 7 m (Barrett and Mullin 1968). However, these distributions are confused in the transition zone discussed above (Bethune and Langdon 1966 and Mergen 1958).

Both varieties of *P. elliottii* were introduced into Southern Africa at the turn of this century. Slash pine was first introduced into Zimbabwe in 1933 from South Africa. South Africa obtained *P. elliottii* seed from the Gulf States in the USA until 1938/39, when sufficient local seed became available (Poynton 1979). It is likely, therefore, that the early introductions to Zimbabwe from South Africa were derived from the Gulf States (Mullin *et al.* 1978). Subsequent seed imports were mainly from South Africa until some seed was obtained from a source in Louisiana, USA, in 1962.

The first *P. elliottii* provenance trials in Zimbabwe were established in 1963 and 1964 at altitudes of 3100, 4100 and 6050 feet (Barrett and Mullin 1968). Only three provenances were available for these trials: one from Mississippi

and two from Florida, including the South Florida slash pine (Barrett and Mullin 1968). This variety was introduced to Zimbabwe in 1961, when a small quantity of seed was received from Broward County, Florida, and subsequently used in provenance trials. The variety grew slowly for the first two years; experience with slash pine led to expectations of rapid growth from the third year onwards. However, these were not fulfilled in South Florida slash pine, and led to its subsequent exclusion from the tree improvement programme.

P. elliottii var *elliottii* Engelm has generally performed well where it has been introduced as an exotic to warm tropical zones. The major plantings of this species have been in Brazil, China, South Africa, Australia and Zimbabwe. The largest areas of slash pine have been established in China, where the species outgrows the native species on infertile soils. By 1988, some 720 000 ha of 14 provenances had been established in three climatic regions (Zhigang 1989). Initial plantings in South Africa were limited by difficulties in obtaining seed; when this constraint was overcome, the area of slash pine established was second only to *P. patula*. The largest plantings are found along the slopes of the escarpment and its foothills in the eastern Transvaal, where the tree is growing successfully on the full range of sites from the hot lowveld to the cool plateau (Poynton 1979). Slash pine has become an important species in South Africa for both timber and for pulp, because of its high wood density and tall oil content. By 1988, 72 140 ha of slash pine had been established (South African Department of Environmental Affairs 1988). In Queensland, Australia,

the species was important for plantation cultivation until the mid-1970's, but is now superseded by its hybrid with *P. caribaea* var. *hondurensis* Barrett and Golfari (Department of Forestry, Queensland 1983). Nevertheless some 65 000 ha of pure *P. elliottii* were established by the Department of Forestry, Queensland and nearly 30 000 ha by a private company, A.P.M. (Department of Forestry, Queensland 1990). Large areas have been established in Brazil, but few details are available. In Zimbabwe, *P. elliottii* is the second most important softwood species, after *P. patula* Schiede and Deppe; approximately 35 000 ha have been established (Forest Research Centre[1] pers. comm.). The advantages of *P. elliottii* in Zimbabwe over the alternative coniferous species, *P. taeda* L. and *P. patula*, are its ability to better withstand adverse planting conditions, drought, and weed competition (Mullin *et al* 1978).

Timber and pulpwood are the major products of both the natural and exotic forests of *P. elliottii*. A variety of other products are also important: for example, in Zimbabwe, the species is also used in particle chipboards for which it is particularly suited because of the resinous nature of the wood. Veneer recovery is usually high because of the relatively small knot size. In Zimbabwe, *P. elliottii* is tapped for resin commercially for the production of rosin and turpentine.

[1] Forest Research Centre, P.O. Box HG 595, Highlands, Harare, Zimbabwe.

Although slash pine has a relatively limited natural distribution, provenance variation is important for many of the traits. Dorman (1976) reported results from 15 provenances out-planted at seven locations, all in the Georgia-Florida area. These showed large differences in growth, survival, susceptibility to fusiform rust, and minor morphological and physiological traits. After 10 years, it was apparent that trees from the extreme northern and southern parts of the range were, on the average, shorter in height than those from the central part of the range. The good oleoresin producers were identified as those from the well drained soil areas in the coastal uplands and flatwoods of south-east Georgia and north-east Florida. Those from the deep sanded areas were characterised by poor volume production. Specific gravity was seen to increase in a north-west to south-east direction through Georgia and Florida. Commercially important provenance variation has also been reported in many exotic locations, which Dorman (1976) has reported comprehensively.

In its natural range, *P. elliottii* is susceptible to fusiform rust infection. Fusiform rust is the most economically-important disease of slash pine in the southern USA, with yield losses of up to US $35 million annually (Cooperative Forest Genetics Research Program 1990). Slash pine resistance to this pest is variable and the subject of intensive breeding efforts: details of this work may be seen in the annual reports of the Cooperative Forest Genetics Research Program (CFGRP) of the University of Florida .

Slash pine is relatively free of pests in most locations where it is grown as an exotic. In Zimbabwe the only pest of concern is *Pineus pini* Gmelin, which causes little commercial damage. However, the species is very susceptible to the fungus *Armillaria mellea* (Vahl ex Fr.) Quel, which causes deaths mainly at lower altitudes where the plantations have been established on indigenous woodland sites (Mullin *et al* 1978).

1.2 - Genetic improvement

The genetic improvement of *P. elliottii* in its natural environment was initiated in the early 1940's, but did not begin in earnest until the 1950's. Activities were oriented to solve practical problems such as grafting or controlled crossing, or to establish basic information such as the extent of provenance variation (Squillace 1979). The breeding strategies became more advanced as they developed, with the more sophisticated usually entailing controlled crossing of original selections made in the wild, establishment of base populations from their progeny, selection of the best individuals to establish new seed orchards. Tree improvement played an important role in the rapid expansion of afforestation in the south, in association with site selection and preparation, seedling quality, and planting technology (Barber 1979). Appreciable gains have been obtained in the programmes; detailed accounts are provided by Squillace (1989) and the CFGRP (1990).

In Queensland, Australia the breeding of slash pine was initiated in 1939 with major emphasis on improvement in stem volume and quality (Allen 1985). Although the establishment of pure slash pine in Australia has ceased in favour of the hybrid with *P. caribaea* var *hondurensis,* breeding of slash pine for the hybrid programme continues. The first hybrids were planted in 1958; further details may be found in Nikles (1970), Allen (1985), Department of Forestry, Queensland (1979,1983), and Nikles and Robinson (1989).

In South Africa, breeding of slash pine initially concentrated on the improvement of volume production, bole straightness, branch size and angle, and wood properties. The appearance of the insect pests *Pineus pini* and *Cinara cronartii* T. et P. soon gave a new dimension to the programme, with vegetative propagation of disease free material becoming very important (South African Department of Environmental Affairs 1988). First generation selections in the base population in the Transvaal were only completed in 1984; the hybrid between *P. elliottii* and *P. caribaea* var *hondurensis* has performed well and is being pursued (van Wyk 1986).

Mullin *et al* (1978) reported the breeding of *P. elliottii* in Zimbabwe; it began in 1958 when the principal concern of breeders was to establish trials to test general combining ability of candidates for the breeding programme and, in some cases, the specific combining abilities. Trials were also established specifically to test the importance of genotype - environment effects. The main emphasis of the programme in the early stages was the selection of as many

plus trees from as many different altitudes as possible. Once identified, these trees were cloned in untested orchards for the commercial production of seed. Over the subsequent 20 year period, a total of 89 plus trees were selected locally and at least 48 clones were imported from elsewhere, primarily South Africa. Resistance to *Pineus pini* was assumed to be heritable, and any tree found to be infested by *Pineus pini* was promptly discarded from the breeding programme so as to reduce the incidence of the pest in plantations. The breeding programme was based on recurrent selection in a single breeding population of plus trees with complete individual tree pedigree control. Single pair, diallel and factorial mating designs were used; seed production was from progeny-tested clonal orchards (Barnes and Mullin 1989).

The breeding philosophy in Zimbabwe underwent a major change in 1981. The large number of plus trees that had been selected in many species were more difficult to manage in single populations. Selection procedures were considered inflexible and cumbersome, and limiting to rapid, short term improvement. It was apparent that a new breeding strategy was necessary; it had to be simple enough to be workable, but complex enough to account for the many different species, environments, purposes of breeding, and availability of genetic material. The multiple population breeding strategy (MPBS) was therefore devised (Namkoong *et al* 1980) and applied to breeding populations in Zimbabwe (Barnes 1981). Basically, this strategy was devised to cope with the breeding of many diversified populations of different species at the same time, and to simplify long-term pedigree control, which was

maintained at the population rather than the individual tree level. It also facilitated the use of genotype-environment interaction and the preservation of variation. Since 1981, its specific application to *P. elliottii* in Zimbabwe has been developed and reported in the annual Plan of Work for the Zimbabwe Forestry Research Programme since 1981 (Barnes 1981-1990), and summarised elsewhere by Barnes (1986 and 1987), and Barnes and Mullin (1989).

To date there are more than 200 plus trees in the multiple population breeding programme, selected in private stands, commercial plantations, provenance and progeny trials. A total of 15 progeny trials of the species have been planted; most are now of second generation selections.

The changes in breeding strategy imply that the results obtained from the analyses of data from the progeny trials established in the era of recurrent selection will have to be interpreted carefully. The second generation selections are members of different sub-populations in the multiple population breeding strategy. The aims in the breeding objectives of the species have also changed with the change in strategy, with *P. elliottii* now being bred for more characteristics than previously. The new strategy is based on the formation and maintenance of separate populations for each of the major objectives and environmental regions. Barnes and Mullin (1989) explained that under a multiple population strategy, a number of populations for a single species are kept separate so as to produce trees with different gene complexes. The objective is the maintenance of different populations while practising

various intensities of breeding with them. As most traits are under multiple gene control, diversity will occur between the sub-populations even if selection criteria, selection pressures and the environments are similar. Also, different sets of genes are brought together in different populations and currently neutral alleles will not be lost in all populations. Crossing these populations at any time will reinstate variation, overcome inbreeding depression and create new populations with specific attributes. In essence, the composition of sub-populations is entirely dependent on the specific needs of the strategy.

A total of 14 sub-populations of *P. elliottii* have been created in Zimbabwe. All have timber production as the main breeding objective; 11 have pulp production and three have oleoresin production as the secondary objective. It is the intention that each sub-population comprises 50 or more trees, but not all are currently of this size (Barnes 1981-1990).

1.3 - Objectives of this study

The general objectives of this study are to examine genetic variation in traits of commercial significance for *P. elliottii* in Zimbabwe, and to use this information to construct selection indices which best meet breeding objectives. Data were available from a series of progeny tests, established in the era of recurrent selection, originating from factorial mating designs, established on three sites in Zimbabwe. The tests were assessed for a multitude of traits in the fifth, eighth and 15th years.

The specific objectives of the study, around which the thesis is structured, are to:

1) estimate additive and dominance variance components and derive genetic parameters in the form of heritabilities, genetic correlations, juvenile-mature correlations and genotype-environment interactions, for production and quality traits at the three ages;
2) use these parameters to develop selection indices for specified breeding objectives relevant to the Zimbabwean breeding programme;
3) investigate the optimum age for selection for the breeding objectives;
4) investigate the consequences of using indices incorporating more complete information from relatives;
5) consider the consequences of these results for the breeding programme of *P. elliottii* in Zimbabwe.

Chapter 2 -

2 - Trends over time in additive and dominance genetic parameters for growth, stem straightness, wood density, resin yield and branching traits

2.1 - Introduction

Estimates of genetic parameters are required for the determination of optimum culling levels and the calculation of genetic gains, both of which contribute to efficient tree breeding (Cotterill and Dean 1990). To use parameter estimates efficiently, the tree breeder needs to know how they are influenced by the environment and time. The objectives of this study are to derive, from additive and dominance variance components, parameters in the form of heritabilities, genetic correlations, juvenile-mature correlations and genotype-environment interactions, for growth, stem straightness, wood density, resin yield and branching traits in Zimbabwean *P. elliottii* at several ages.

2.1.1 - Variances and heritabilities

The variation of a trait in a population, measured on a continuous scale, is expressed as the variance, which can be partitioned into that due to the environment and that due to genetic effects (Falconer 1981). The latter can be partitioned further into that due to the additive genetic effects and that due to non-additive effects, which include the dominance effects. Additive genetic effects express the extent to which phenotypes are determined by the average effect of genes transmitted from their parents, and for this reason they are important to breeding programmes (Falconer 1981). Non-additive genetic effects arise from dominance and epistatic gene action (Nicholas 1987) and are more important, for example, in clonal forestry where both additive and non-additive genetic effects are utilised (Cotterill and Dean 1990).

Narrow sense heritability is defined as the variation due to the additive genetic effects expressed as a proportion of the total phenotypic variation (Falconer 1981). The function of the heritability estimate is predictive in that it expresses reliability of the phenotypic value of individuals as a guide to the breeding value, *ie*, their genetic worth (Falconer 1981). The literature reports many estimates of the extent of genetic control of various traits for industrial tree species. Growth traits of *Pinus* species between the ages of five and 16 years have been found to be under low to moderate genetic control, with heritabilities ranging from 0.10 to 0.50, and standard errors ranging from 0.05 to 0.23 (*eg*, Barnes *et al* 1992a and b, for *P. patula*; Cotterill and Dean 1988, for

P. radiata D. Don; Cotterill *et al* 1987, for *P. elliottii, P. pinaster* Ait. and *P. radiata*; Woolaston *et al* 1990, for *P. caribaea*). Similarly, stem straightness at the same ages has been found to be under low to moderate genetic control, ranging from 0.10 to 0.30, with standard errors ranging from 0.11 to 0.15 (*eg* Cotterill and Dean 1988, for *P. radiata*; Cotterill *et al* 1987, for *P. pinaster, P. radiata* and *P. elliottii*; Woolaston *et al* 1990, for *P. caribaea*). Megraw's (1985) review and Zobel and van Buijtenen (1989) report that wood density in *Pinus* species is generally under strong genetic control, ranging between 0.4 and 0.7 with standard errors ranging from 0.1 to 0.20. Branch traits (branch diameters and internode length) have also been found to be under moderate to high genetic control, ranging from 0.14 to 0.63 with standard errors ranging from 0.07 to 0.20 (*eg*, Barnes *et al* 1992 a, for *P. patula*; Dean *et al* 1986 and Volker and Cameron 1988, for *P. radiata*).

2.1.2 - Genetic and phenotypic correlations

Genetic correlations are defined as associations between the breeding values of two traits, whereas phenotypic correlations are associations between the phenotypic values of two traits. The main genetic cause of correlations is pleiotropy, that is, one gene may influence more than one trait thereby causing simultaneous variation in the affected traits. A knowledge of correlations is important for the efficient conduct of a breeding program in that it will indicate the extent to which selection on a particular trait may influence others (Falconer 1981). Estimates of correlations are required to predict genetic gains

in correlated traits when selection is practised as well as how effectively many traits can be changed simultaneously (Cotterill and Dean 1990).

Literature review reveals that many studies have been carried out to estimate genetic and phenotypic correlations in industrial tree species. Growth traits (height, diameter and volume) have been found to be strongly correlated, typically at levels between 0.40 and 0.90 with standard errors ranging between 0.03 and 0.19 (*eg*, Barnes *et al* 1992a and b for *P. patula*; Cotterill and Dean 1988, for *P. radiata*; Cotterill *et al* 1987, for *P. pinaster*, *P. radiata* and *P. elliottii*; Woolaston *et al* 1990, for *P. caribaea*). These studies also report genetic correlations between stem straightness and growth traits that range from low to moderate (0.10 to 0.30 with standard errors between 0.11 and 0.29). Dean *et al* (1986) reported strong negative genetic correlations between growth traits and branching traits (-0.24 to -0.79 and standard errors between 0.16 and 0.30) for *P. caribaea*, and Birks and Barnes (1991) reported negative genetic correlations between growth traits and wood density for *P. patula*, ranging between -0.3 and -0.4 with standard errors between 0.01 and 0.30.

2.1.3 - Juvenile - mature correlations

Juvenile-mature correlations, specific genetic correlations defined as associations between the breeding values of traits at earlier and later ages, are of interest because of their potential to facilitate early selection, which can increase the rate of genetic improvement of long lived organisms (Franklin

1979). Selecting earlier than the rotation age shortens the generation interval; although it may lead to greater genetic gains per year, it is usually at the expense of gain per generation (Matheson *et al* 1988). The success of early selection is dependent on trends over time in heritabilities and genetic correlations of the early and mature traits under study (Cotterill and Dean 1988). These trends have been the subject of numerous studies (*eg* Borralho *et al* 1992, Cotterill and Dean 1988, Foster 1986, Kang 1985, Lambeth 1980, Lambeth *et al* 1983, McKeand 1988, Squillace and Gansel 1974, Nanson 1976).

Juvenile-mature correlations have been reported for many industrial species and, in most cases, it is evident that juvenile-mature correlations in growth traits are at least moderate and often high (r_a ranges between 0.5 and unity and standard errors between 0.01 and 0.15, depending on ages of assessment). High juvenile-mature correlations between growth traits have been reported for many *Pinus* species (*eg*, Cotterill and Dean 1988, for *P. radiata*; Foster 1986, Lambeth *et al* 1983, for *P. taeda*; Reimenscheneider 1988, for *P. banksiana* Lamb.; Squillace and Gansel 1974, for *P. elliottii*). These correlations have been estimated both as phenotypic correlations of family means (*eg* Squillace and Gansel 1974, for *P. elliottii;* Wakeley 1971, for *P. elliottii* and other *Pinus* species) and as correlations of breeding values (*eg* Cotterill and Dean 1988 for *P. radiata;* Gill 1987, for *Picea sitchensis* Bongard; Namkoong and Conkle 1976, for *P. ponderosa* Dougl. ex Laws.).

As a result of these studies, different selection ages have been suggested as the

most efficient in terms of realising genetic gains *eg*, between five and 10 years for *P. taeda* and *P. elliottii* (Lambeth 1980, Lambeth *et al* 1983, Nanson 1976, Squillace and Gansel 1974). The most efficient age for selection has also been expressed in terms of average tree size, *eg* seven metres for *P. radiata* (Cotterill and Dean 1988) or eight metres for *Eucalyptus globulus* Labill. ssp. *globulus* (Borralho *et al* 1992).

In this study, the term "juvenile-mature correlation" is used to describe genetic correlations between traits at an age considered juvenile, *viz*, five or eight years, and that considered to equate to maturity, *viz*, 15 years, which commercially is equivalent to half the rotation age.

2.1.4 - Genotype-environment interaction

The concept of genotype-environment interaction (gei) has been defined as the varying relative performance of genotypes according to environment (Burdon 1977). If individuals of one population are to be planted in different environments, it is important to know whether genotype-environment interaction exists, and if it is of practical consequence. There is substantial literature on genotype-environment interaction in pine species: for example, for *P. elliottii* (Goddard and Smith 1969); *P. radiata* (Burdon 1977, Johnson and Burdon 1990, Matheson and Raymond 1984a, Pederick 1990); *P. taeda* (Owino 1977); and *P. caribaea* (Nikles 1972, Woolaston *et al* 1990). Gei has also been the subject of various reviews, for example, those of Gibson (1982), Matheson and

Raymond (1984a), Matheson and Cotterill (1990) and Shelbourne (1972).

There is also an extensive literature on methodologies applied to the analysis of genotype-environment interaction (*eg*, Burdon 1977, Finlay and Wilkinson 1963, Freeman and Perkins 1971, Matheson and Raymond 1984a, Pederson 1974, Shelbourne 1972). Much of this work has been directed to establishing whether interaction is present. However, as Robertson (1959) commented, "these statistical statements do not specify whether any of this statistically significant interaction has any biological importance or whether the design was such that biologically important interactions would have been detected". Used in this sense, "biologically important" genotype-environment interaction presumably implies either, or both, genetic and economic consequences. Genetic consequences include losses in the efficiency of selection, and therefore gain, and the optimal structure of the breeding population; each has economic implications.

Matheson and Raymond (1984a) reviewed approaches to the study of genotype-environment interactions, distinguishing between those for which the primary objective was identification, and those which sought explanation of the interaction. Only the former is of interest here.

Neither the presence nor the importance of genotype-environment interaction in Zimbabwean *P. elliottii* populations have been studied in detail, although the species has been planted across a range of environments which represent

a variety of site types and elevations. This study is concerned not only with determining the statistical significance of genotype-environment interaction but, more importantly, with considering the practical implication of any such interaction.

2.2 - Experimental material

2.2.1 - Progeny test location and management

The progeny tests from which data originate are part of a series established by the Zimbabwe Forestry Commission. They were planted on three different sites in Zimbabwe, and are identified locally as tests 23a, 23b and 23c. Test details are summarised in Table 2.1. Tests 23a and 23b are located on much more productive sites than is 23c, which is located on a site with poorer soil and lower rainfall. Test 23c was established with the primary purpose of investigating genotype-environment interaction with respect to tests 23a and 23b. Locations for tests 23a and 23b are typical of those in the Zimbabwean eastern highlands on which commercial plantations of *P. elliottii* are established.

Table 2.1 Details of progeny tests used in this study.

Identification	Test 23a	23b	23c
Location	Tarka, E. Highlands	Stapleford, E.Highlands	Grasslands, Marondera
Latitude	19° 59'S	18° 44'S	18° 10'S
Longitude	32° 56'E	32° 49'E	31° 30'E
Altitude (m)	967	1760	1646
Mean annual rainfall (mm)	2279	1836	884.7
Mean annual temperature	16.6°C	14.1°C	17.1°C
Soil type	Dolerite/quartzite-derived; varying from reddish brown fine grained sandy loams to red brown clays.	Quartzite/dolerite- derived; brown red clays.	Granite/dolerite-derived; greyish brown medium-grained sands, of lower fertility.
Parental origin	Bulk commercial ex Georgia, Lousiana and South Carolina, USA, via South Africa.		
Mating design	Factorial 24♀ x 9♂	Factorial 23♀ x 9♂	Factorial 25♀ x 4♂
	Diallel 9♀ x 9♂	Diallel 9♀ x 9♂	Diallel 9♀ x 9♂

	Number of crosses					
	Produced	Possible	Produced	Possible	Produced	Possible
Factorial	157	216	145	207	51	100
Diallel	53	81	46	81	9	81

2.2.2 - Silviculture and field design

After disc-harrowing of the sites, the progeny tests were planted between January and February 1976, at a spacing of 2.44 m x 2.44 m. The tests were established as randomised complete blocks with six replications. Each family was represented in every replicate by a 10 - tree line plot. No fertilization was carried out in the field. Weeding was manual when necessary during the tests' early life. The tests were pruned at five years, and thinned at eight years by systematically removing every other tree, leaving 50 percent of the original trees standing.

2.2.3 - Genetic material

The three progeny tests included a total of 216 full-sib families from factorial mating designs, in which each member of a group of one sex is mated with each member of a group of the other sex (Bridgewater 1992). The progeny tests also included a total of 53 full-sib families in a diallel mating design embedded within the factorial design; in full diallels each entry is mated with every entry (Bridgewater 1992), here, matings represented an incomplete diallel without selfs. The 33 parents used in these factorials and diallels were selected as superior phenotypes from unimproved plantations in both Zimbabwe and South Africa. Little is known of their origin or degree of relatedness, but it is assumed that they are unrelated since they were widely distributed within plantations. The South African plantations in which parents were selected originated from seedlots from Georgia, S. Carolina and Central Louisiana, USA; the Zimbabwean plantations were derived from seed collected in South African plantations. The crosses represented in the tests are shown in Table 2.2. The subset of families common to the three progeny tests, on which genotype-environment interaction analyses were based, is presented in Table 2.3.

Table 2.2 Families included in the three progeny tests, where A, B, C, refer to those present in tests 23a, 23b and 23c, respectively. Crosses in the shaded block represent the diallel design. The A crosses in the lower inner block represent those in the 8 x 8 factorial sampled for resin yield in test 23a.

	Males								
Females	22	23	45	49	129	137	177	9	130
22		AB			AB	AB		AB	
23				ABC	ABC	AB	AB	ABC	A
45	AB	A		AB	AB	AB	AB	AB	A
49	A	AB	AB		AB	ABC		AB	
129	A	AB	AB	AB		AB		AB	AB
137	AB	AB	AB	AB	AB			AB	AB
177	AB	A	ABC	ABC	AB	ABC		AB	AB
9	AB	AB	ABC	ABC	AB		ABC		A
130									
58	AB	AB	AB	ABC	AB	AB	ABC	ABC	
76	AB	AB	AB	ABC	AB	AB	ABC	AB	
87	A	AB	AB	AB	AB	AB	AB	AB	
126	AB	AB	AB	AB	AB	AB	ABC	AB	
128	AB	AB	AB	ABC	AB	AB	ABC	ABC	
174	AB	ABC	AB	AB	AB	AB	AB	AB	
175	AB	ABC	AB	ABC	AB	AB	ABC	AB	B
200	AB	ABC	AB	ABC	AB	AB	AB	ABC	AB
28	AB	A		AB		A	AB	AB	
43	AB	ABC		AB	AB			AB	
57	AB	ABC	AB		AB	AB	AB	ABC	
125	AB	ABC		A	AB		ABC	ABC	
132	AB	ABC	AB	ABC	AB	AB	AB	BC	
138	AB	AB	AB	AB	A		AB	AB	AB
172	AB	ABC		AB			A	AB	
173		ABC	AB	ABC		AB	ABC	ABC	AB
176	AB	ABC			AB	AB	ABC		A
86			AB	AB			AB	ABC	
88	AB	ABC	AB	ABC	A	AB		ABC	
89	A	ABC		AB	AB	AB	ABC		
178				A			A		
203		AB		A			ABC	ABC	
224	A	AB		ABC	AB		AB	AB	
234	AB	A		A	A	A	A	B	A

Table 2.3 Parental representation in families common to the three progeny tests (A, B, C), on which genotype-environment interaction analyses were based.

	Males				Total
Females	23	49	177	9	
58		ABC	ABC	ABC	3
76		ABC	ABC		2
126			ABC		1
128		ABC	ABC	ABC	3
174	ABC				1
175	ABC	ABC	ABC		3
200	ABC	ABC		ABC	3
43	ABC				1
57	ABC			ABC	2
125	ABC		ABC	ABC	3
132	ABC	ABC			2
172	ABC				1
173	ABC	ABC	ABC	ABC	4
176	ABC		ABC		2
86				ABC	1
88	ABC	ABC		ABC	3
89	ABC		ABC		2
203				ABC	1
224		ABC			1
Total	12	9	9	9	39

2.2.4 - Measurement, assessment and derivation of traits

The three progeny tests were measured for height and diameter and assessed for stem straightness at five, eight and 15 years. Wood density and resin yield were assessed at 15 years after planting. Branching characteristics were assessed only at five years. Details of traits measured or derived are given in Table 2.4.

Table 2.4 Traits measured and derived at five, eight and 15 years in the three progeny tests, and their units of measure.

Trait	Code	Unit
5 years		
Total height	HT5	m
Stem diameter over bark at 1.3 m height	DBH5	cm
Volume over bark	VOL5	dm^3
Stem straightness	STR5	rating 1-7
Number of branches counted in the two whorls nearest breast height	BRCT5	number
Branch diameter (five centimetres from branch insertion point).	BRDM5	mm
Average internode length (excludes section between the ground and the first whorl)	AIL5	m
8 years		
Total height	HT8	m
Stem diameter over bark at 1.3 m	DBH8	cm
Total stem volume over bark	VOL8	dm^3
Stem straightness	STR8	rating 1-7
15 years		
Total height	HT15	m
Stem diameter over bark at 1.3 m	DBH15	cm
Total stem volume over bark	VOL15	dm^3
Wood density	DENS15	kg/m^3
Resin quantity	RESQ15	g/wk
Stem straightness	STR15	rating 1-7

Height was measured with metre rods, from the base of the tree to the tip of the growing shoot. Stem diameter was measured at 1.3 m (breast height) with a girth tape. Stem volume over bark at five (VOL5), eight (VOL8) and 15 years (VOL15) was calculated from the height and diameter measurements using the volume function :-

$$VOL_i = 0.45\pi (DBH_i/2)^2 HT_i \quad (2.1)$$

VOL_i = the volume at five, eight or 15 years;

DBH_i = the diameter over bark at 1.3 m at five, eight or 15 years;

HT_i = the height at five, eight or 15 years;

and 0.45 is the form factor appropriate for the species (Mills[1] pers. comm.).

Wood density was assessed in only three replicates of each test. Each of the three progeny tests had two five millimetre bark to bark increment cores taken through the pith at breast height (1.3 m) of each tree in three replicates. Where the trees were too large for the five millimetre borer, an eight millimetre borer was used. The cores were taken away from the nodal swellings so as to avoid compression wood and branch scarring. If the nodes were at 1.3 m height, drilling was positioned a few centimetres above or below, depending on which was closest to breast height.

Bark was removed from the cores; they were measured then preconditioned in water at approximately 4°C for 24 hours, until saturated. The cores were then dried in a conventional oven at 102°C for at least 48 hours, or until the weight was constant.

Wood density was calculated following Heinrichs and Lassen (1971):-

---

[1] Mr W. R. Mills, Forest Research Centre, Harare, Zimbabwe.

$$DENS15 = \frac{dry\ weight(grams)}{green\ volume(cm^3)} . 1000 \qquad (2.2)$$

where DENS15 = density in kg/m^3.

Resin was tapped from living trees in a subset of families in test 23a which consisted of an 8 x 8 factorial design (Table 2.2). Resin was collected over a three month period (October to December). Bark was stripped across half the width of the tree, east facing and approximately 30 cm from the ground, to expose the sapwood (a process called chipping). Gutters were laid at an angle of 45^0 to the chipped part of the tree to guide the resin flow into the glass bottle of known weight placed at one end of the gutter. The gutters were supported by nails. A horizontal strip of bark three centimetres high was then removed along the chipped area, a process known as streaking. Fifty percent sulphuric acid was sprayed on to the freshly stripped wound to encourage the flow of resin, as the streaking was not deep enough to open the resin ducts.

At the end of every week the amount of resin in each bottle was weighed and recorded. The bottles were rinsed out with solvent and water, and replaced on the tree. Re-streaking was carried out after every measurement, by extending the cut upwards by another three centimetres. After every fourth week sulphuric acid was resprayed to encourage resin flow. Weights of all resin samples collected over the 12 week period were summed, and this value divided by 12 to express the amount of resin produced in grams per week (RESQ15 g/wk).

Three traits were measured to assess branching excellence. The branch count (BRCT5) involved counting all branches in the two whorls nearest breast height. This trait was assessed as a measure of the average number of branches per whorl on each tree. The average branch diameter (BRDM5) was calculated as the mean of the diameters of all branches in these two whorls, measured at approximately five centimetres from the base of each. It was assessed as an indication of the general branch size. The internode length (AIL) was measured as the average internode length along the stem, excluding the section between the ground and the first whorl (Barnes 1973). This trait was assessed to characterise the frequency of whorls along the stem. It is important to note that internode length is not in this case equivalent to growth for a growing season, as it might be in a temperate region; in Zimbabwe, trees grow continuously throughout the year.

Stem straightness (STR5, STR8, STR15) was assessed on a predetermined scale of 1 (crooked) to 7 (straight), as defined in Table 2.5.

Table 2.5 Stem straightness categories and corresponding classifications, as applied by the Zimbabwean Forestry Commission (Barnes and Mullin 1968).

Category	Straightness characteristics of the main length	Comparable classification in general terms and note on value as a pole
7	No deviation which would appreciably reduce utilisation value	Straight: meets the transmission pole specification
6	(i) basically as 7 but with one minor defect slightly affecting utilisation OR (ii) basically slightly inferior to 7 but no specific defect	Nearly straight: meets any but the most exacting requirements
5	(i) basically as 7 but with one major defect appreciably reducing utilisation value OR (ii) as 6 (ii) but with a minor defect	Very slightly crooked: straight enough for most uses but not for transmission poles
4	basically as 6 (ii) but with either (i) a major defect OR (ii) several minor defects	Slightly crooked: has some value as a long pole
3	basically as 6 (ii) but with (i) at least two major defects OR (ii) a series of minor defects	Crooked: has practically no value as a long pole
2	basically inferior to (ii) and with specific defects such that utilisation would be confined to short straight lengths	Very crooked: suitable only for very short poles and for fuel wood
1	basically as 2 but with major and minor defects restricting utilisation to fuel or industrial wood	Malformed: has no value as a pole

2.3 - Analysis of data

Data from the diallel design were not analysed separately because the diallel was small, incomplete and unbalanced, and it was not clear that it would yield any more information than that already provided by analysis of the factorial design.

2.3.1 - Estimation of variance components

Variance components were estimated by the Residual Maximum Likelihood (REML) technique. Details of the technique and its function are described by Harville (1977), Patterson and Thompson (1971 & 1975) and Searle (1971 & 1987).

REML was developed mainly for the analysis of unbalanced data and is therefore appropriate for this study, where there is a substantial proportion (27 - 49%) of missing crosses. The program has no restrictions on the number of fixed and random effects, or covariates. The estimation of variance components is by maximum likelihood methods (Patterson and Thompson (1971 & 1975). The assumptions underlying the model are that the levels of each random factor are uncorrelated and normally distributed with a common variance. The residuals in the vector of random errors are also assumed to be normally distributed and uncorrelated with each other and with the other terms in the model (Robinson, 1987).

In the analyses, parents were treated as random effects, as they represented a sample of all parents of interest in the population about which inferences were made. The linear model used for the analyses of data from an individual site was:-

$$Y_{ijkl} = \mu + F_i + M_j + R_k + FM_{ij} + FMR_{ijk} + e_{ijkl} \qquad (2.3)$$

where Y_{ijkl} = individual tree observation;

μ = population mean;

F_i = random effect of the i^{th} female parent;

M_j = random effect of the j^{th} male parent;

R_k = fixed effect of the k^{th} replicate;

FM_{ij} = random effect of the ij^{th} family (female and male interaction);

FMR_{ijk} = random effect of the ij^{th} family by k^{th} replicate interaction;

e_{ijkl} = residual error.

2.3.2 - Phenotypic, additive and dominance variances

Estimates of additive and dominance variances were derived from the covariances between half and full-sibs, as described by Becker (1975) and Cotterill *et al* (1987), following expectations derived in Table 2.6.

Table 2.6 Genetic and environmental interpretation of the components together with the assumptions made (Becker 1975).

Variance components and relationships to covariance of relatives	σ^2_A	σ^2_D	σ^2_{AA}	σ^2_{AD}	σ^2_{DD}	σ^2_{AAA}	σ^2_c	σ^2_e
σ^2_m = cov HS_m	1/4	0	1/16	0	0	1/64	0	0
σ^2_f = cov HS_f	1/4	0	1/16	0	0	1/64	0	0
σ^2_{fm} = cov FS - (covHS_f + covHS_m)	0	1/4	1/8	1/8	1/16	3/32	0	0
$\sigma^2_w = \sigma^2_p$ - covFS	1/2	3/4	3/4	7/8	15/16	56/64	0	1

where σ^2_A = variance due to additive genetic effects;

σ^2_D = dominance genetic variance;

σ^2_c = variance due to the maternal environmental effects;

σ^2_{AA} = epistatic variance due to interactions of additive effects of two or more loci;

σ^2_{AD} = epistatic variance due to interaction of additive and dominance effects at two loci;

σ^2_{DD} = epistatic variance due to interactions of dominance effects at two loci;

σ^2_p = total phenotypic variance;

σ^2_e = the variance due to the environment;

σ^2_m = random effect of the j^{th} male parent;

σ^2_f = random effect of the i^{th} female parent;

σ^2_{fm} = random effect of the ij^{th} family (female and male interaction);

σ^2_w = contains the remainder of genetic variance plus all the environmental variance.

When the coefficient of inbreeding among the parents (F) is assumed to be 0, the variance component due to the maternal effects (σ^2_f) is equal to the genetic covariance among maternal groups of half-sib offspring:-

$$\sigma^2_f = COVHS_f = \frac{1}{4}\sigma^2_A + \frac{1}{16}\sigma^2_{AA} + \frac{1}{64}\sigma^2_{AAA} + \ldots\sigma^2_c \qquad (2.4)$$

where σ^2_A, σ^2_{AA}, σ^2_c and σ^2_p are as defined above.

If epistatic effects are assumed negligible, $4\sigma^2_f$ is used as an estimate of additive variance and hence:-

$$4\sigma_f^2 \approx \sigma_A^2 + 4\sigma_c^2 \qquad (2.5)$$

Maternal effects are often considered to be of importance in animal breeding, but they are usually assumed negligible in plants; if they are large, σ^2_A may be overestimated. There are few studies on the magnitude of maternal effects for *P. elliottii* or other *Pinus* species. The most relevant of these studies are those by Barnes (1973) for *P. patula*, and Cotterill *et al* (1987) for *P. pinaster*, *P. radiata* and *P. elliottii*, both of whom found maternal effects to be negligible. In the absence of other information, this result will be assumed to apply in this study, such that:-

$$\sigma_A^2 = 4\sigma_f^2 \qquad (2.6)$$

The genetic covariance among paternal groups of half-sib offspring is estimated as:-

$$\sigma_m^2 = covHS_m = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 + \frac{1}{64}\sigma_{AAA}^2 + \ldots \qquad (2.7)$$

The paternal component can be used to estimate directly the additive variance, if epistatic effects are assumed negligible; it has the additional advantage of generally being considered to be free of confounding effects, although exceptions have been recorded (see Neale *et al* 1986). Here, the additive genetic variance from the male parent was estimated as follows:-

$$\sigma_A^2 = 4\sigma_m^2 \tag{2.8}$$

In factorial designs where the number of male parents is much fewer than that of the female parents, this estimate is therefore likely to be less precise than that estimated from the variance due to female parents.

The average of the paternal and maternal components provides another estimate of additive variance under the assumptions that maternal effects are either absent or negligible and that both are equally reliable. Therefore:-

$$\sigma_A^2 \approx 2(\sigma_f^2 + \sigma_m^2) \tag{2.9}$$

The component σ^2_{fm} is an estimate of the covariance of full sibs, less the covariance of both maternal and paternal half-sibs, that is:-

$$\sigma_{fm} = covFS - (covHS_f + covHS_m) = \frac{1}{4}\sigma_D^2 + \frac{1}{8}\sigma_{AA}^2 + \frac{1}{16}\sigma_{DD}^2 + \frac{1}{64}\sigma_{AAA}^2 + \ldots \tag{2.10}$$

where σ^2_D, σ^2_{AD} and σ^2_{DD} are as defined in section 2.3.2.

In the above equation it is assumed that maternal variance is negligible. Given this assumption and that of negligible epistatic effects, it is possible to estimate dominance genetic variance:-

$$\sigma_D^2 \approx 4\sigma_{fm}^2 \tag{2.11}$$

The total phenotypic variance was estimated as:-

$$\sigma_p^2 = \sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_{fmr}^2 + \sigma_w^2 \tag{2.12}$$

where σ^2_p is the total phenotypic variance σ^2_f, σ^2_m, σ^2_{fm} are as described above, σ^2_{fmr} is the variance component due to family-replicate interaction or plot mean variance, and σ^2_w that due to residual which also contains the remainder of the genetic variance and the environmental variance, *ie*, the within family variance.

2.3.3 - Heritabilities

Estimates of narrow-sense heritabilities on an individual tree basis were derived separately from maternal and paternal half-sib covariances;

$$h_f^2 = \frac{4\sigma_f^2}{\sigma_p^2} \tag{2.13}$$

where h^2_f = narrow-sense heritability estimated from the maternal variance;

$$h_m^2 = \frac{4\sigma_m^2}{\sigma_p^2} \tag{2.14}$$

where h^2_m = narrow-sense heritability estimated from the paternal variance. Standard errors were estimated by the program REML.

It would also be possible to derive an average estimate from the female and male estimates, either as an unweighted average or some weighted basis, for example, weighting by the inverse of the standard error as described by Cunningham (1977), but this was not seen to be of any additional utility here.

The heritabilities calculated from equations 2.13 to 2.14 are block-adjusted (that is, the replicates are treated as fixed effects), as discussed by Cotterill (1987), Cotterill and Dean (1990) and Woolaston *et al* (1990).

2.3.4 - Phenotypic and genetic correlations

Phenotypic and genetic correlations between traits were estimated using a generalised least-square program (Harvey 1987). The additive correlations were based only on the maternal half-sib variances and covariances, as they were derived from a much larger number of parents and were therefore assumed to be more reliable and representative. Additive genetic correlations for height at age five were estimated from the whole population; correlations at eight years were estimated from that half of the population that was thinned systematically, as measurements were made only on this part of the population; correlations at 15 years were estimated from that half of the population that was left standing after the 50 percent thinning at eight years. As the thinning at eight years was systematic, it is expected that the data should still be representative of the whole population.

Analyses followed the linear model :-

$$Y_{ijkl} = \mu + F_i + M_j + FM_{ij} + R_k + e_{ijkl} \quad (2.15)$$

where Y_{ijkl} = individual tree observation;

μ = population mean;

F_i = random effect of the i^{th} female;

M_j = fixed effect of the j^{th} male;

FM_{ij} = random effect of the ij^{th} family;

R_k = fixed effects of the k^{th} replicate;

e_{ijkl} = residual error.

This model assumes that interactions of female with other fixed effects, such as replicates, are negligible. This simplification results from a limitation in the program. The model has the same assumptions as does that used by REML, that is, the levels of each random factor are uncorrelated, and normally distributed with a common variance. Standard errors were calculated according to Becker (1975).

As resin yield and wood density were assessed in different replicates and height measurements were recorded at eight years for thinned trees only, it was not possible to calculate correlations with these traits using the above methodology. Correlations between family means were assumed to be the best proxy, and were estimated, following Burdon (1977), as in equation (2.16):-

$$r_{A_{xy}} = \frac{corr\ \bar{N}_{f_{xy}}}{(\sqrt{h^2_{fx}})\ (\sqrt{h^2_{fy}})} \qquad (2.16)$$

where r_{Axy} = genetic correlation of family means of the traits x and y;

corr $\bar{N}_{fxy}$ = correlation of family means between trait x and trait y;

$h^2_{fx,}$ h^2_{fy}= heritability of family means for traits x and y respectively.

2.4 - Approaches to the analysis of genotype-environment interaction

Individual heritabilities derived from maternal variances, which originated from a much larger number of parents than did those from paternal variances, were used in the estimation of genotype-environment interaction. The study was based on 39 families common to all three tests (Table 2.3); the genotype-environment interaction discussed in this study therefore represents the interaction between family and environment. Five approaches were used to infer the extent and importance of genotype-environment interaction. They represent only a sample of the variety of methodologies reported in the literature and were used because of their relevance to the particular objectives of this study. The methodologies adopted are summarised in Table 2.7 and discussed in more detail below.

Table 2.7 Methodologies used in this study of genotype-environment interaction.

Method	Key references	Advantages	Disadvantages
Estimation of variance components	Patterson and Thompson (1971, 1975) Harville (1977) Searle (1971, 1987)	Strength is dependent on the design but it is a general test of variation and it is robust in many respects.	Assumptions are not always met by data; when they do not hold the power of the test is reduced. Heterogeneity of variance may falsely signal significant interactions and, if interactions are found to be present, the test does not indicate whether they are of practical importance.
Ranks	Matheson and Raymond (1984a)	Allows families to be compared and those that contribute most to the interaction, on the basis of rank changes, to be identified.	Sensitive only to rank changes, therefore the implications of a significant result should be considered carefully.
Spearman's rank correlation	Siegel and Castellan (1988) Snedecor and Cochran (1989)	Tests for a trend, ie, if there is a broad agreement between ranks. It has confidence limits and does not assume normal distribution.	As for ranks.
Genetic correlation	Falconer (1981) Robertson (1959) Burdon (1977)	The correlation is independent of whether environments represent a fixed or a random effect and is a quantitative measure of the importance of interaction.	Arbitrary definition of the values below which the correlation should fall before it is considered of practical importance; subject to usual difficulties of estimating genetic correlations (Robertson 1959).
Efficiency of selecting at one environment for planting on another	Burdon (1977) Matheson and Raymond (1984a) Woolaston *et al* (1990)	Indication of the losses to be expected from g x e. Easy to compute and the information obtained can be used for regionalisation.	Relies on accurate estimation of genetic parameters; arbitrary definition of values of practical importance.

2.4.1 - Analysis of variance

The linear equation used for the combined analysis with REML was as follows:-

$$Y_{ijklm} = \mu + F_i + M_j + S_k + FM_{ij} + FS_{ik} + MS_{jk} + FMS_{ijk} + RS_{lk} + e_{ijklm} \quad (2.17)$$

where μ = population mean;

F_i = random effect of the i^{th} female parent;

M_j = random effect of the j^{th} male parent;

S_k = random effect of the m^{th} site;

FM_{ij} = random effect of the ij^{th} family (female x male interaction);

FS_{ik} = random effect of the im^{th} female x site interaction;

MS_{jk} = random effect of the jm^{th} male x site interaction;

FMS_{ijk} = random effect of the ijm^{th} family x site interaction;

RS_{lk} = random effect of the km^{th} replicate within site interaction;

e_{ijklm} = residual error.

Assumptions of the model are as those in equation (2.3).

The proportion of total variance calculated from the variance components indicates the relative importance of each of the sources of variation.

2.4.2 - Ranks

Least square means (LSM) of each family were ranked for each trait (*eg* height) at each of the sites, as illustrated in Table 2.8.

Table 2.8 Least square site means for height and their rankings, for an illustrative sample of families.

Family	LSM 23a	Rank	LSM 23b	Rank	LSM 23c	Rank
88 x 49	6.000	3	6.555	4	6.000	3
224 x 49	5.996	4	4.669	5	3.100	6
58 x 9	4.331	5	7.065	3	8.000	2
88 x 23	7.458	2	8.000	2	5.333	4
86 x 9	9.000	1	9.000	1	9.000	1
203 x 9	2.000	6	1.000	7	2.000	7
176 x 23	1.000	7	5.000	6	5.000	5

The magnitude of rank changes across sites for each family suggested, on an arbitrary basis, those that were interactive.

Absolute rank deviations from average across-site rankings were calculated as in Matheson and Raymond (1984a). Absolute rank deviations identify those families which are interactive; families with the highest rank deviations are the most interactive. The following steps are involved in the process:

1) Cross-site arithmetic means for the families were calculated for each trait and ranked as illustrated in Table 2.9.

Table 2.9 Cross site arithmetic means and their ranking, for an illustrative sample of families.

Family	Arithmetic mean	Rank
88 x 49	8.556	2
224 x 49	8.550	3
58 x 9	4.125	6
88 x 23	2.324	7
86 x 9	9.200	1
203 x 9	5.321	5
176 x 23	7.687	4

2) The rank deviations are calculated by subtracting the ranking of each family at each site (Table 2.8) from the average cross-site ranking (Table 2.9).

3) Absolute deviations were calculated as the sum of the absolute values of the ranks at each site (Table 2.10).

Table 2.10 Individual site rank deviations and absolute rank deviations, for an illustrative sample of families.

Family	Difference in ranks			Absolute Deviation
	23a	23b	23c	
88 x 49	-1	-2	-1	4
224 x 49	-1	-2	-3	6
58 x 9	1	3	4	8
88 x 23	5	5	3	13
86 x 9	0	0	0	0
203 x 9	-1	-2	-2	5
176 x 23	-3	-2	-1	6

The more interactive families are those with the highest rank deviations. However, only arbitrary decisions are possible about the magnitude of acceptable rank deviations.

2.4.3 - Spearman's rank correlation

The Spearman's rank correlation coefficient describes the relationship between the ranks, rather than that between the absolute values, of a pair of observations (Snedecor and Cochran 1989). In this case, the variables tested were pairs of ranks of family means for all combinations of the three sites, and the hypothesis that there is no correlation between the ranks of two variables was tested for significance, in this case at the five percent level.

The assumptions of this approach are minimal: both variables must be measured on at least an ordinal scale, so that the objects or individuals under study may be ranked in two ordered series (Siegel and Castellan 1988).

2.4.4 - Genetic correlations

The estimation of genetic correlations between performances (Type B correlations in Burdon's 1977 nomenclature) across environments provides a measure of the importance of cross-site interactions (Robertson 1959, Burdon 1977), which can be expressed in terms of the variance due to average genetic effects over the two environments (Robertson 1959). This method was first applied by Falconer (1952) with mice, and was adapted to plant breeding by Robertson (1959) and to tree improvement by Yamada (1962) and Burdon (1977). The advantages of this form of analysis are as discussed by Burdon (1977). Traits measured in different environments are regarded as distinct

traits (Robertson 1959, Burdon 1977); the closer the value of the correlation to +1, the smaller the interaction. A genetic correlation of less than one means that genotype-environment interaction may be biologically important (Eisen and Saxton 1983). There are only arbitrary guidelines as to the significance of values of the correlation; Robertson (1959) suggested a threshold of 0.8 below which gei would be of practical importance. An important attribute of this genetic correlation is that it is independent of whether the environments represent a fixed or random effect (Burdon 1977).

The genetic correlations were estimated following the methodology presented in Burdon (1977), and previously described by Falconer (1981). Genetic correlations were estimated as in Equation (2.18):-

$$r_{Gxy} = \frac{r_{Fxy}}{(\sqrt{h_x^2})\,(\sqrt{h_y^2})} \qquad (2.18)$$

where h^2_x and h^2_y are the heritability of family means for traits x and y, respectively, calculated as in Falconer (1981) :-

$$h_f^2 = \frac{h^2(1+(n-1)\,r)}{(1+(n-1)\,t)} \qquad (2.19)$$

where r_{Fxy} = the correlation of family means between sites x and y;

h^2_f = heritability of family means for the relevant trait;

h^2 = the individual heritability for the relevant trait;

n = number of individuals in each family (here, 60 at five years, and 30 at eight and 15 years, due to the 50 percent thinning at age

eight years);

r = coefficient of relationship (assumed 0.50 for full sibs);

t = intra-class correlation between members of families.

2.4.5 - Efficiency of phenotypic selection

The efficiency of phenotypic selection at site x for planting at environment y, relative to both selecting and planting at site y, was estimated as in Burdon (1977). The estimates of efficiencies indicate the relative loss in gain for selecting on one site for planting on another. Efficiencies of selection were calculated as in equation 2.20:-

$$E = \frac{r_{Axy} h_x}{h_y} \qquad (2.20)$$

where E = efficiency of phenotypic selection on a trait at site x for planting at environment y relative to both selecting at and planting at y, with the same intensity of selection at the two sites (ie $i_x = i_y$);

r_{Axy} = genetic correlation of family means, and;

h_x and h_y are the square roots of the individual heritabilities for the traits under study at environments x and y, respectively.

2.5 - Results and discussion

2.5.1 - Family means and differences

Table 2.11 summarises the overall means and their standard deviations for all traits measured and assessed, at five, eight and 15 years, based on the 39 families common to all three tests.

Table 2.11 Trait means and their standard deviations in the three progeny tests at ages five, eight and 15 years estimated from 39 common families.

	Test		
Trait	23a	23b	23c
Survival (%)	84	83	80
HT5 (m)	5.57 ± 0.95	5.60 ± 1.12	3.80 ± 1.06
DBH5 (cm)	10.51 ± 2.02	10.46 ± 2.42	6.50 ± 2.12
VOL5 (dm^3)	23.48 ± 9.74	24.45 ± 13.61	7.17 ± 5.26
BRCT5 (No)	6.76 ± 1.74	8.44 ± 2.15	6.52 ± 2.16
BRDM5 (mm)	14.89 ± 3.27	13.00 ± 3.40	13.07 ± 3.34
AIL5 (m)	0.39 ± 0.11	0.32 ± 0.09	0.35 ± 0.11
STR5 (rating)	4.09 ± 0.90	3.68 ± 0.75	3.73 ± 0.77
HT8 (m)	10.26 ± 1.24	8.91 ± 1.74	6.40 ± 1.78
DBH8 (cm)	16.15 ± 2.78	15.26 ± 3.59	11.32 ± 2.95
VOL8 (dm^3)	100.29 ± 40.74	82.85 ± 45.96	34.24 ± 20.70
STR8 (rating)	4.07 ± 0.75	3.46 ± 0.84	2.55 ± 0.72
HT15 (m)	18.99 ± 1.81	15.93 ± 2.89	11.70 ± 1.81
DBH15 (cm)	24.35 ± 4.20	23.03 ± 6.57	19.02 ± 3.12
VOL15 (dm^3)	415.73 ± 156.59	346.99 ± 216.11	158.47 ± 65.50
DENS15 (kg/m^3)	425.71 ± 53.90	372.72 ± 44.58	432.05 ± 38.23
RESQ15 (g/wk)	31.5 ± 14.9	-	-
STR15 (rating)	4.00 ± 0.71	4.11 ± 0.95	3.82 ± 0.84

Survival was good in all tests, averaging around 80 percent. At five years, little difference was apparent in growth and stem straightness between tests 23a and 23b. Growth in test 23c, a drier and less fertile site, was substantially

less. By age eight it was evident that test 23a was located on the most favourable site and this trend was still apparent at age 15. The branch traits (branch count, branch diameter and the average internode length) varied in the three tests, with trees in test 23b having on average two branches more than those in tests 23a and 23c; this may be due to the lack of flowering in test 23b (Barnes[2] pers. comm.). The average internode length differed little in the three tests.

There is no consistent relationship between growth and wood density across the three sites. Average wood density was highest in test 23c and lowest in test 23b, with a difference of approximately 59 kg/m^3; the difference between tests 23c and 23a was much smaller (6 kg/m^3). This result corresponds to that for *P. caribaea* reported by Barnes *et al* (1977), who found the highest density occurred at the driest site.

As resin yield was assessed in one test only, it was not possible to make comparisons across tests. However, resin yield is low compared with previous results for *P. elliottii* in Zimbabwe (Zimbabwe Forestry Commission unpublished data), which suggest a weekly average of 80 g per tree. The low amounts of resin produced in this test may result from the fact that rain was reported for eight of the 12 weeks during which resin was collected. Coppen *et al* (1984) observed that high temperatures encouraged the flow of

---

[2] Dr. R.D. Barnes, Oxford Forestry Institute, Department of Plant Sciences, South Parks Road, OX1 3RB, UK.

resin while prolonged rainfall did not. It may also be that three months is too short a period over which to gain a good average estimate of production. Timing of collection in relation to opening of the wound may also be important, as when the wound is first opened, the area from which resin flows is small, but when the wound is enlarged the surface area increases and more resin flows. Here, for example, an average of 37.1 g was recorded over the first two weeks, but by the 11^{th} and 12^{th} weeks, the average weekly yield was 95.1 g.

Table 2.12 presents a summary of the analyses of variance for the 39 families common to the three tests, at five, eight and 15 years of age. Analyses were restricted to the 39 families common to the three tests to allow direct comparison of results between the tests.

The F-test for ANOVAs derived from unbalanced data such as these should be interpreted with care (Searle 1987; p14). For example, ratios of mean squares for mixed models do not follow the distribution appropriate for fixed models. Furthermore, the hypothesis being tested depends on the pattern of crosses completed, and therefore tests the particular set of crosses in the experiment rather than the parent population.

It is apparent from Table 2.12 that at five, eight and 15 years, differences in all traits between both female and male parents were almost always significant ($P < 0.05$) in the three tests.

Table 2.12 Mean squares and significance levels for all traits in 39 common families at ages five, eight and 15 years in the three progeny tests.

	Mean Squares																
Source	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	RESQ15	STR15
23a																	
Female	8.4**	40.9**	1405.9**	13.1**	57.9*	0.1**	4.0*	10.1*	39.7ns	9590.6*	2.0*	14.1*	112.5**	179580.0**	22337.0**	22865.0**	1.4**
Male	35.7**	201.6**	6050.2**	72.3**	21.8ns	0.6**	28.3**	52.4**	429.8**	92895.0**	8.0**	52.6**	653.5**	904890.0**	76291.0**	20754.0*	1.0ns
FemxMale	1.3**	8.9**	206.0**	2.9ns	21.3**	0.02**	1.7**	3.2*	19.4*	3455.9**	0.7ns	4.8**	20.5ns	24289.0ns	3532.1**	2392.8**	0.7*
FamxRep	0.8	5.3	135.3	2.9	18.7	0.01	1.1	1.3	6.4	1426.3	0.7	4.2	17.1	24252.0	2416.7	2391.7	0.7
Residual	0.4	1.8	51.1	2.2	8.0	0.01	0.5	1.1	5.7	1131.3	0.5	2.4	12.4	16359.0	2415.5	1346.9	0.4
23b																	
Female	18.9**	80.8**	2629.2**	25.5**	68.6**	0.1**	5.4**	20.5*	68.1**	11861.0**	4.2**	46.7ns	230.8*	254520.0*	17777.0**		2.9ns
Male	131.4**	672.4**	22707.0**	323.3**	353.3**	0.4**	35.6**	236.3**	1148.6**	194900.0**	22.0**	760.3**	4481.8**	4776100.0**	59231.0**		42.5**
FemxMale	5.3**	20.5**	615.0**	4.5ns	16.3ns	0.01*	1.3**	7.1**	22.8**	3645.4**	1.1*	24.6**	87.1**	88556.0**	2191.7**		1.7ns
FamxRep	1.0	6.6	178.3	4.5	12.1	0.01	0.8	2.2	8.9	1281.0	0.8	5.8	27.0	28180.0	1869.8		0.7
Residual	0.7	3.4	104.4	3.7	10.2	0.01	0.4	1.7	7.7	1206.0	0.5	5.2	25.0	27012.0	1441.6		0.7
23c																	
Female	15.4**	57.7**	374.5**	10.4ns	51.1ns	0.1*	4.1ns	18.8**	50.0**	2735.4**	2.0*	21.5*	56.1**	27512.0**	5932.9**		1.2ns
Male	30.0**	61.4**	759.4**	60.9**	73.3ns	0.3**	7.4ns	29.1**	60.1*	5441.1**	6.0**	16.0*	193.2**	72164.0**	81375.0**		5.4**
FemxMale	3.7**	10.9**	70.6**	6.3ns	50.6**	0.04**	1.9**	5.1**	13.7**	812.2**	0.7*	4.4**	9.5*	4462.0*	945.8ns		0.9**
FamxRep	1.9	6.5	36.8	6.2	14.2	0.02	1.1	4.1	9.2	456.8	0.7	3.9	9.5	3963.2	944.4		0.7
Residual	0.7	3.1	18.4	4.4	9.9	0.01	0.5	1.9	6.2	267.9	0.4	1.7	5.6	2412.0	797.0		0.4

* = significant at P<0.05
** = significant at P<0.01
ns = not significant

The female x male interaction effects were generally significant at all ages in all three tests, with some exceptions; for example, for BRCT5. There was little consistency across tests in the traits for which these effects were not significant, though differences between female or male parents in stem straightness were not significant at one site, at least, at all ages, and female x male effects in branch traits at five years were generally significant in test 23b.

2.5.2 - Variance components

The magnitude of variance components, their standard errors and relative proportions of total variability, for all traits assessed at five, eight and 15 years, are shown in Tables 2.13, 2.14 and 2.15, respectively. Figures 2.1, 2.2 and 2.3 depict the proportions of total variance and Figures 2.4 - 2.7 depict the trends over time in variance components for those traits which were assessed on successive occasions, *viz*, growth traits and stem straightness. In order to increase accuracy of the estimates, variance components were derived from all available data in each test, unlike the analyses of variance described previously, which were limited to the 39 families common to the three tests.

The within-plot error (residual) was the most important source of variation for all traits, accounting for between 50-96% of the total phenotypic variation at five, eight and 15 years.

Table 2.13 Variance components, associated standard errors, and proportions of total variance (in brackets) for growth, stem straightness and branching traits for all families at five years in the three progeny tests.

Test	Source	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5
	Female							
23a		0.07±0.02 (9.5)	0.25±0.08 (8.3)	9.87±3.18 (10.3)	0.08±0.05 (2.5)	0.08±0.07 (0.8)	0.001±0.0002 (7.6)	0.02±0.01 (3.6)
23b		0.12±0.03 (10.4)	0.58±0.16 (11.3)	20.29±5.57 (12.1)	0.09±0.09 (2.0)	0.62±0.18 (5.0)	0.001±0.0001 (8.1)	0.03±0.01 (5.7)
23c		0.14±0.06 (12.3)	0.58±0.22 (13.1)	4.12±1.63 (13.3)	0.08±0.05 (1.7)	0.001±0.27 (0.01)	0.0003±0.0002 (2.4)	0.03±0.02 (5.3)
	Male							
23a		0.09±0.05 (13.2)	0.34±0.18 (11.4)	14.22±7.29 (14.9)	0.08±0.05 (2.5)	0.03±0.04 (0.3)	0.001±0.001 (7.6)	0.03±0.01 (4.5)
23b		0.14±0.07 (12.2)	0.77±0.39 (15.0)	26.12±13.40 (15.6)	0.37±0.19 (8.4)	1.21±0.62 (9.8)	0.001±0.0004 (8.1)	0.04±0.02 (7.6)
23c		0.11±0.10 (9.7)	0.26±0.23 (5.9)	3.17±2.82 (10.2)	0.09±0.09 (1.9)	0.001±0.10 (0.01)	0.001±0.001 (7.9)	0.01±0.01 (1.8)
	Fem x Male							
23a		0.02±0.004 (2.7)	0.06±0.02 (1.9)	2.93±0.69 (3.1)	0.01±0.01 (0.32)	0.64±0.12 (6.1)	0.0001±0.0001 (0.8)	0.003±0.003 (0.5)
23b		0.05±0.01 (0.9)	0.17±0.03 (3.3)	6.13±1.06 (3.7)	0.06±0.02 (1.4)	0.19±0.48 (1.5)	0.0002±0.00004 (0.02)	0.01±0.002 (1.9)
23c		0.02±0.02 (1.8)	0.05±0.07 (1.1)	0.85±0.62 (2.8)	0.0004±0.04 (0.01)	0.90±0.39 (7.5)	0.0003±0.0002 (2.4)	0.01±0.01 (1.8)
	Fam x Rep							
23a		0.05±0.01 (6.9)	0.39±0.03 (13.0)	8.69±0.75 (9.1)	0.17±0.02 (5.4)	1.11±0.10 (10.6)	0.001±0.0001 (7.6)	0.07±0.01 (11.7)
23b		0.04±0.01 (3.5)	0.23±0.03 (4.5)	7.27±0.85 (4.4)	0.08±0.02 (1.8)	0.30±0.06 (2.4)	0.0002±0.00004 (0.02)	0.04±0.004 (7.6)
23c		0.16±0.03 (14.0)	0.44±0.08 (9.9)	2.53±0.51 (8.2)	0.10±0.06 (2.1)	0.36±0.17 (3.0)	0.001±0.0002 (7.9)	0.07±0.01 (12.3)
	Residual							
23a		0.47±0.01 (67.7)	1.94±0.03 (65.2)	59.93±0.92 (62.7)	2.81±0.04 (89.2)	8.60±0.13 (82.2)	0.01±0.0002 (76.3)	0.48±0.01 (79.7)
23b		0.80±0.01 (69.6)	3.40±0.05 (66.0)	107.5±1.50 (64.3)	3.83±0.05 (86.5)	10.05±0.14 (81.2)	0.01±0.001 (80.7)	0.41±0.01 (77.4)
23c		0.71±0.02 (62.3)	3.11±0.10 (70.1)	20.28±0.68 (65.5)	4.41±0.15 (94.2)	10.80±0.36 (89.5)	0.01±0.0003 (79.4)	0.45±0.02 (79.0)

Table 2.14 Variance components, standard errors, and proportions of total variance (in brackets) for growth and stem straightness at eight years for all families in the three progeny tests.

Test	Source	HT8	DBH8	VOL8	STR8
	Female				
23a		0.13±0.04 (8.0)	0.62±0.18 (7.7)	154.19±43.8 (9.0)	0.03±0.01 (5.3)
23b		0.32±0.09 (11.4)	1.18±0.34 (10.0)	220.8±62.5 (11.3)	0.05±0.02 (7.5)
23c		0.36±0.15 (12.6)	1.00±0.40 (11.9)	53.6±21.6 (12.3)	0.03±0.0.01 (6.3)
	Male				
23a		0.13±0.07 (8.0)	0.85±0.44 (10.6)	209.6±108.9 (12.2)	0.03±0.02 (5.3)
23b		0.37±0.19 (13.1)	2.10±1.09 (17.6)	345.0±177.1 (17.7)	0.05±0.03 (7.5)
23c		0.21±0.19 (7.3)	0.56±0.50 (6.7)	47.4±41.8 (10.9)	0.03±0.03 (6.3)
	Fem x Male				
23a		0.05±0.01 (3.1)	0.28±0.06 (3.5)	69.6±13.7 (4.0)	0.01±.003 (1.8)
23b		0.16±0.03 (5.7)	0.48±0.09 (4.0)	82.5±15.7 (4.2)	0.02±0.01 (3.0)
23c		0.02±0.07 (0.7)	0.12±0.17 (1.4)	11.23±10.0 (2.6)	0.00003±0.01 (0.01)
	Fam x Rep				
23a		0.07±0.02 (4.3)	0.32±0.07 (4.0)	81.6±15.2 (4.7)	0.03±0.01 (5.3)
23b		0.11±0.02 (3.9)	0.40±0.10 (3.4)	61.1±15.3 (3.1)	0.05±0.01 (7.5)
23c		0.62±0.10 (21.7)	0.83±0.24 (10.0)	45.7±11.7 (10.5)	0.08±0.02 (16.7)
	Residual				
23a		1.25±0.03 (76.7)	5.97±0.12 (74.3)	1206.6±.24.3 (70.1)	0.47±0.01 (82.5)
23b		1.86±0.04 (66.0)	7.77±0.16 (65.1)	1245.3±26.1 (63.7)	0.50±0.01 (74.6)
23c		1.65±0.08 (57.5)	5.90±0.29 (70.2)	277.6±13.70.02 (63.7)	0.34±0.02 (70.8)

Table 2.15 Variance components and their standard errors, and proportions of total variance (in brackets) for growth, wood density, resin yield and stem straightness for all families at 15 years in the three progeny tests.

Test	Source	HT15	DBH15	VOL15	DENS15	RESQ15	STR15
	Female						
23a		0.20±0.06 (7.6)	1.68±0.47 (9.3)	2514.1±708.3 (9.4)	218.45±65.14 (7.3)	17.03±10.71 (7.6)	0.02±0.01 (3.7)
23b		0.82±0.25 (10.0)	4.45±1.28 (10.7)	4764.8±1374.4 (10.9)	194.88±56.63 (9.7)		0.04±0.01 (4.7)
23c		0.38±0.17 (12.5)	1.26±0.51 (12.6)	641.9±268.0 (14.3)	167.05±57.66 (11.3)		0.03±0.18 (5.4)
	Male						
23a		0.22±0.11 (8.4)	1.84±0.96 (10.2)	3057.5±1588.0 (11.4)	270.20±141.75 (9.1)	10.73±7.35 (4.8)	0.03±0.02 (5.5)
23b		1.10±0.58 (13.4)	8.80±4.50 (21.2)	8638.9±4435.6 (19.7)	255.98±132.98 (12.7)		0.07±0.04 (8.1)
23c		0.14±0.10 (4.6)	1.71±1.48 (17.1)	712.7±620.5 (15.9)	460.08±378.08 (31.2)		0.03±0.03 (5.4)
	Fem x Male						
23a		0.09±0.02 (3.4)	0.77±0.15 (4.3)	1220.6±225.23 (4.6)	77.54±29.01 (2.6)	0.02±5.67 (0.01)	0.01±0.003 (1.9)
23b		0.63±0.10 (7.7)	2.23±0.37 (5.4)	2388.7±396.80 (5.5)	21.92±19.45 (1.1)		0.04±0.01 (4.7)
23c		0.12±0.10 (4.9)	0.29±0.25 (2.9)	219.9±132.35 (4.9)	0.08±16.51 (0.01)		0.02±0.02 (3.6)
	Fam x Rep						
23a		0.21±0.03 (8.0)	0.63±0.16 (3.5)	1098.5±379.7 (4.1)	0.24±37.54 (0.01)	39.76±9.15 (17.8)	0.04±0.01 (7.4)
23b		0.19±0.06 (2.3)	0.52±0.29 (1.3)	677.7±310.10 (1.6)	87.31±29.00 (4.4)		0.02±0.01 (2.3)
23c		0.77±0.12 (25.5)	1.30±0.30 (13.0)	547.17±128.93 (12.2)	49.75±32.38 (3.4)		0.10±0.02 (17.9)
	Residual						
23a		1.91±0.04 (72.6)	13.17±0.27 (72.8)	18828.0±379.70 (70.5)	2415.5±69.51 (81.0)	156.2±8.04 (69.8)	0.44±0.01 (81.5)
23b		5.42±0.11 (66.4)	25.58±0.54 (61.5)	27400.0±578.0 (62.5)	1441.6±43.04 (72.0)		0.69±0.02 (80.0)
23c		1.61±0.09 (53.3)	5.47±0.32 (54.5)	2361.3±136.2 (52.7)	796.00±45.95 (54.0)		0.38±0.02 (67.9)

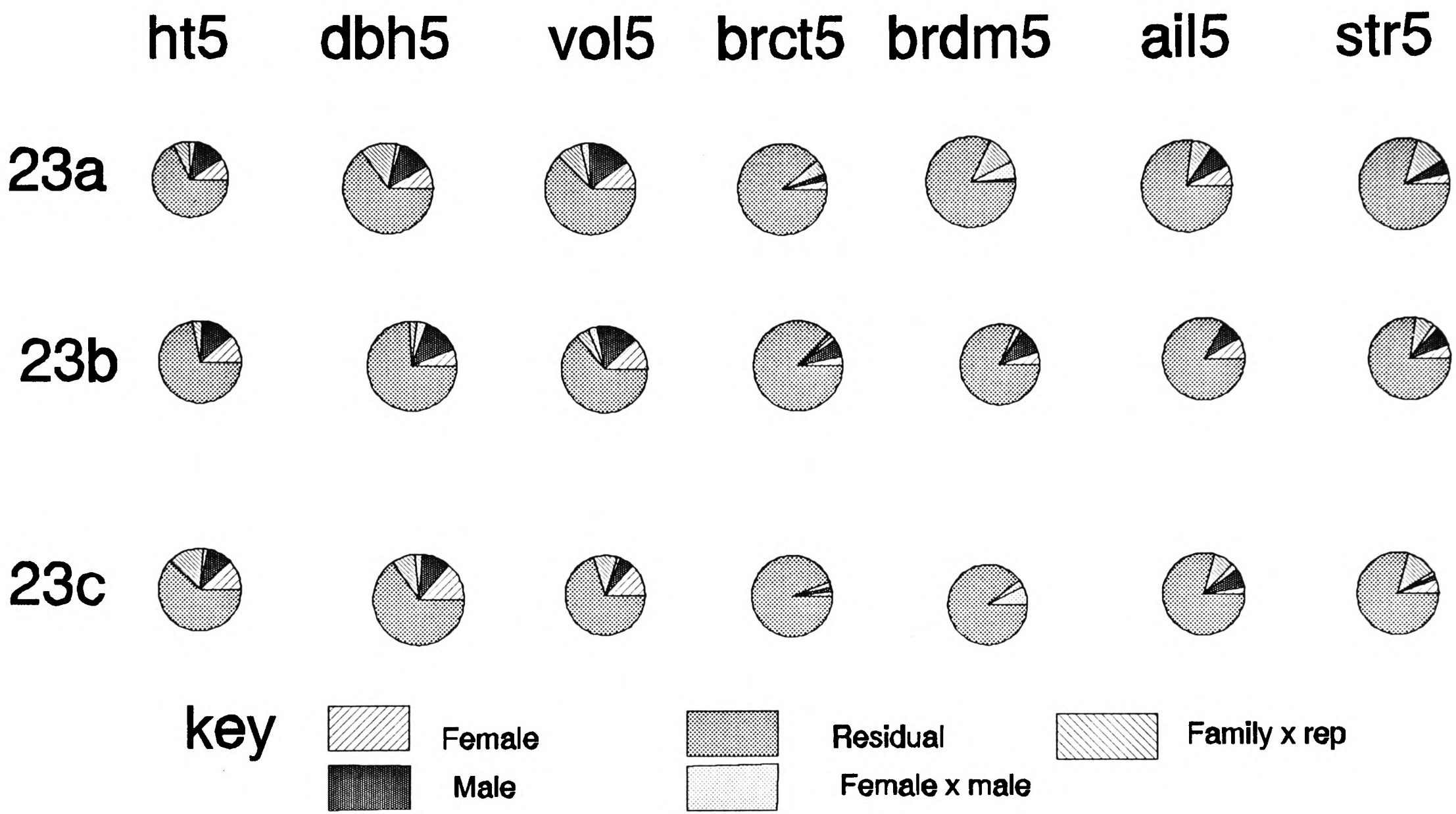


Figure 2.1. Proportions of total variance for all traits at 5 years in the three progeny tests.

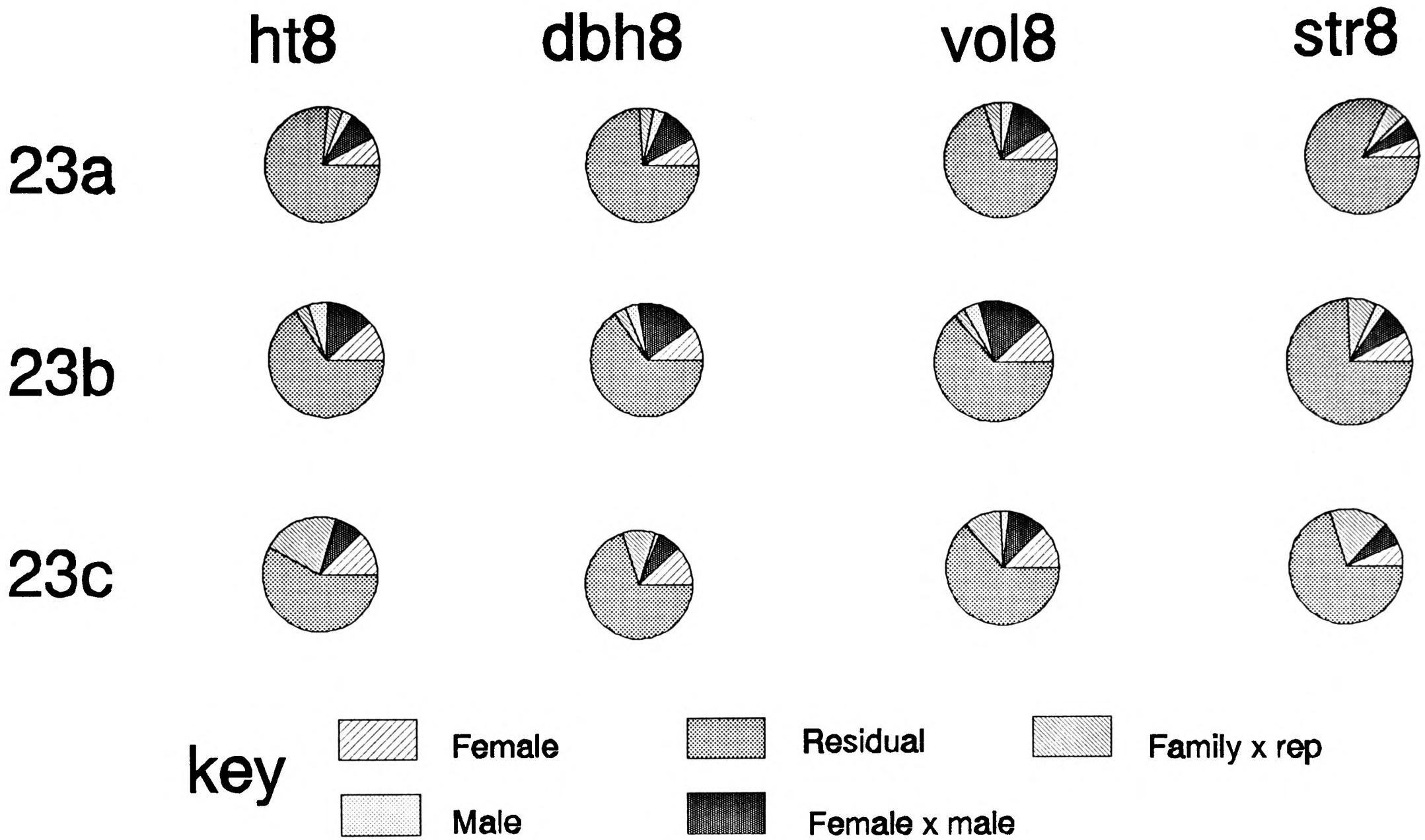


Figure 2.2. Proportions of total variance for all traits at 8 years in the three progeny tests.

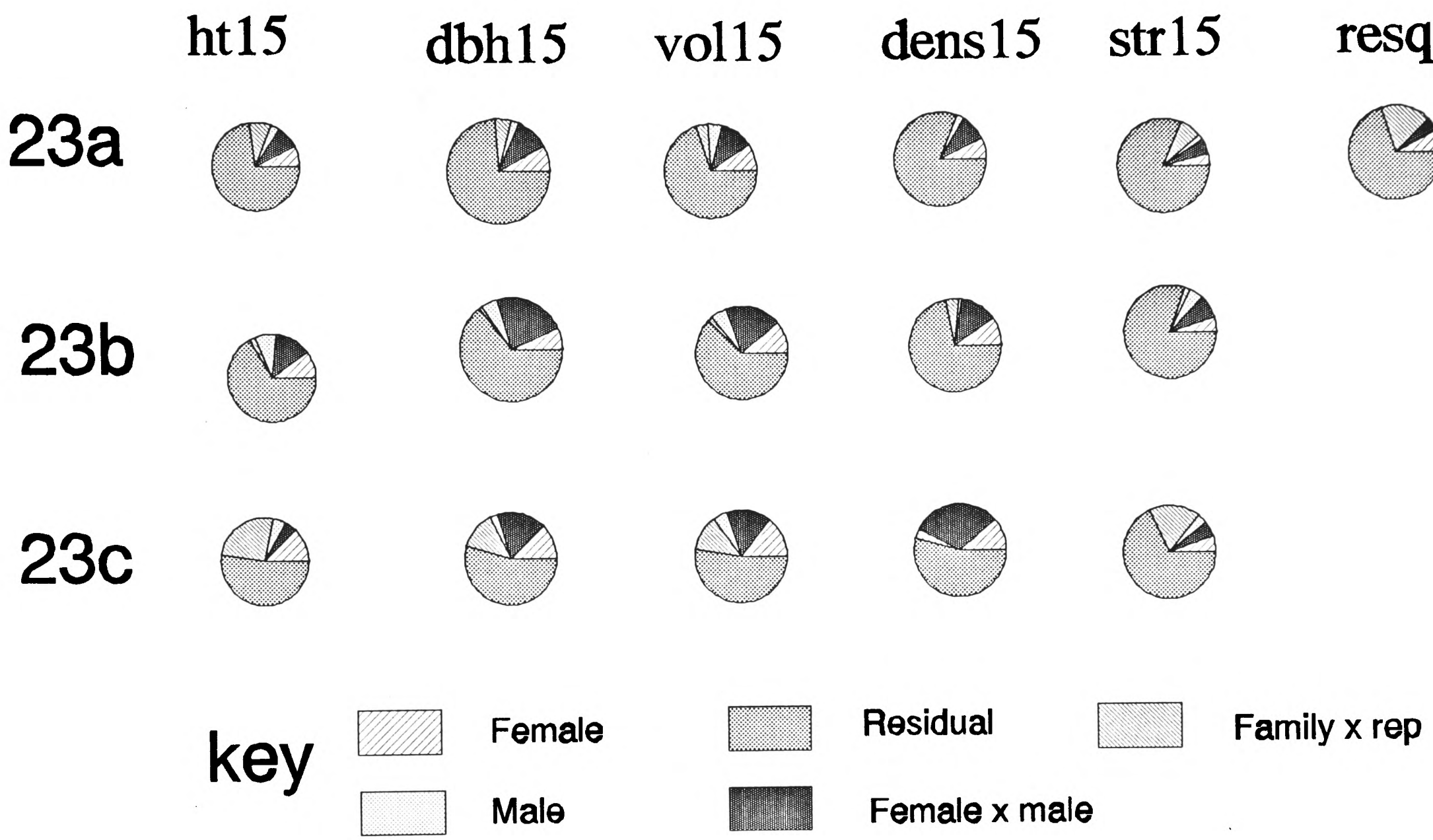


Figure 2.3. Proportions of total variance for all traits at 15 years in the three progeny tests.

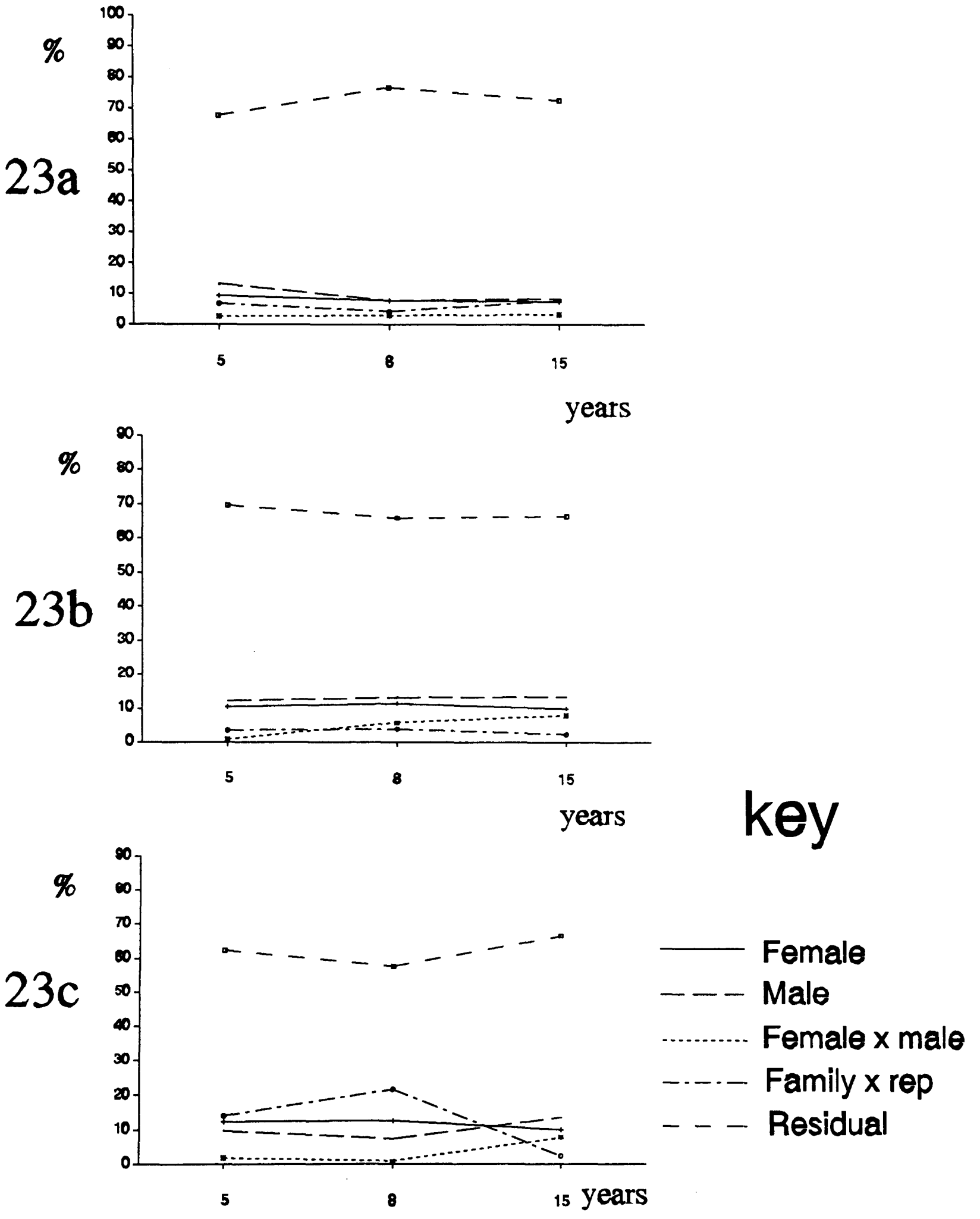


Figure 2.4. Trends over time in variance components for height in the three progeny tests.

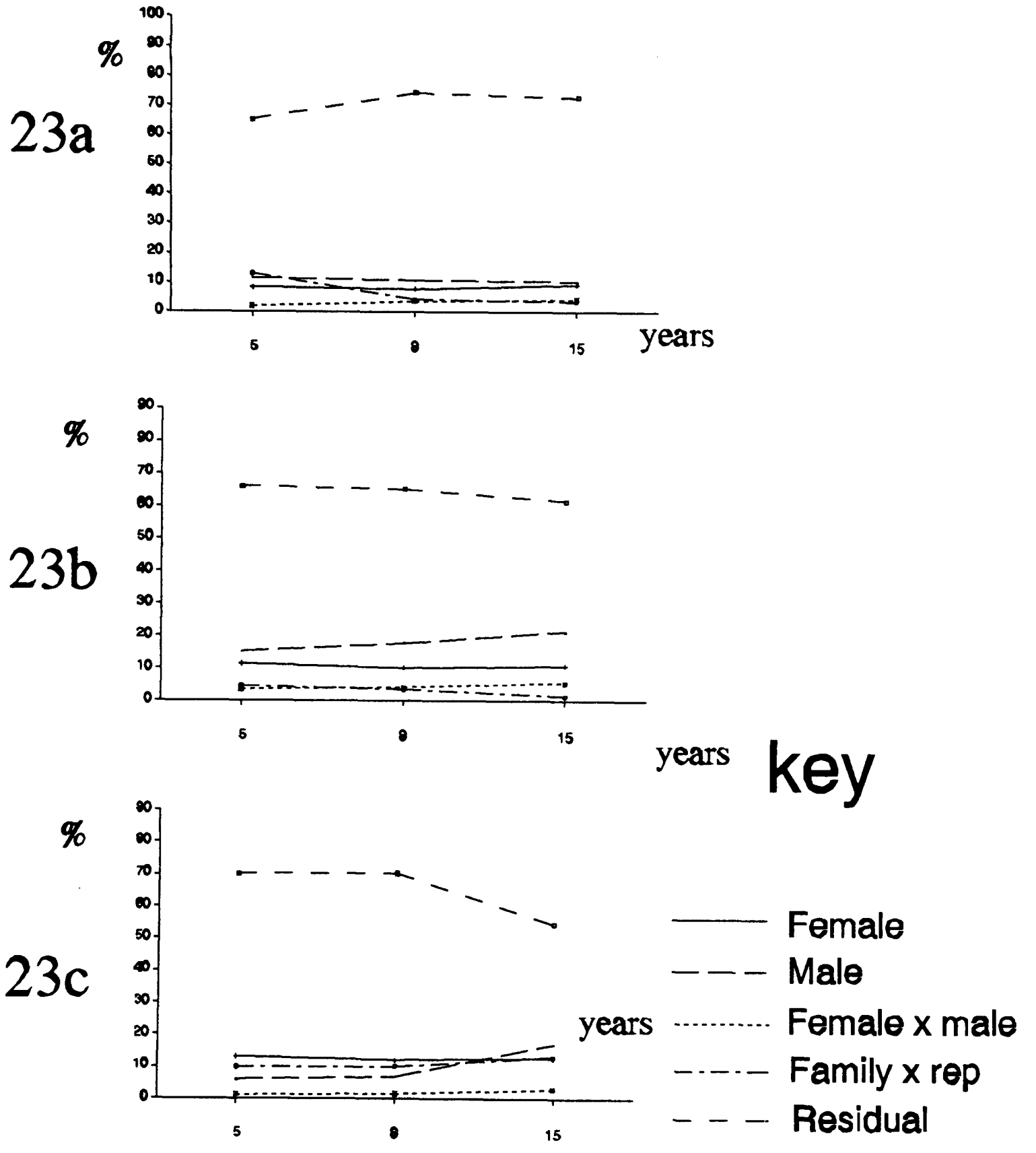


Figure 2.5. Trends over time in variance components for diameter in the three progeny tests.

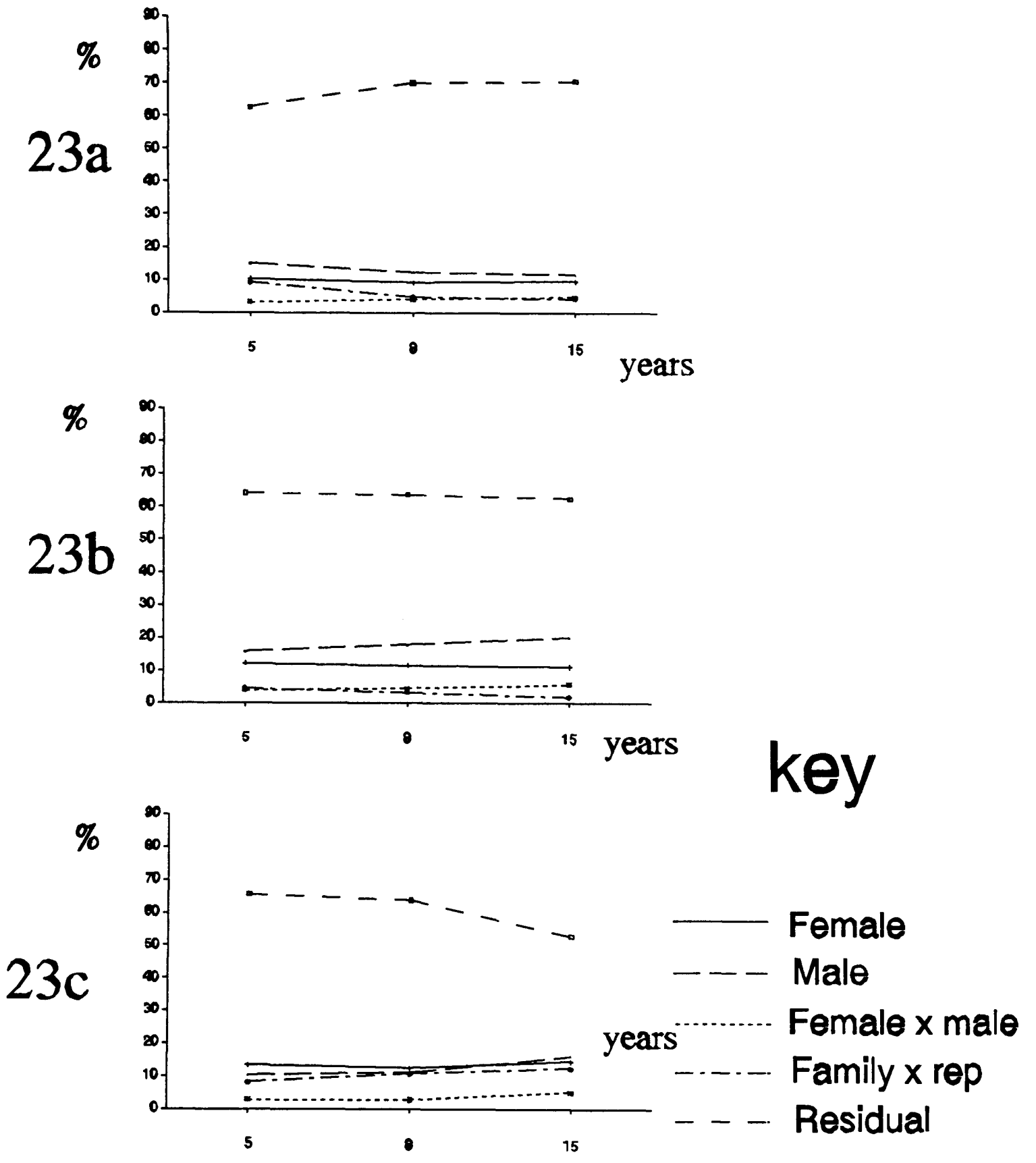
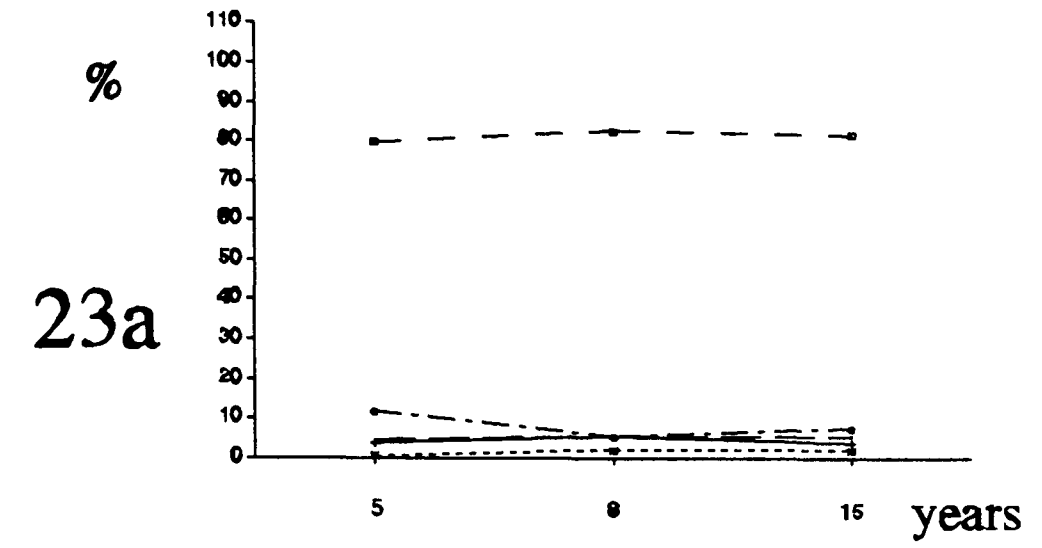
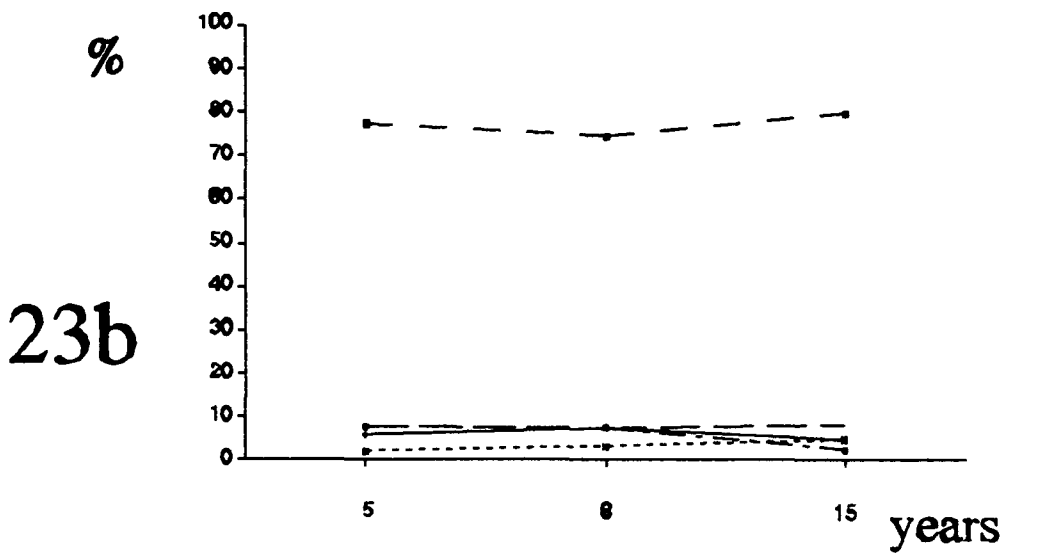


Figure 2.6. Trends over time in variance components for volume in the three progeny tests.





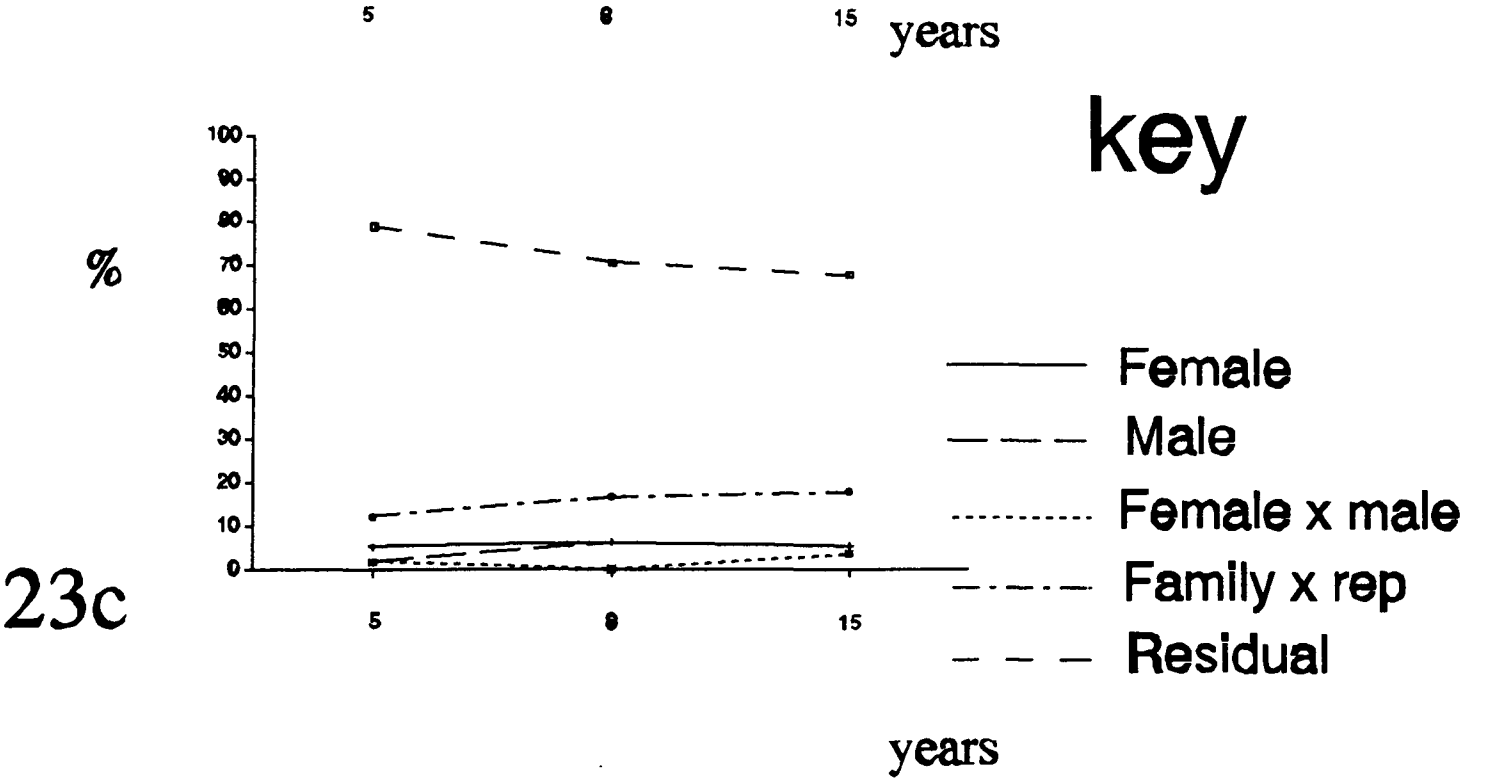


Figure 2.7. Trends over time in variance components for stem straightness in the three progeny tests.

In most cases, within-plot variance increased between ages five and 15 years, with the exception of stem straightness for which it decreased slightly. However, this increase in the variance was low in all cases. The large within-plot error in this study may indicate the inefficiency of the design used to account for the variation present. The female and male components were generally the next most important sources of variation for all traits, with the exception of HT15 in test 23c and RESQ15 in test 23a. The magnitudes of the male components were greater than those of the female components in tests 23a and 23b; the converse was true in test 23c at five and eight years. By 15 years of age the male components were larger than the female components in all three tests for all traits, with the exception of height in 23c. The standard errors of the male components are also higher, which may reflect the smaller number of male parents used in the analysis. However, in all cases, the changes over time in variance components derived from both female and male parents were small.

Resin yield was atypical in that effects of the family x replicate interaction were more important than those of the female and male components. The female x male interaction components were lower than either the male or female components in all tests at all ages for all traits but BRDM5, for which the female x male interaction components were usually greater than the male component.

In a few cases, the interaction between family x replicate was a more important source of variation than that between females x males; for example, in the traits BRCT5, BRDM5 and STR5 in all three tests, and HT15 and STR15 in test 23c. Estimates from test 23c should be interpreted with care because they derive from a much smaller and more unbalanced data set than do estimates from the other two tests.

2.5.3 - Additive and dominance genetic variances

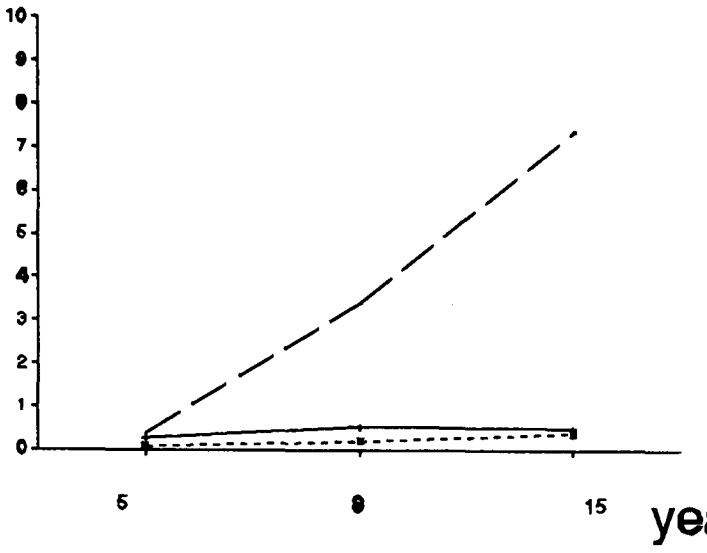
Table 2.16 lists the additive and dominance genetic variances estimated on various bases from the three progeny tests at five, eight and 15 years, respectively. Figures 2.8 - 2.11 depict the trends over time in the additive genetic variances for growth and stem straightness.

Generally, the ratios of additive genetic variances estimated from female parents to those estimated from male parents are less than one for growth traits, stem straightness and wood density in tests 23a and 23b. The results are a result of the larger variances derived from the male parents, caused by the smaller number of male parents sampled. Conversely, ratios of female to male additive genetic variances for these traits in test 23c were generally above one. The inconsistency in these results may be due to the smaller data set in test 23c. Ratios of additive to dominance genetic variances are above one for all traits in all tests at the three ages, with the exception of BRDM5 in tests 23a and 23c.

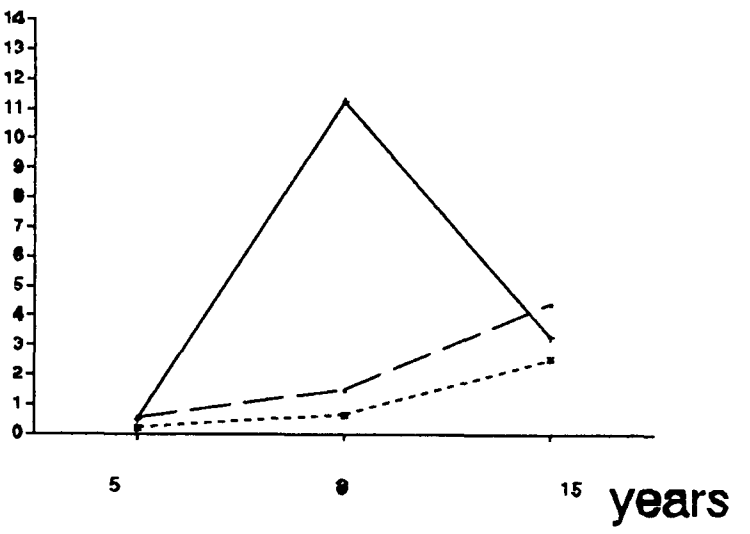
Table 2.16 Additive ($4\sigma^2_f$, $4\sigma^2_m$) and dominance ($4\sigma^2_{fm}$) variances, and ratios of the two estimates of additive variance and of additive to dominance variance, for all traits in the three progeny tests at five, eight and 15 years.

Trait	$4\sigma^2_f$	$4\sigma^2_m$	σ^2_f/σ^2_m	$4\sigma^2_{fm}$	σ^2_f/σ^2_{fm}	σ^2_m/σ^2_{fm}
23a - 5 yrs						
HT5	0.26	0.37	0.70	0.08	3.47	4.84
DBH5	0.99	1.38	0.72	0.22	4.43	6.14
VOL5	39.50	56.9	0.69	11.7	3.37	4.85
BRCT5	0.36	0.32	1.13	0.04	9.00	8.00
BRDM5	0.34	0.11	3.09	2.54	0.13	0.04
AIL5	0.004	0.004	1.00	0.0004	10.0	10.0
STR5	0.09	0.11	0.82	0.01	7.30	9.0
8 yrs						
HT8	0.52	0.52	1.00	0.20	2.60	2.60
DBH8	2.48	3.40	0.73	1.12	2.21	3.04
VOL8	616.8	838.4	0.74	278.4	2.21	3.01
STR8	0.12	0.12	1.00	0.04	3.00	3.00
15 yrs						
HT15	0.80	0.88	0.91	0.36	2.22	2.44
DBH15	6.72	7.36	0.91	3.08	2.18	2.39
VOL15	10056.40	12230.0	0.82	4882.4	2.06	2.51
DENS15	873.8	1080.8	0.81	310.2	2.82	3.49
RESQ15	703.7	631.1	1.1	0.54	1306.1	1171.4
STR15	0.08	0.12	0.67	0.04	2.00	3.00
23b - 5 yrs						
HT5	0.48	0.56	0.86	0.20	2.40	2.80
DBH5	2.32	3.08	0.75	0.68	3.40	4.50
VOL5	81.16	104.48	0.78	24.52	3.31	4.26
BRCT5	0.36	1.48	0.24	0.24	1.50	6.17
BRDM5	2.48	4.84	0.51	0.76	3.26	6.37
AIL5	0.004	0.004	1.00	0.001	5.00	5.00
STR5	0.12	0.20	1.00	0.08	2.50	2.50
8 yrs						
HT8	11.28	1.48	0.87	0.64	2.00	2.31
DBH8	4.72	8.40	0.56	1.92	2.46	4.38
VOL8	883.20	1380.0	0.64	330.0	2.68	4.18
STR8	0.20	0.20	1.00	0.08	2.50	2.50
15 yrs						
HT15	3.28	4.40	0.75	2.52	1.30	1.75
DBH15	17.8	35.20	0.51	8.92	2.00	3.95
VOL15	19059.20	34555.60	0.55	9554.80	2.00	3.62
DENS15	779.5	1023.9	0.76	87.66	8.89	11.68
STR15	0.16	0.28	0.57	0.16	1.00	1.75
23c - 5 yrs						
HT5	0.56	0.44	1.27	0.08	7.00	5.50
DBH5	2.32	1.04	2.23	0.20	11.60	5.20
VOL5	16.48	12.68	1.30	3.40	4.85	3.73
BRCT5	0.32	0.36	0.89	0.002	200.0	225.0
BRDM5	0.004	0.004	1.00	3.60	0.001	0.001
AIL5	0.001	0.004	0.30	0.001	3.33	3.33
STR5	0.12	0.04	3.00	0.04	3.00	1.00
8 yrs						
HT8	1.44	0.84	0.71	0.08	18.0	10.5
DBH8	4.00	2.24	1.79	0.48	8.30	4.70
VOL8	214.40	189.60	1.13	44.90	4.80	4.20
STR8	0.12	0.12	1.00	0.0001	1000.0	1000.0
15 yrs						
HT15	1.52	0.56	2.71	0.48	3.17	1.17
DBH15	5.04	6.84	0.74	1.16	4.30	5.90
VOL15	2567.6	2850.80	0.90	879.60	2.92	3.24
DENS15	668.2	1840.3	0.36	0.32	2088.1	5751.0
STR15	0.12	0.12	1.00	0.08	1.50	1.50

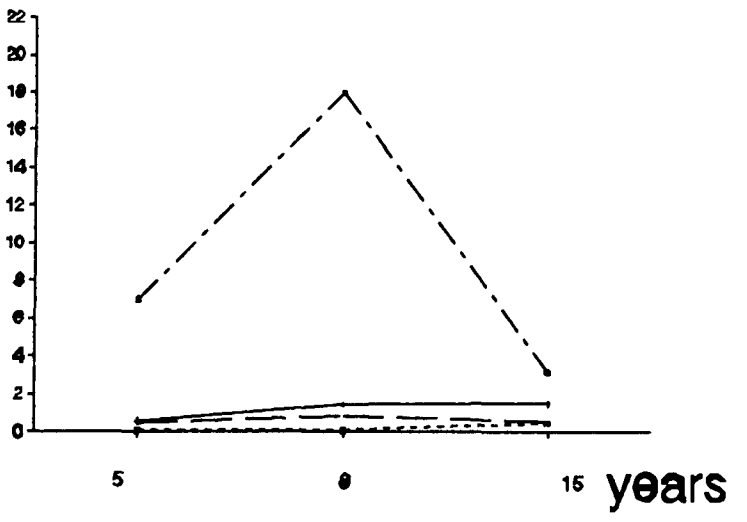
23a



23b



23c



key

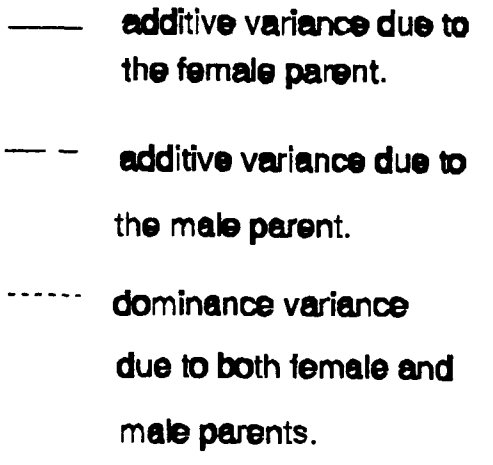
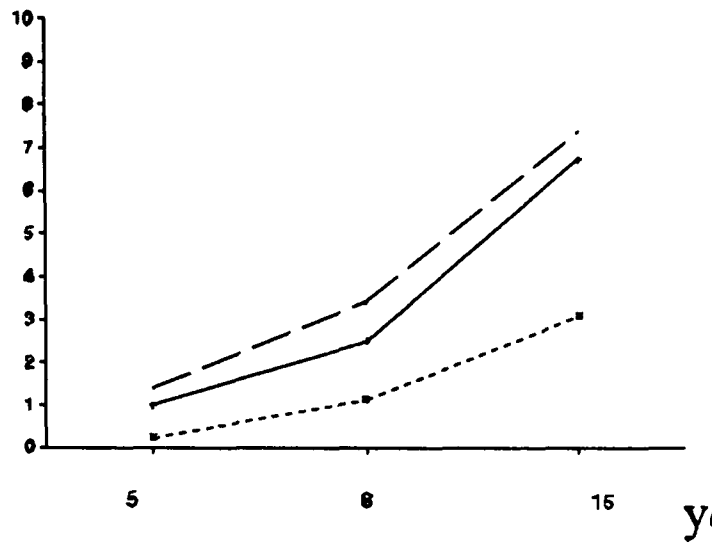
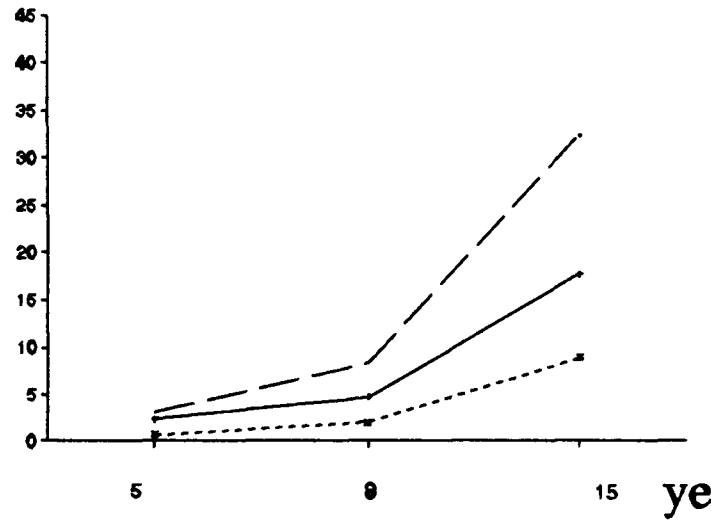


Figure 2.8. Trends over time in additive and dominance variances for height in the three progeny tests.

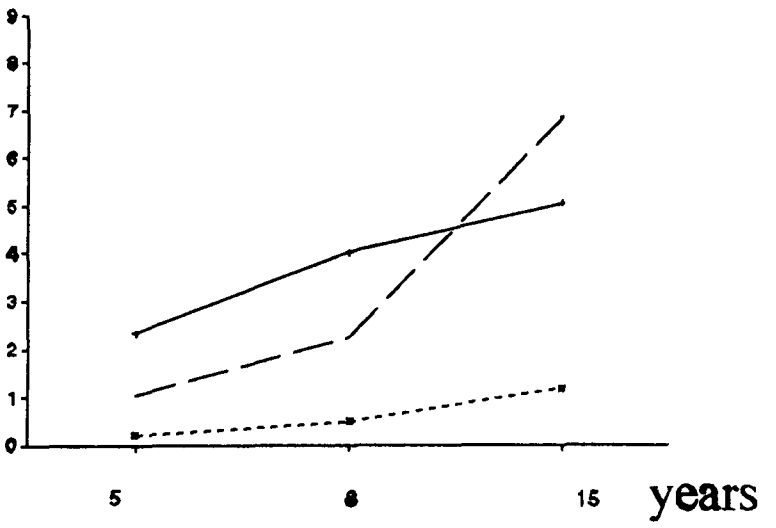
23a



23b



23c



key

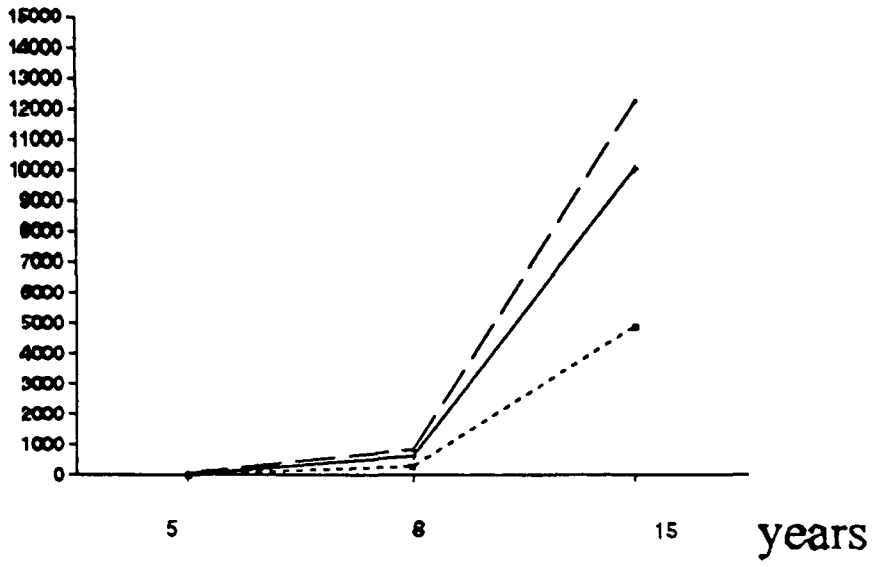
——— additive variance due to the female parent.

— — additive variance due to the male parent.

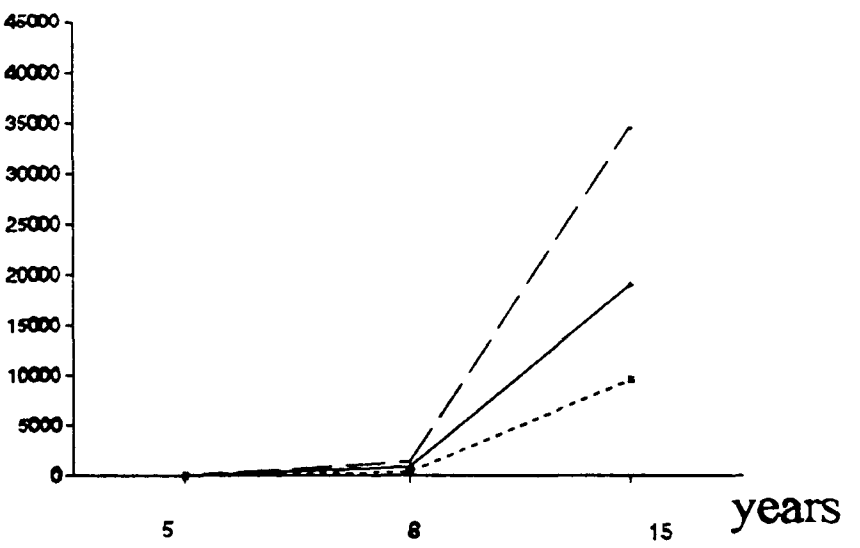
------ dominance variance due to both female and male parents.

Figure 2.9. Trends over time in additive and dominance variances for diameter in the three progeny tests.

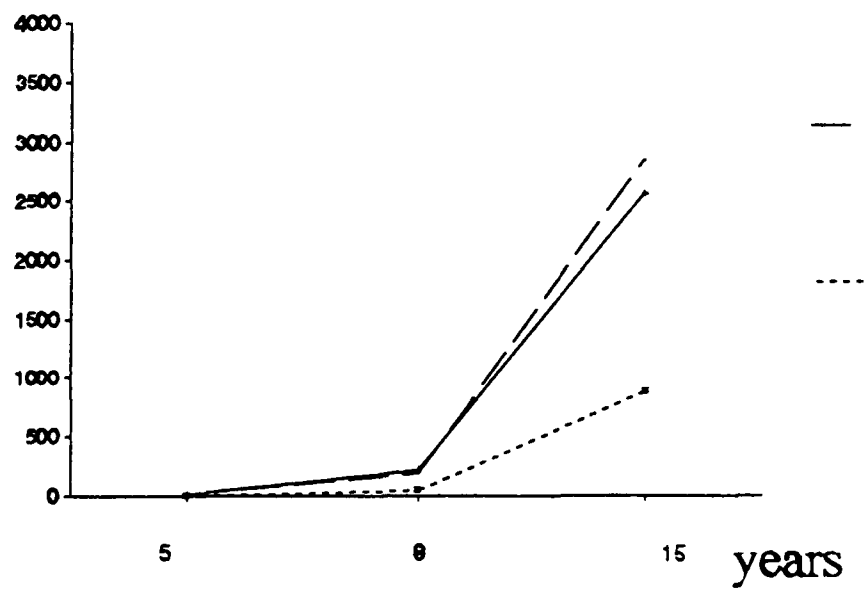
23a



23b



23c



key

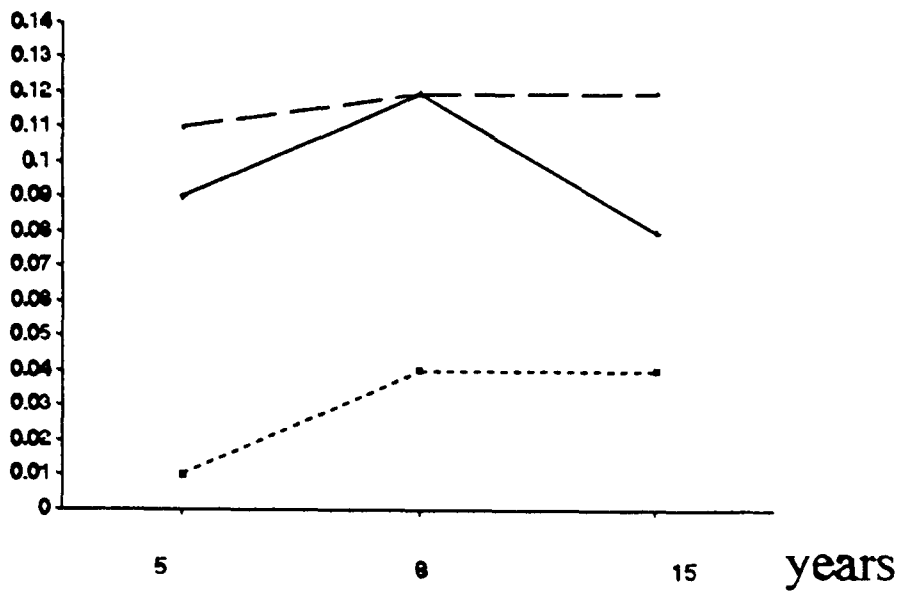
—— additive variance due to the female parent.

— — additive variance due to the male parent.

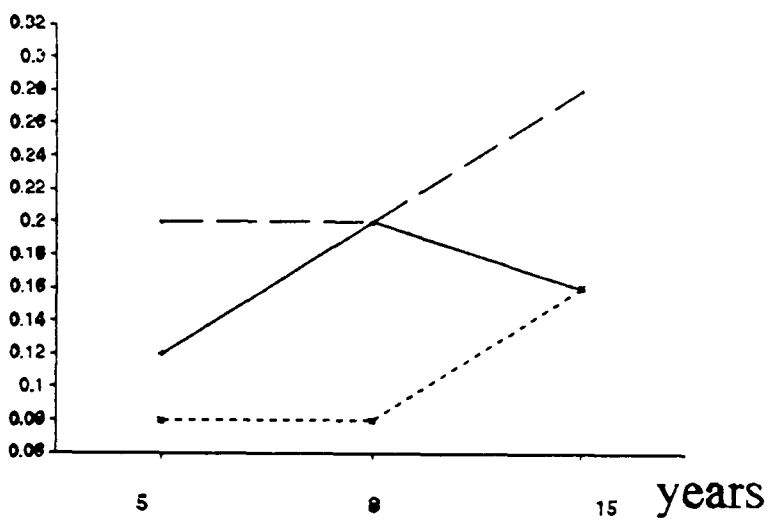
------ dominance variance due to both female and male parents.

Figure 2.10. Trends over time in additive and dominance variances for volume in the three progeny tests.

23a

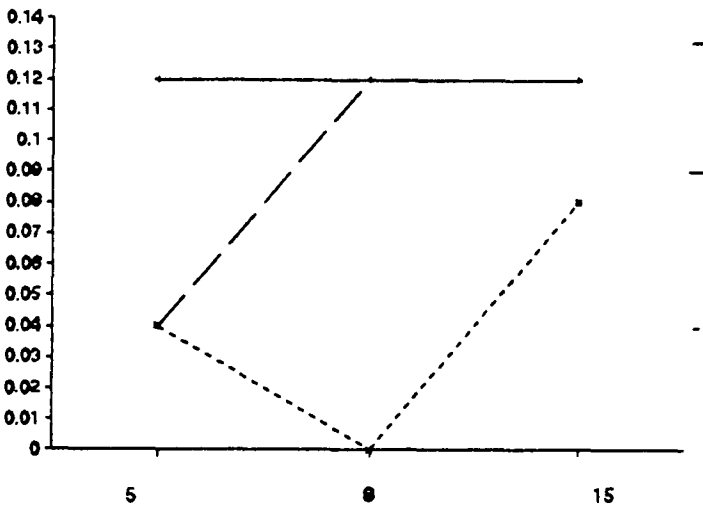


23b



key

23c



——— additive variance due to the female parent.

— — additive variance due to the male parent.

----- dominance variance due to both female and male parents.

Figure 2.11. Trends over time in additive and dominance variances for stem straightness in the three progeny tests.

Ratios of additive to dominance variances for growth traits and stem straightness estimated at five and eight years are in agreement with other published estimates for various pine species, summarised by Cotterill *et al* (1987). The results suggest that additive genetic effects are the most important in the control of all measured traits in this population of *P. elliottii*, with the probable exception of branch diameters. For growth traits at ages eight and 15 years, the magnitude of additive variance was between two and four times greater that of than non-additive variance. Similarly, Carson (1986 in Dean 1990) and Volker and Cameron (1988), both working with *P. radiata*, reported additive genetic variances at least four times greater than dominance genetic variances for height, diameter, sectional area, stem straightness and branch quality.

Both additive and dominance genetic variances of all traits increase as the trees age, though the latter does so at a slower rate than the former. The lower additive genetic variance at age five years may be due to the effects of competition among trees, although this can only be speculation as there are no data at earlier ages. Although selective thinning has been found to affect the magnitude of additive and phenotypic variances, increasing the former and decreasing the latter (Matheson and Raymond 1984b), the thinning practised here was systematic and should have had no such effects.

2.5.4 - Heritabilities

Table 2.17 summarises narrow-sense heritabilities for all measured traits estimated from the three tests at five, eight and 15 years. Figures 2.12 - 2.15 illustrate the trends over time for heritabilities of growth traits and stem straightness.

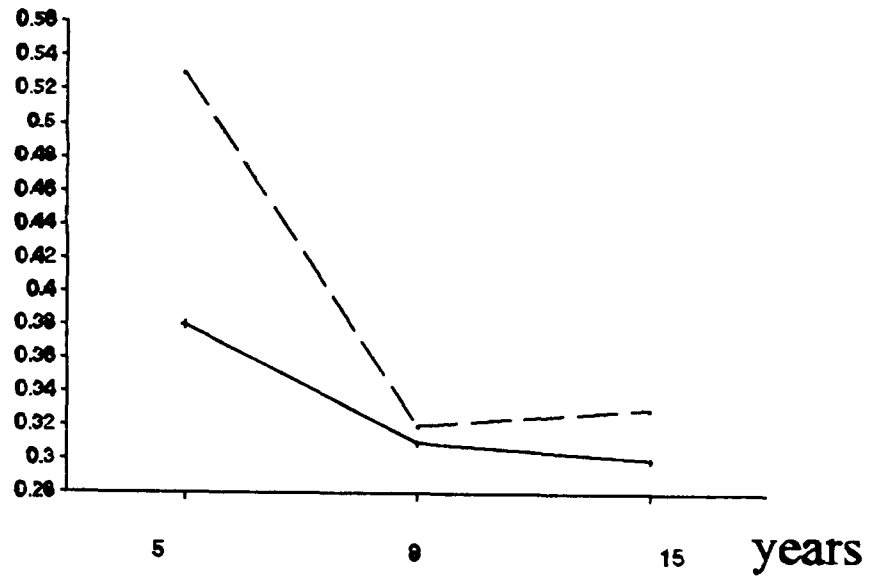
Growth traits, resin yield, wood density and stem straightness are under moderate to strong genetic control in all tests at all ages. Heritabilities for branch traits range from low to moderate. In tests 23a and 23b, estimates from male parents are higher than those from female parents at all three ages; the reverse is true in test 23c at five and eight years, reflecting the pattern in the variance components. Correspondingly, standard errors of male estimates in test 23c are also greater at all ages, and of approximately the same magnitude as the estimates. In all cases, this reflects the lower number of males represented in the tests.

The difference between male and female estimates was not as great for branching characteristics and stem straightness as for growth traits. These traits are under weaker genetic control than is growth. Estimates of heritabilities for resin yield based on male and female parents were of equal magnitude, as were the associated standard errors.

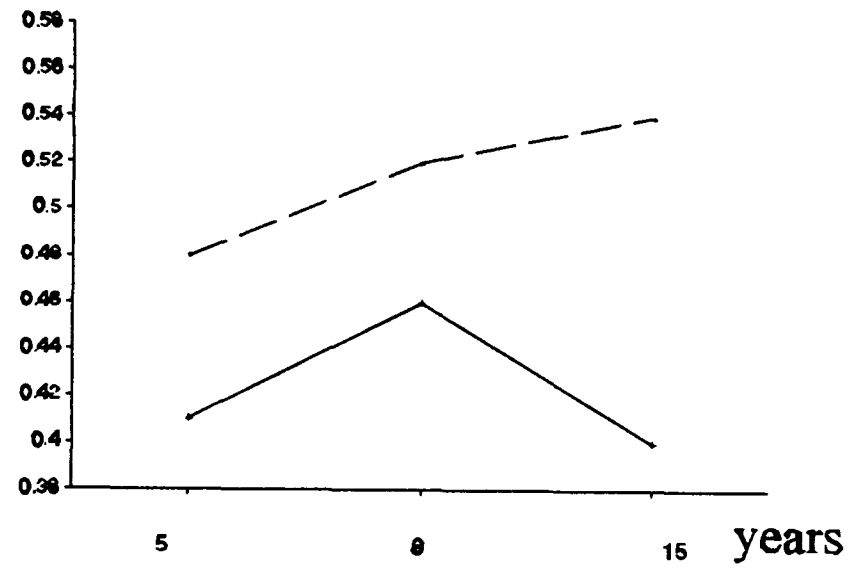
Table 2.17 Heritabilities and associated standard errors for all measured traits in the three tests at ages five, eight and 15 years.

Trait	Female	Male
23a - 5 yrs		
HT5	0.38 ± 0.11	0.53 ± 0.24
DBH5	0.33 ± 0.10	0.46 ± 0.21
VOL5	0.41 ± 0.12	0.60 ± 0.26
BRCT5	0.15 ± 0.05	0.12 ± 0.06
BRDM5	0.03 ± 0.03	0.01 ± 0.02
AIL5	0.25 ± 0.08	0.37 ± 0.17
STR5	0.15 ± 0.05	0.18 ± 0.09
8 yrs		
HT8	0.31 ± 0.08	0.32 ± 0.16
DBH8	0.31 ± 0.08	0.42 ± 0.20
VOL8	0.36 ± 0.10	0.49 ± 0.22
STR8	0.20 ± 0.06	0.24 ± 0.12
15 yrs		
HT15	0.30 ± 0.08	0.33 ± 0.16
DBH15	0.37 ± 0.10	0.41 ± 0.19
VOL15	0.38 ± 0.10	0.46 ± 0.21
DENS15	0.29 ± 0.08	0.36 ± 0.17
RESQ15	0.37 ± 0.20	0.33 ± 0.19
STR15	0.15 ± 0.05	0.23 ± 0.11
23b - 5 yrs		
HT5	0.41 ± 0.11	0.48 ± 0.22
DBH5	0.45 ± 0.12	0.60 ± 0.26
VOL5	0.49 ± 0.12	0.62 ± 0.27
BRCT5	0.17 ± 0.05	0.33 ± 0.15
BRDM5	0.20 ± 0.06	0.39 ± 0.18
AIL5	0.27 ± 0.07	0.37 ± 0.17
STR5	0.22 ± 0.06	0.29 ± 0.14
8 yrs		
HT8	0.46 ± 0.12	0.52 ± 0.24
DBH8	0.40 ± 0.11	0.71 ± 0.30
VOL8	0.45 ± 0.12	0.71 ± 0.30
STR8	0.30 ± 0.08	0.28 ± 0.14
15 yrs		
HT15	0.40 ± 0.11	0.54 ± 0.25
DBH15	0.43 ± 0.12	0.85 ± 0.34
VOL15	0.43 ± 0.12	0.79 ± 0.33
DENS15	0.39 ± 0.11	0.51 ± 0.23
STR15	0.18 ± 0.06	0.34 ± 0.16
23c - 5 yrs		
HT5	0.48 ± 0.18	0.38 ± 0.31
DBH5	0.52 ± 0.17	0.23 ± 0.20
VOL5	0.53 ± 0.19	0.41 ± 0.33
BRCT5	0.07 ± 0.04	0.08 ± 0.07
BRDM5	0.0004 ± 0.09	0.0004 ± 0.03
AIL5	0.10 ± 0.08	0.25 ± 0.22
STR5	0.19 ± 0.11	0.06 ± 0.08
8 yrs		
HT8	0.51 ± 0.18	0.30 ± 0.25
DBH8	0.48 ± 0.17	0.26 ± 0.22
VOL8	0.49 ± 0.18	0.44 ± 0.34
STR8	0.23 ± 0.11	0.28 ± 0.24
15 yrs		
HT15	0.51 ± 0.21	0.19 ± 0.18
DBH15	0.50 ± 0.20	0.68 ± 0.49
VOL15	0.57 ± 0.23	0.64 ± 0.47
DENS15	0.45 ± 0.18	1.00 ± 0.71
STR15	0.20 ± 0.13	0.20 ± 0.18

23a



23b



23c

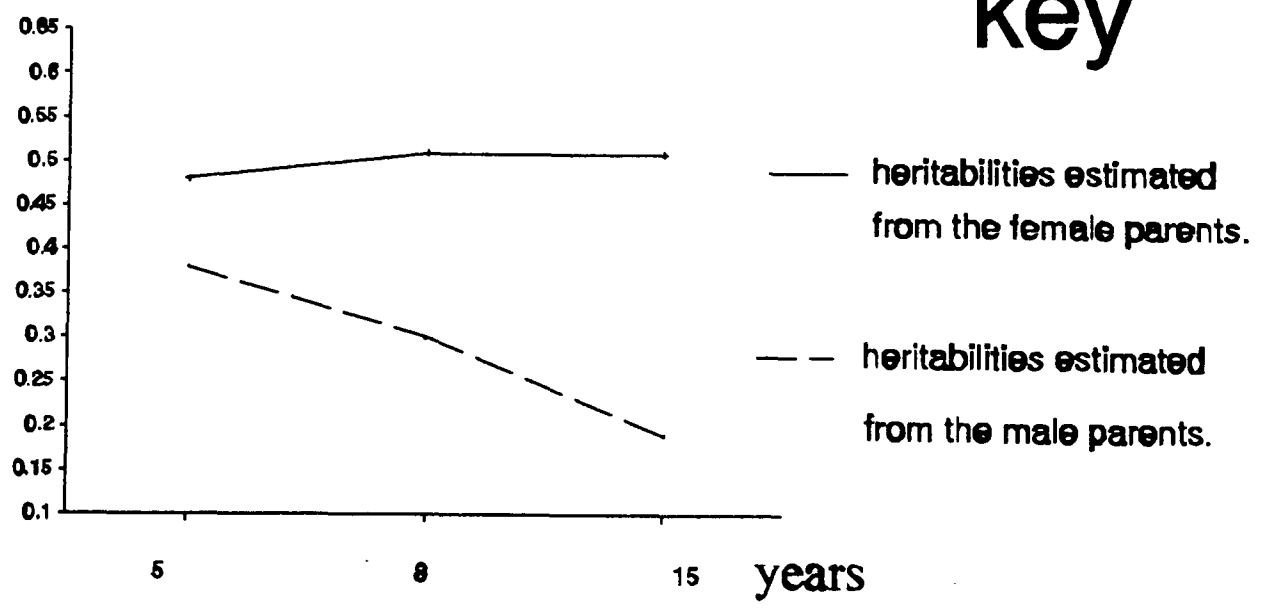
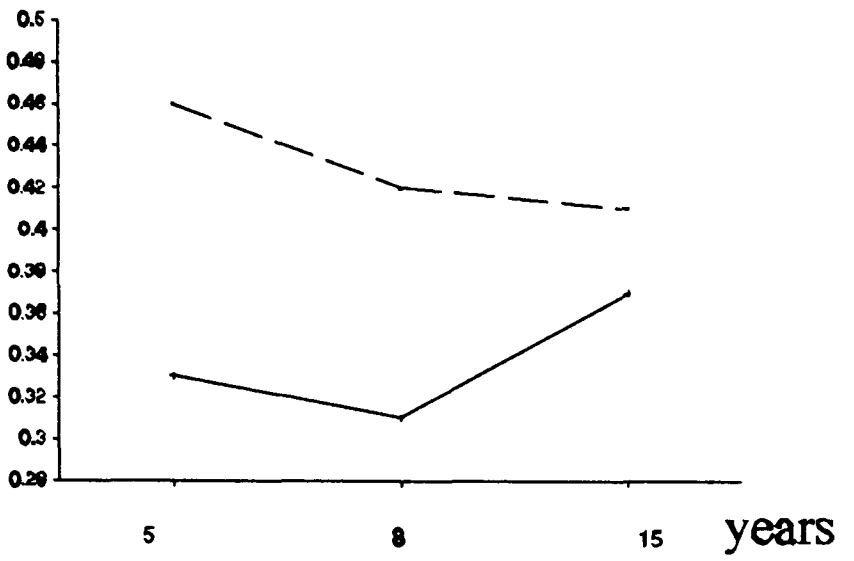
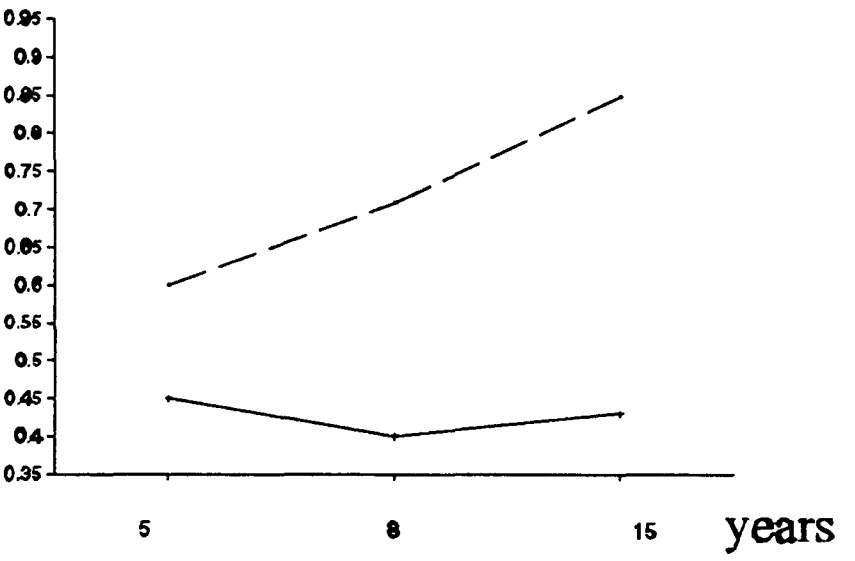


Figure 2.12. Trends over time in heritabilities for height in the three progeny tests.

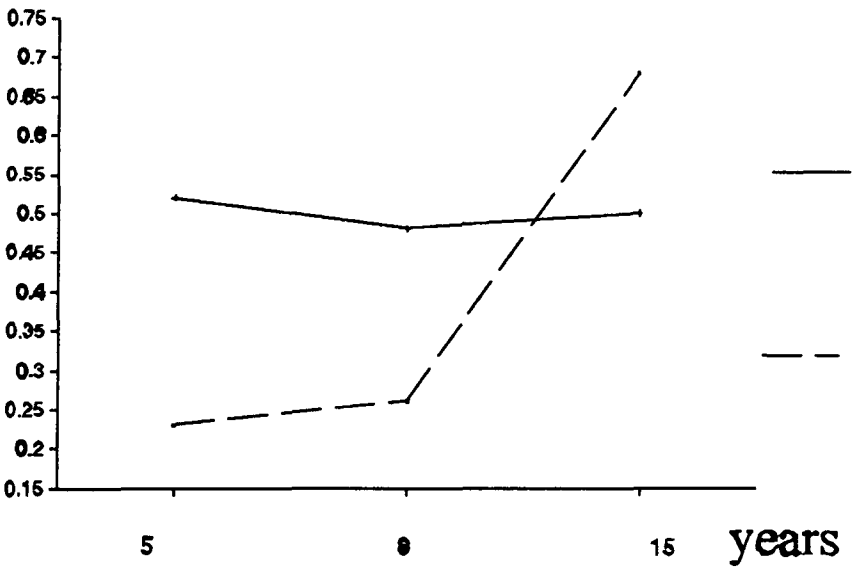
23a



23b



23c



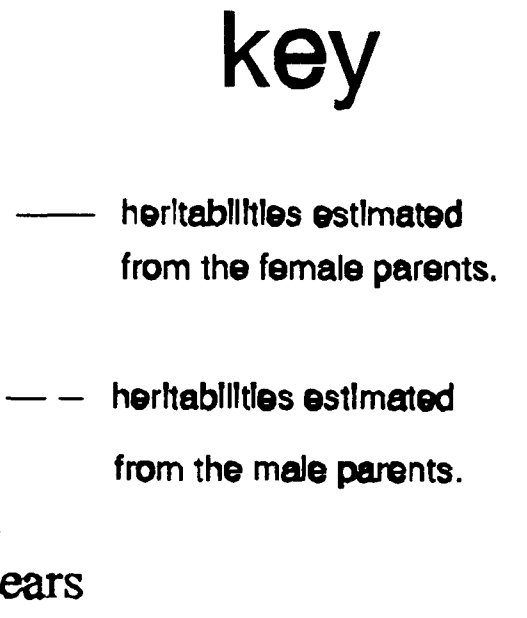
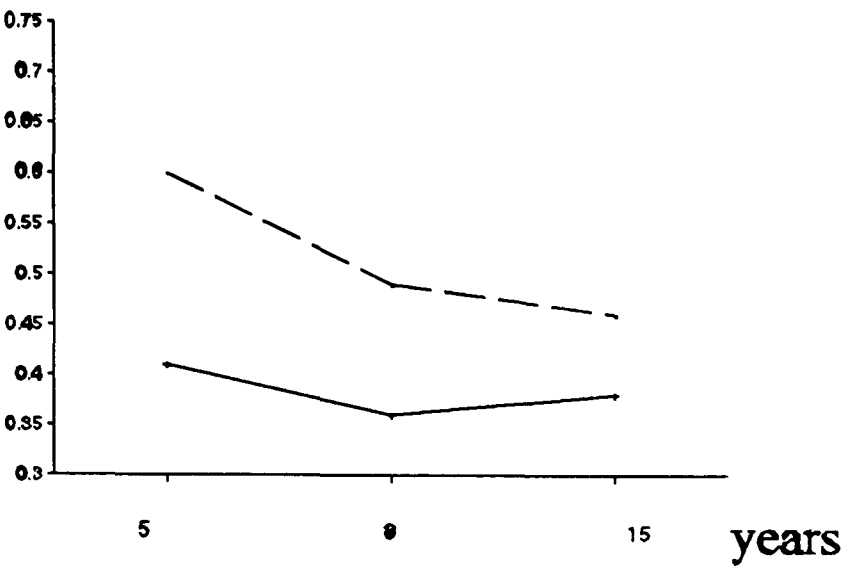
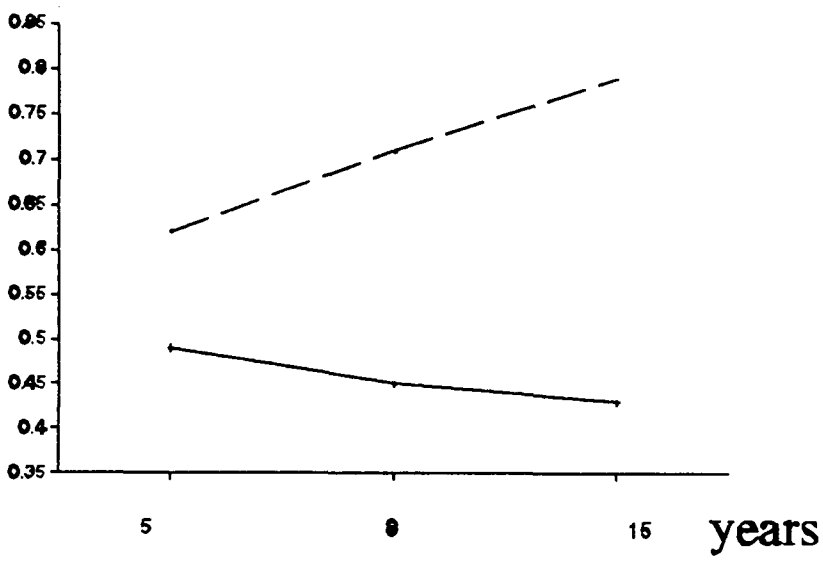


Figure 2.13. Trends over time in heritabilities in diameter in the three progeny tests.

23a

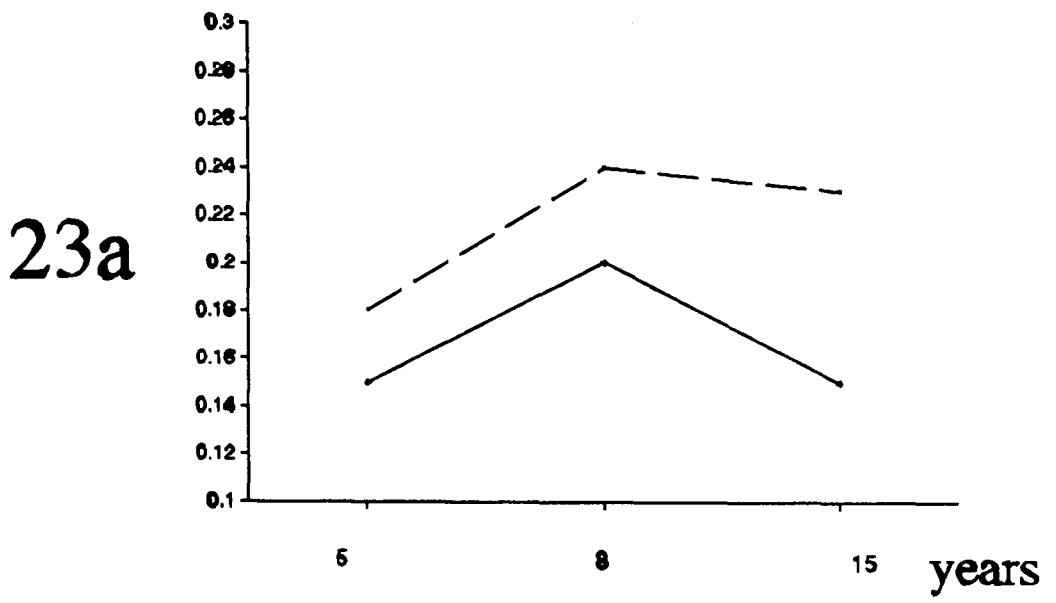


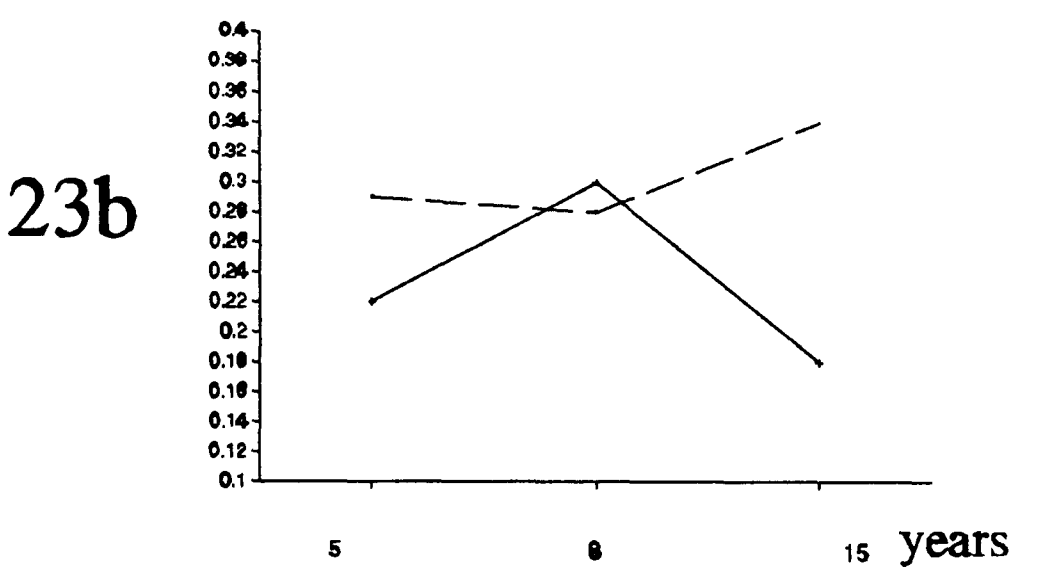
23b



23c

Figure 2.14. Trends over time in heritabilities for volume in the three progeny tests.





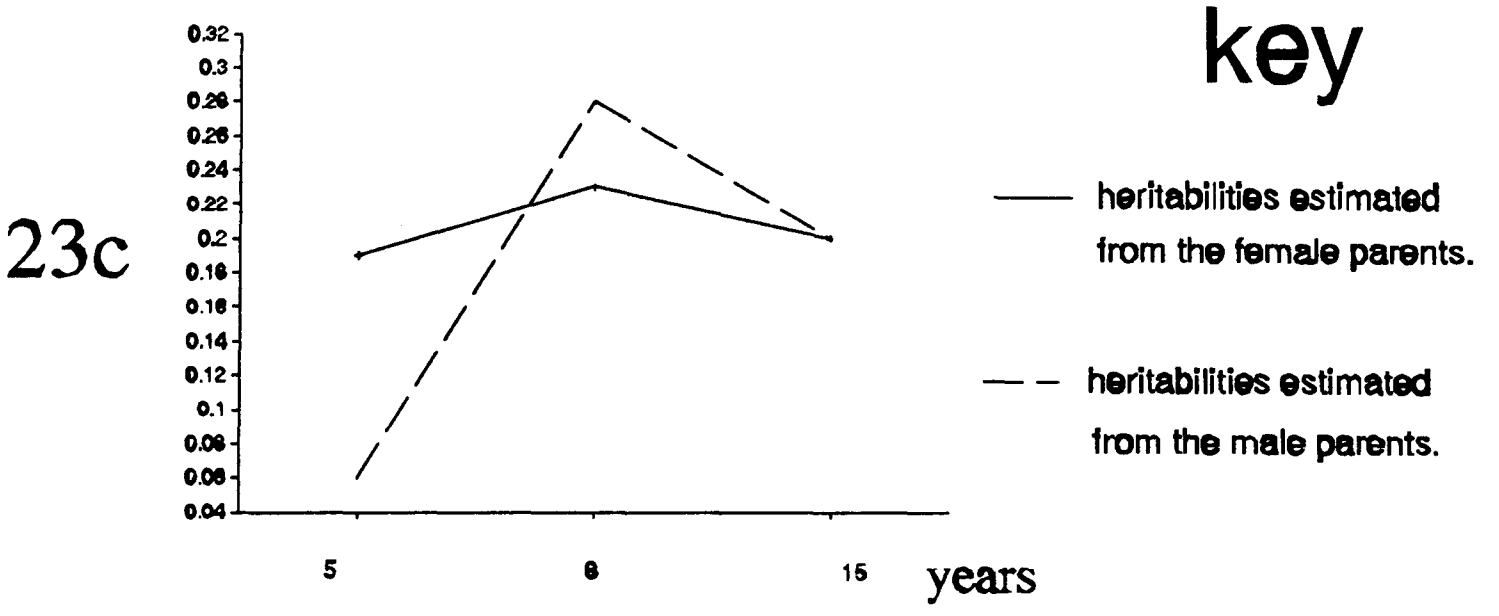


Figure 2.15. Trends over time in heritabilities for stem straightness in the three progeny tests.

Heritabilities for wood density in tests 23a and 23b were slightly lower, at 0.3-0.4, than those reported in literature; for example, Goddard and Cole (1966), Institute of Paper Chemistry (1962) and Sohn and Goddard (1974) reported heritabilities of this trait in *P. elliottii* ranging between 0.47 to 0.65 with standard errors ranging between 0.1 and 0.23, and Birks (1990) reported heritabilities ranging between 0.51 and 0.63 with standard errors ranging between 0.21 and 0.32 in Zimbabwean *P. patula*. Generally, heritabilities of wood density in conifers have been found to range between 0.4 and 0.7 with standard errors ranging between 0.1 and 0.20 (Megraw 1985, Zobel and van Buijtenen 1989). In all tests, heritability estimates changed little between five and 15 years. Notable exceptions were those from male parents in test 23b, in which the eight and 15 year estimates were much higher than those at age five. The heritabilities for stem straightness were generally moderate and tended to be highest at age eight years.

Estimates of heritability found in this study are generally consistent with those reported elsewhere for *P. elliottii*, for example, by Allen (1985) and Dorman and Squillace (1974), and for other *Pinus* species, *eg*, Barnes *et al* (1992a and b) for *P. patula*, Cotterill *et al* (1987) for *P. pinaster*, *P. radiata* and *P. elliottii*, Dean (1990) for *P. radiata*, Woolaston *et al* 1990 for *P. caribaea*, and Foster (1986) for *P. taeda*.

2.5.5 - Genetic and phenotypic correlations

Tables 2.18, 2.19 and 2.20 summarise the estimates of genetic and phenotypic correlations between traits assessed at five, eight and 15 years of age, respectively.

2.5.5.1 - Growth traits

Additive genetic correlations between growth traits in all tests were large and positive, above 0.65 at all ages in all tests, with moderate or low standard errors. Additive genetic correlations between volume and height or diameter were high, which is expected given that volume is derived from both height and diameter. Phenotypic correlations were generally of comparable magnitude to genetic correlations. Additive genetic correlations between growth traits generally increased between the ages of five and eight and decreased between eight and 15 years. The magnitude of genetic correlations found in this study are generally similar to those reported in the literature for *P. elliottii* (Cotterill *et al* 1987, Allen 1978, Sohn and Goddard 1974), and for other species, *eg, P. patula* (Barnes *et al* 1992a and b), *P. banksiana* (Reimenscheneider 1988), *P. caribaea* (Woolaston *et al* 1990), *P. pinaster, P. radiata* and *P. elliottii* (Cotterill *et al* 1987), *P. radiata* (Cotterill and Dean 1988), *P. taeda* (Foster 1986), *Pseudotsuga menziesii* (Mirb.) Franco (King *et al* 1988) and *Eucalyptus globulus* (Borralho *et al* 1992).

Table2.18 Genetic correlations and associated standard errors (upper triangle), estimated from maternal components of variance, and phenotypic correlations (lower triangle) for all traits at five, eight and 15 years for progeny test 23a.

Trait	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	RESQ15	DENS15	STR15
HT5		0.65±0.12	0.84±0.06	0.29±0.20	-0.45±0.20	-0.26±0.20	0.50±0.17					0.93±0.04	0.75±0.10	0.82±0.07	0.07±0.41	0.15±0.19	-0.10±0.22
DBH5	0.72		0.96±0.02	0.47±0.17	0.16±0.24	0.02±0.22	0.32±0.20					0.54±0.16	0.94±0.03	0.92±0.04	0.06±0.41	-0.31±0.18	-0.01±0.23
VOL5	0.83	0.92		0.42±0.18	-0.19±0.24	-0.11±0.21	0.41±0.18					0.72±0.11	0.96±0.02	0.97±0.02	0.11±0.40	-0.16±0.19	-0.06±0.23
BRCT5	0.16	0.22	0.19		-0.19±0.24	0.52±0.16	-0.09±0.22					0.30±0.18	0.31±0.18	0.33±0.17		0.05±0.21	0.06±0.20
BRDM5	0.02	0.12	0.06	-0.09		-0.21±0.24	-0.33±0.23					-0.68±0.12	-0.19±0.18	-0.29±0.18		-0.28±0.20	-0.28±0.19
AIL5	0.10	0.12	0.09	0.14	0.06		-0.23±0.21					0.04±0.19	0.03±0.19	0.002±0.19		0.04±0.20	0.16±0.19
STR5	0.31	0.21	0.23	0.05	-0.04	0.04						0.64±0.14	0.34±0.20	0.42±0.19	0.59±0.30	0.23±0.20	0.54±0.17
HT8									0.69±0.12	0.88±0.06	0.15±0.24	0.97	0.84	0.88	0.10	-0.09	0.08
DBH8								0.90		0.97±0.02	-0.07±0.24	0.56±0.15	0.96±0.02	0.93±0.03	0.08±0.41	-0.30±0.18	-0.04±0.23
VOL8								0.76			-0.01±0.24	0.88	1.00	1.00	0.32	-0.23	0.08
STR8								0.66	0.56	0.35		0.35±0.20	0.11±0.23	0.15±0.22	0.55±0.36	-0.12±0.21	0.83±0.08
HT15	0.52	0.36	0.45	0.08	-0.06	0.11	0.15	0.85	0.47	0.78	0.14		0.67±0.12	0.76±0.09	0.24±0.42	0.19±0.19	0.09±0.23
DBH15	0.61	0.66	0.72	0.11	0.06	0.07	0.18	0.75	0.87	0.91	0.14	0.56		0.99±0.01	0.10±0.42	-0.18±0.19	0.04±0.23
VOL15	0.59	0.61	0.68	0.10	0.03	0.07	0.17	0.77	0.79	0.92	0.13	0.63	0.91		0.09±0.42	-0.11±0.20	0.05±0.23
RESQ15	0.13	0.06	0.09				0.02	0.14	0.10	0.31	-0.06	0.06	0.09	0.09		-0.42	0.60±0.34
DENS15	0.02	-0.12	-0.08	-0.05	-0.05	-0.03	-0.01	-0.08	-0.09	-0.20	-0.002	0.08	-0.01	-0.01	-0.36		-0.45±0.17
STR15	0.12	0.09	0.11	0.003	-0.04	0.02	0.23	0.06	0.17	0.07	0.51	0.20	0.23	0.21	0.03	0.01	

Table 2.19 Genetic correlations and associated standard errors (upper triangle), estimated from maternal components of variance, and phenotypic correlations (lower triangle) for all traits at five, eight and 15 years for progeny test 23b.

Trait	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	STR15
HT5		0.83±0.07	0.88±0.05	0.24±0.21	0.38±0.19	0.31±0.20	0.17±0.21					0.83±0.07	0.58±0.15	0.64±0.13	-0.02±0.20	0.26±0.22
DBH5	0.82		0.99±0.004	0.44±0.18	0.65±0.13	0.34±0.19	0.07±0.22					0.66±0.13	0.77±0.09	0.81±0.08	-0.37±0.17	0.22±0.23
VOL5	0.86	0.94		0.41±0.19	0.59±0.15	0.36±0.19	0.07±0.22					0.71±0.11	0.76±0.10	0.81±0.08	-0.28±0.18	-0.20±0.23
BRCT5	0.24	0.32	0.29		0.43±0.19	0.74±0.11	-0.27±0.21					0.44±0.16	0.49±0.15	0.46±0.16	-0.10±0.21	0.08±0.20
BRDM5	0.21	0.41	0.34	-0.03		0.28±0.21	0.10±0.22					0.45±0.16	0.63±0.12	0.61±0.12	0.05±0.21	0.26±0.19
AIL5	0.32	0.28	0.29	0.16	0.32		-0.07±0.22					0.37±0.17	0.36±0.17	0.36±0.17	0.10±0.20	0.21±0.19
STR5	0.31	0.22	0.23	0.03	0.02	0.05						0.18±0.22	0.02±0.23	0.02±0.23	0.02±0.21	0.79±0.10
HT8									0.80±0.08	0.87±0.06	0.26±0.21	0.97	0.84	0.88	0.06	0.08
DBH8								0.82		0.99±0.01	0.17±0.22	0.66±0.13	0.92±0.04	0.91±0.04	-0.34±0.18	-0.22±0.23
VOL8								0.86			0.12±0.22	0.91	1.00	1.00	-0.15	0.88
STR8								0.45	0.38	0.35		0.11±0.23	-0.07±0.23	-0.07±0.23	-0.01±0.21	0.87±0.07
HT15	0.72	0.66	0.66	0.16	0.22	0.23	0.32	0.88	0.77	0.85	0.44		0.74±0.10	0.79±0.09	0.15±0.19	0.43±0.20
DBH15	0.60	0.74	0.71	0.20	0.36	0.19	0.71	0.85	0.90	0.94	0.39	0.80		0.98±0.01	-0.25±0.18	0.37±0.21
VOL15	0.59	0.70	0.71	0.19	0.33	0.19	0.71	0.88	0.84	0.97	0.35	0.59	0.94		-0.25±0.19	0.37±0.21
DENS15	-0.02	-0.16	-0.14	-0.08	-0.04	-0.01	-0.14	0.05	-0.08	-0.13	-0.001	0.07	-0.08	-0.09		-0.22±0.20
STR15	0.42	0.41	0.39	0.10	0.15	0.08	0.39	0.73	0.60	0.77	0.59	0.77	0.60	0.55	0.003	

Table 2.20 Genetic correlations and associated standard errors (upper triangle), estimated from maternal components of variance, and phenotypic correlations (lower triangle) for all traits at five, eight and 15 years for progeny test 23c.

Trait	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	STR15
HT5		0.71±0.12	0.87±0.06	0.43±0.42	-0.45±0.34	0.63±0.19	0.72±0.15					0.96±0.04	0.82±0.09	0.93±0.05	0.32±0.27	0.23±0.31
DBH5	0.74		0.97±0.02	0.47±0.41	-0.09±0.37	0.78±0.14	0.78±0.13					0.94±0.05	0.97±0.03	1.00±0.01	0.19±0.28	0.44±0.28
VOL5	0.86	0.93		0.59±0.39	0.02±0.37	0.70±0.17	0.77±0.13					0.95±0.04	0.90±0.06	0.97±0.02	0.30±0.27	0.37±0.29
BRCT5	0.01	0.05	0.08		0.55±0.63	0.72±0.46	-0.56±0.46					0.51±0.33	0.86±0.26	0.98±0.27	-1.00±0.40	0.33±0.39
BRDM5	-0.03	-0.04	-0.03	-0.02		-0.71±0.36	-1.00±0.29						Unable to estimate - data too limited			
AIL5	0.56	0.78	0.70	0.02	0.00		0.51±0.25					0.29±0.28	0.27±0.28	0.10±0.32	1.00±0.87	0.01±0.34
STR5	0.54	0.56	0.46	0.01	-0.06	0.34						0.63±0.45	1.00±0.60	1.00±0.57	-0.81±1.00	0.05±0.64
HT8									0.92±0.05	0.95±0.03	0.99±0.06	0.89	0.85	0.88	-0.03	0.60
DBH8								0.86		0.98±0.02	1.00±0.06	0.86±0.08	0.99±0.01	1.00±0.01	0.08±0.28	0.50±0.27
VOL8								0.85	0.89		0.97±0.08	0.92	0.97	1.00	-0.12	0.49
STR8								0.60	0.54	0.49		0.64±0.48	0.54±0.49	0.85±0.48	0.05±0.38	0.58±0.49
HT15	0.73	0.64	0.58	0.001		0.33	0.44	0.80	0.68	0.83	0.37		0.80±0.10	0.92±0.05	0.14±0.28	0.29±0.30
DBH15	0.66	0.73	0.70	0.07		0.24	0.36	0.79	0.87	0.90	0.32	0.65		0.98±0.01	-0.05±0.29	0.29±0.30
VOL15	0.70	0.72	0.75	0.08		0.25	0.36	0.82	0.85	0.93	0.32	0.65	0.95		0.08±0.29	0.28±0.30
DENS15	0.04	-0.03	-0.01	0.07		-0.01	-0.01	0.03	-0.05	-0.11	-0.05	0.07	-0.06	-0.03		-0.13±0.33
STR15	0.32	0.27	0.22	0.03		0.08	0.36	0.49	0.30	0.40	0.43	0.44	0.32	0.32	0.05	

Additive genetic correlations between juvenile heights (HT5 and HT8) and diameters (DBH5 and DBH8) *vs* mature height (HT15), diameter (DBH15) or volume (VOL15) were generally high (0.7 and above). Juvenile-mature correlations between growth traits generally increased with age in tests 23a and 23b but decreased in test 23c. Genetic correlations between growth traits were associated with low standard errors (0.1 and below), and phenotypic correlations between growth traits were generally high (0.6 and above). Additive genetic correlations were generally higher than phenotypic correlations. The high genetic correlations between growth traits found in this study are consistent with those reported by Paschke (1979) for *P. taeda*, and Wakeley (1971) for a variety of southern pines.

2.5.5.2 - Stem straightness

Genetic correlations between stem straightness and growth traits ranged from moderately negative to strongly positive in all three tests. Highly positive genetic correlations between stem straightness and growth traits were also reported for *P. elliottii* by Cotterill *et al* (1987). These correlations were generally associated with large standard errors.

Juvenile-mature correlations between stem straightness and growth traits were consistently low in test 23a, but ranged between low and moderate, with occasional high correlations, in tests 23b and 23c. They were relatively stable over time and were associated with large standard errors. Phenotypic

correlations between stem straightness and growth traits were generally low to moderate.

2.5.5.3 - Wood density

The additive genetic correlations between wood density and height were positive in all three tests, though low (0.07 to 0.19). Correlations between wood density and diameter or volume were negative, ranging from low to moderate (-0.11 to -0.23) in the three tests. Correlations between wood density and stem straightness were also negative, ranging from low to moderate. These results are consistent with those reported in the literature, where slightly positive correlations between height and density and a negative correlation between density and diameter have been observed, for example by Sohn and Goddard (1974) and Squillace and Kraus (1962). Phenotypic correlations between the traits were generally low, also as reported in the literature.

Additive genetic correlations between wood density at 15 years and juvenile height ranged from low negative values (-0.02 ± 0.20) to moderately positive values (0.32 ± 0.27). Correlations with mature height were positive for all tests, while those with diameter were generally negative and moderate for tests 23a and 23b, but more variable in test 23c. The magnitude of correlations with diameter decreased with increasing age in all tests. Additive genetic correlations with volume followed the same pattern as that of diameter. Correlations with stem straightness were variable between all ages and tests.

The positive genetic correlations between height and wood density, and the negative correlation with diameter at age 15, found in this study are in keeping with those reported, for example, by Dean (1990) and Megraw (1985). It has also been suggested that this could be due to the loss of the live crown and the distance from the live crown of the area from which the core was taken (Barnes[3] pers. comm.); as Megraw (1985) proposed, it may be that as a tree grows taller and the vigorous crown moves upward, diameter growth slows at a given height and specific gravity increases, such that there is a definite inverse relationship between specific gravity and growth rate. The negative correlations between wood density and diameter weakened with age.

2.5.5.4 - Branching traits

Additive genetic correlations between the branching traits and growth traits ranged from low ($r_a = 0.01 \pm 0.37$) to high ($r_a = 0.78 \pm 0.14$) with no particular pattern across tests. Correlations between the number of branches per whorl and stem straightness at five years were negative, but - as with other branching traits, which had more variable correlations with stem straightness at five years - correlations with straightness at 15 years were positive. Standard errors of correlations involving branching traits tended to be high.

In all three tests, correlations between the number of branches per whorl and

[3] Dr. R.D. Barnes, Oxford Forestry Institute, Department of Plant Sciences, South Parks Road, OX1 3RB, UK.

internode length were high and positive; correlations between internode length and volume at 15 years were also positive. This result suggests that, were a "long internode" population to be developed, as has been done for *P. radiata* in New Zealand, the nodes would be large and knotty, with consequent difficulties for processing (Carson and Inglis 1986). The results are similar to those reported by Barnes *et al* (1992a) for *P. patula*, Carson and Inglis (1986) for *P. radiata*, and Dean *et al* (1986) and Woolaston *et al* (1990) for *P. caribaea*.

2.5.5.5 - Resin yield

Correlations between resin yield and height were moderate and positive, while those with diameter or volume were low but also positive. Coppen *et al* (1984) reported that trees with large diameters yielded more resin, but this relationship was not found to be strong in this population of *P. elliottii*. Instead, the highest correlation of resin yield was with stem straightness at 15 years (0.60 ± 0.34). Correlations between resin yield and wood density were moderate but negative. All correlations involving resin yield were associated with high standard errors, and it is possible that the data set was not large enough to give reliable results (only three replicates were sampled). Phenotypic correlations of resin yield with most traits were low, with the exception of that with wood density, which was moderately negative.

Juvenile-mature correlations between resin yield and growth traits ranged from low to moderate, and those with stem straightness were high (0.5 and

above). Correlations were reasonably consistent over time for each trait. Standard errors of genetic correlations were generally high. Phenotypic correlations were moderate and similarly consistent over time.

2.6 - Genotype-environment interaction

2.6.1 - Analysis of variance

Results of the combined analysis of variance of the 39 families common to all sites are presented in Table 2.21. All sources of variation had a significant effect ($P < 0.05$) on all traits at all ages. This result is typical of those reported in the literature (see Matheson and Raymond 1984a).

2.6.2 - Variance components

The magnitude of variance components, their standard errors and relative proportions of total variability, for growth and stem straightness at five, eight and 15 years, and wood density at 15 years, are shown in Tables 2.22, 2.23 and 2.24 respectively.

Together, the components of variance for the residual and for site account for at least 70% of the variation for all traits at all ages. The female and male components were generally the next most important sources of variation.

Table 2.21 Mean squares for growth, stem straightness and branching traits at ages five, eight and 15 years from the combined analysis of the 39 families present in all three tests.

Source	Mean Squares												
	HT5	DBH5	VOL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	STR15
Site	2106.1	10621.0	183670.0	125.0	3324.5	5921.4	1082100.0	478.2	11384.0	6356.2	14806000.0	1066300.0	22.3
Rep in Site	16.5	61.5	1230.9	5.9	27.2	39.5	4476.0	5.2	33.2	44.7	71266.0		13.3
Female	31.1	130.5	3203.4	7.41	32.5	105.3	17631.0	2.8	53.8	284.6	325760.0	36400.0	3.2
Male	161.1	674.6	19340.0	58.7	239.5	1137.4	198470.0	26.5	387.8	3116.6	3083800.0	127250.0	19.2
Fem x Male	6.1	23.0	498.0	2.6	11.0	34.9	5434.0	1.0	16.8	72.2	74197.0	3203.3	1.4
Fem x Site	5.1	20.8	491.9	2.9	8.4	25.7	2641.2	2.3	14.0	47.6	50695.0	2837.4	1.5
Male x Site	12.0	89.4	4158.2	4.6	21.8	132.7	30726.0	4.3	118.4	600.9	781640.0	5444.9	10.6
Fam x Site	2.2	8.9	198.5	1.2	2.6	10.1	1302.6	0.5	7.8	22.6	23002.0	2283.8	0.9
Residual	0.7	3.0	66.1	0.5	1.7	6.8	979.91	0.5	3.6	16.5	18163.0	1913.6	0.6

All sources of variation had significant effects ($P < 0.05$) on all traits at all ages.

Table 2.22 Variance components, their standard errors and proportions of total variance (in brackets) for growth traits and stem straightness estimated from the combined site analysis for the 39 families present in all three progeny tests at five years.

Source	HT5	DBH5	VOL5	STR5
Site	1.07±1.09 (51.9)	5.45±5.52 (54.7)	93.83±96.67 (46.9)	0.06±0.06 (9.0)
Rep in Site	0.05±0.02 (2.4)	0.17±0.06 (1.7)	3.32±1.28 (1.66)	0.02±0.01 (3.0)
Female	0.08±0.04 (3.9)	0.37±0.17 (3.7)	9.29±4.13 (4.7)	0.01±0.01 (1.5)
Male	0.11±0.10 (5.3)	0.46±0.44 (4.6)	12.60±12.86 (6.3)	0.04±0.03 (6.0)
Fem x Male	0.02±0.01 (1.0)	0.09±0.05 (0.9)	1.84±1.08 (0.9)	0.01±0.01 (1.5)
Fem x Site	0.03±0.01 (1.5)	0.11±0.05 (1.1)	2.79±1.23 (1.4)	0.02±0.01 (3.0)
Male x Site	0.02±0.01 (1.0)	0.16±0.10 (1.6)	7.82±4.82 (3.9)	0.01±0.01 (1.5)
Fam x Site	0.03±0.01 (1.5)	0.11±0.04 (1.1)	2.39±0.86 (1.2)	0.01±0.01 (1.5)
Residual	0.65±0.01 (31.6)	3.04±0.05 (30.5)	66.14±1.18 (33.1)	0.49±0.01 (73.1)

Table 2.23 Variance components, their standard errors and proportions of total variance (in brackets) for growth traits and stem straightness estimated from the combined site analysis from the 39 families present in all three progeny tests at eight years.

Source	HT8	DBH8	VOL8	STR8
Site	3.83±3.89 (59.7)	6.57±6.73 (39.2)	1163.3±1197.5 (42.9)	0.56±0.57 (47.0)
Rep in Site	0.16±0.06 (2.5)	0.19±0.09 (1.13)	21.02±9.86 (0.8)	0.03±0.01 (2.5)
Female	0.11±0.09 (1.7)	0.42±0.28 (2.5)	81.53±45.80 (3.0)	0.001±0.01 (0.08)
Male	0.31±0.29 (4.8)	1.45±1.40 (8.7)	253.65±249.15 (9.4)	0.03±0.03 (2.5)
Fem x Male	0.11±0.05 (1.7)	0.31±0.16 (1.9)	52.81±23.95 (2.0)	0.01±0.004 (0.8)
Fem x Site	0.13±0.05 (2.0)	0.29±0.14 (1.7)	25.13±14.00 (0.9)	0.04±0.01 (3.4)
Male x Site	0.09±0.06 (1.4)	0.56±0.33 (3.3)	120.38±72.26 (4.4)	0.02±0.01 (1.7)
Fam x Site	0.03±0.02 (0.5)	0.13±0.09 (0.8)	12.57±11.83 (0.5)	0.001±0.01 (0.08)
Residual	1.65±0.04 (25.7)	6.83±0.18 (40.8)	979.91±25.60 (36.2)	0.50±0.01 (50.0)

Table 2.24 Variance components, their standard errors and proportions of total variance (in brackets) for height, diameter, volume, wood density and stem straightness estimated from the 39 families present in all three progeny tests at 15 years.

Source	HT15	DBH15	VOL15	DENS15	STR15
Site	13.12±13.28 (70.8)	6.86±7.59 (20.6)	16826.0±17787.0 (36.5)	1117.71±1130.70 (31.5)	0.0001±0.03 (0.01)
Rep in Site	0.19±0.08 (1.0)	0.17±0.10 (0.5)	333.79±165.17 (0.7)		0.08±0.03 (11.0)
Female	0.24±0.15 (1.3)	1.51±0.80 (4.5)	1853.5±903.92 (4.0)	193.07±54.16 (5.4)	0.01±0.01 (1.4)
Male	0.45±0.53 (2.4)	4.35±4.38 (13.0)	4129.2±4446.5 (9.0)	249.40±129.67 (7.0)	0.01±0.03 (1.4)
Fem x Male	0.12±0.08 (0.7)	0.66±0.34 (2.0)	684.04±345.86 (1.5)	30.43±13.94 (0.9)	0.01±0.01 (1.4)
Fem x Site	0.12±0.08 (0.7)	0.52±0.27 (1.6)	587.75±283.55 (1.3)	8.21±8.33 (0.2)	0.01±0.01 (1.4)
Male x Site	0.47±0.29 (2.5)	2.55±1.55 (7.7)	3383.9±2024.8 (7.3)	7.97±8.54 (0.2)	0.04±0.03 (5.5)
Fam x Site	0.17±0.07 (0.9)	0.24±0.22 (0.7)	185.07±219.01 (0.4)	26.06±16.83 (0.7)	0.02±0.01 (2.7)
Residual	3.64±0.10 (19.7)	16.48±0.44 (49.4)	18163.0±485.32 (39.4)	1913.6±35.37 (54.0)	0.56±0.02 (76.7)

The female x site and the male x site interactions were comparable in magnitude, but lower than the female or male components at the three ages, with the exception of the male x site interaction at 15 years. The magnitudes of family x site interactions were variable at all ages but generally smaller than those for all other sources of variation (0.8 - 1.5%).

2.6.3 - Rank changes and genetic correlations

Ranks of Least Square means for growth, wood density and stem straightness traits in the three progeny tests at five, eight and 15 years are listed in Tables 2.1 to 2.13 of Appendix I. Absolute deviations of family rankings at each site, for all traits and ages, are presented in Tables 2.25, 2.26 and 2.27.

The values of Spearman's rank correlation coefficient between family means for each trait across sites at each age, are presented in Table 2.28. Genetic (type B) correlations between family means at each site, for all traits at each of the three ages, are presented in Table 2.29.

2.6.3.1 - Growth traits and wood density

The values of Spearman's rank correlation coefficient, or the genetic correlation, between family means across the three sites was consistently high for growth traits for the three ages represented. In the case of wood density, correlations were effectively or actually unity.

Table 2.25 The deviation of family rankings at individual sites from the overall family site ranking for growth traits and stem straightness at five years.

Family	HT5	DBH5	VOL5	STR5
88 X 49	1	0	2	7
224 X 49	11	9	10	21
88 X 9	2	0	2	17
128 X 9	13	0	0	13
128 X 49	4	5	3	12
58 X 49	21	19	18	28
200 X 49	4	8	6	0
173 X 49	7	8	9	28
172 X 23	9	9	7	20
76 X 49	28	19	12	29
58 X 9	6	7	7	8
88 X 23	8	12	13	10
86 X 9	9	5	10	16
174 X 23	17	14	20	17
175 X 49	5	7	6	3
203 X 9	12	9	5	21
128 X 177	8	12	14	17
58 X 177	3	2	1	14
132 X 49	18	15	15	16
57 X 9	4	10	10	10
203 X 177	13	14	9	2
176 X 177	13	5	6	4
176 X 23	15	8	13	6
200 X 9	16	15	16	11
76 X 177	11	5	9	8
125 X 177	4	4	4	12
126 X 177	7	16	15	10
173 X 23	12	7	5	11
173 X 177	11	14	13	7
125 X 9	11	15	18	8
89 X 177	10	18	18	17
57 X 23	4	8	8	12
89 X 23	3	7	4	8
132 X 23	14	15	14	36
200 X 23	9	15	10	4
125 X 23	7	10	3	19
175 X 23	3	4	5	8
175 X 177	10	4	1	8
43 X 23	2	7	1	13

Table 2.26 The deviation of family rankings at individual sites from the overall family site ranking for growth traits and stem straightness at eight years.

Family	HT8	DBH8	VOL8	STR8
88 X 9	2	0	0	34.5
88 x 49	2	2	0	37
128 X 9	0	2	13	11
224 X 49	9	5	5	7
58 X 49	17	14	18	17
200 X 49	5	6	7	0
76 X 49	28	22	17	18
128 X 49	6	8	7	11
58 X 9	11	16	17	6
172 X 23	16	17	20	26
57 X 9	9	10	13	17
128 X 177	17	11	14	15
88 X 23	6	9	14	20
173 X 49	9	12	9	10
203 X 9	9	4	8	22
86 X 9	7	8	12	16
58 X 177	8	8	3	13
200 X 9	9	9	11	13
125 X 177	6	9	11	17
132 X 49	14	10	12	20
175 X 49	13	3	8	9.5
203 X 177	8	1	6	2
125 X 9	12	8	12	13
176 X 23	9	12	8	26
176 X 177	6.5	5	6	16
174 X 23	12.5	7	9	25
76 X 177	12	6	6	9
57 X 23	11	11	10	29
126 X 177	12	21	14	10
89 X 23	8	4	5	21
173 X 23	7	7	7	20
125 X 23	5	5	6	26
173 X 177	11	7	7	11
89 X 177	6	9	8	12
200 X 23	5	15	6	21
175 X 23	2	4	1	14
175 X 177	14	1	0	9
132 X 23	15	17	13	30
43 X 23	7	10	2	16

Table 2.27 The deviation of family rankings at individual sites from the overall site ranking for growth traits, wood density and stem straightness at 15 years.

Family	HT15	DBH15	VOL15	DENS15	STR15
43 x 23	4	7	2	15	36
57 x 23	7	5	9	5	17
57 x 9	10	7	12	9	28.5
58 x 49	14	12	12	3	9
58 x 177	10	8	6	6	19
58 x 9	7	3	3	0	20
76 x 49	26	20	16	10	17
76 x 177	11	10	8	4	8
86 x 9	5	8	10	5	14
88 x 23	14	21	22	11	19
88 x 49	5	2	1	9	23.5
88 x 9	3	0	0	1	21.5
89 x 23	14	11	9	1	23
89 x 177	1	5	1	6	23
125 x 23	16	11	10	5	28
125 x 177	10	8	3	11	27
125 x 9	1	3	11	4	16.5
126 x 177	13.5	8	14	3	15
128 x 177	15	12	9	11.5	33
128 x 49	20	24	16	9	22
128 x 9	8	2	2	7	24
132 x 23	30	7	10	16	20
132 x 49	15	23	29	8	55.5
172 x 23	13.5	12	18	7	24
173 x 23	14	2	4	3	21
173 x 49	6.5	3	2	3	20
173 x 177	4	3	2	3	18
174 x 23	29	17	23	16	7
175 x 23	4	2	6	6	25
175 x 49	19	5	9	5.5	12
175 x 177	1	2	1	6	7
176 x 23	13.5	12	9	4	17
176 x 177	12	11	12	2	11
200 x 23	8	3	3	7	26
200 x 49	15	9	7	4	0
200 x 9	15	3	9	2	17
203 x 177	17	6	10	8	8
203 x 9	14	2	0	1	33
224 x 49	14	6	6	1	23.5

Table 2.28 Estimates of Spearman's rank correlation coefficients for growth traits, wood density and stem straightness across the three sites at ages five, eight and 15. All values were significant at P <0.05.

Trait	Site	Sites 23b	23c
HT5	23a	0.86	0.80
	23b		0.80
DBH5	23a	0.91	0.78
	23b		0.78
VOL5	23a	0.89	0.85
	23b		0.83
STR5	23a	0.81	0.55
	23b		0.59
HT8	23a	0.91	0.75
	23b		0.77
DBH8	23a	0.94	0.81
	23b		0.75
VOL8	23a	0.94	0.83
	23b		0.80
STR8	23a	0.55	0.43
	23b		0.65
HT15	23a	0.73	0.85
	23b		0.70
DBH15	23a	0.89	0.95
	23b		0.87
VOL15	23a	0.88	0.94
	23b		0.83
DENS15	23a	0.97	0.97
	23b		0.98
STR15	23a	0.23	0.54
	23b		0.39

Table 2.29 Estimates of genetic correlations (type B) between family means for growth traits, wood density and straightness across the three sites at ages five, eight and 15 years.

Trait	Sites		
	Site	23b	23c
HT5	23a	0.86	0.78
	23b		0.80
DBH5	23a	0.89	0.80
	23b		0.78
VOL5	23a	0.90	0.88
	23b		0.86
STR5	23a	0.80	0.58
	23b		0.64
HT8	23a	0.91	0.74
	23b		0.78
DBH8	23a	0.94	0.84
	23b		0.78
VOL8	23a	0.95	0.88
	23b		0.84
STR8	23a	0.60	0.42
	23b		0.61
HT15	23a	0.77	0.86
	23b		0.76
DBH15	23a	0.87	1.00
	23b		0.92
VOL15	23a	0.87	0.98
	23b		0.88
DENS15	23a	1.00	1.00
	23b		1.00
STR15	23a	0.21	0.64
	23b		0.48

The values of Spearman's coefficient were always significant at P <0.05. It is apparent from comparison of family rankings for growth traits at different sites (Appendix I, Table 2.1 to 2.13), and from the differences between family rankings across sites and those at individual sites (Tables 2.25 to 2.27), that fewer rank changes occur between tests 23a and 23b, which are environmentally similar, than between these tests and test 23c, which is a very different site type (see site details in Table 2.1).

2.6.3.2 - Stem straightness

The values of rank and genetic correlations between family means across environments were generally lower and more variable for stem straightness than for growth traits. However, the values of Spearman's correlation were always significant ($P < 0.05$). Similarly, the rankings of families across sites are less consistent for stem straightness than for growth and wood density (Tables 2.1 to 2.13 of Appendix I), and there are greater differences between average ranks and those at each site. There is no apparent explanation for the atypically low correlations between tests 23a and 23b at age 15. It may well be due to sampling or assessment error or to the nature of the subjective assessment scale, which was described in Table 2.5 and is discussed further in **2.6.4.**

2.6.3.3 - Efficiencies of selection

Efficiencies of selection (see page 45) for each trait for all combinations of testing and planting sites are presented in Table 2.30. In the case of growth traits at all ages, it is inefficient to select on site 23a for planting at the other sites, and almost invariably more efficient to select at site 23c for planting at site 23a. At 8 years, it would also be more efficient to select at site 23b for planting on site 23a. In the case of wood density, it is most efficient to select at site 23c for planting at the other sites and least efficient to select at site 23a for planting on sites 23b or 23c. Selecting on test 23b for planting on test 23a is also more efficient than selection at site 23a.

The results show that it is always better to select on the site with high heritabilities (in this case 23c - see Table 2.17) and hence a better resolution of progeny differences. Burdon (1977) reported a similar result for *P. radiata* in New Zealand. However, the results from test 23c must be interpreted with caution because they are derived from a much smaller data set.

Although test 23c had the highest efficiencies of selection for planting on the other sites, it is not likely in practice that selections would be effected in this test, as it includes only a limited number of families. However, the results demonstrate the potential for further investigation of selection sites distinct from those at which operational establishment will take place.

Table 2.30 Estimates of efficiencies of selection for height, diameter, volume, wood density and stem straightness from all combinations of screening and planting sites at five, eight and 15 years.

Trait	Planting Site	Selection of seed parents on progeny performance		
		Selection Site		
		23a	23b	23c
HT5	23a		0.89	0.88
	23b	0.83		0.87
	23c	0.69	0.74	
DBH5	23a		1.04	1.00
	23b	0.76		0.84
	23c	0.64	0.73	
VOL5	23a		0.98	1.00
	23b	0.82		0.89
	23c	0.77	0.83	
STR5	23a		0.97	0.65
	23b	0.66		0.60
	23c	0.52	0.69	
HT8	23a		1.11	0.95
	23b	0.75		0.82
	23c	0.58	0.74	
DBH8	23a		1.07	1.05
	23b	0.83		0.86
	23c	0.68	0.71	
VOL8	23a		1.06	1.03
	23b	0.85		0.88
	23c	0.75	0.81	
STR8	23a		0.74	0.45
	23b	0.49		0.53
	23c	0.39	0.70	
HT15	23a		0.89	1.12
	23b	0.67		0.86
	23c	0.66	0.67	
DBH15	23a		0.94	1.16
	23b	0.81		0.99
	23c	0.86	0.85	
VOL15	23a		0.92	1.28
	23b	0.82		1.01
	23c	0.80	0.76	
DENS15	23a		1.16	1.25
	23b	0.86		1.07
	23c	0.80	0.93	
STR15	23a		0.23	0.74
	23b	0.19		0.50
	23c	0.55	0.46	

Consistent with the rank and correlation results reported above, there were few cases where selection for stem straightness would be more efficiently accomplished at a site other than that at which planting is to take place.

2.6.4 - Discussion - genotype-environment interaction

Although the analysis of variance results suggest that genotype-environment interaction is statistically significant for all traits at all ages in these tests, the results of other analyses suggest that the interaction is generally of little practical importance. Some of the statistical significance is probably due to the presence of relatively few highly interactive families, for example, 76 x 49, 174 x 23, 200 x 9 and 58 x 49. Matheson and Raymond (1984a) reported similar results for *P. radiata* in Australian tests, and suggested that the interactive families may be particularly sensitive to particular site factors. Conversely, there are other families, for example, 200 x 49, 58 x 9, 89 x 23 and 125 x 177, which are stable across sites.

On these sites, wood density does not appear to be subject to genotype-environment interaction of any magnitude, despite the statistical significance of the relevant terms in Table 2.21. Hamilton and Harris (1965) found little gei for wood density in *P. elliottii* in the south-east USA, and Barnes *et al* (1992b) reported similarly for *P. patula* in Zimbabwe.

The apparently greater sensitivity of stem straightness than growth traits to

site differences may be real, or may be a consequence of the use of a standard, absolute, assessment scale and the relative difficulty of attempting to apply it across all sites. There has been considerable debate about the merits of standard versus site-specific scales for the assessment of stem straightness; see Cotterill *et al* (1987), Shelbourne and Namkoong (1966), Hans (1972), Miller (1975), Gibson (1982), Kanowski *et al* (1986) and Raymond and Cotterill (1990). One of the major arguments advanced in favour of a single scoring system was that it would facilitate comparisons across sites. While this may be true in one sense (*ie* the average quality of sites is easily apparent), the restricted scale thus used on some sites (for example, where trees are all relatively crooked or relatively straight), and the difficulty of maintaining standardisation across sites, may limit the utility of these data in genetic analyses. Results reported by Johnson and Burdon (1990) and Woolaston *et al* (1990), both of which were based on assessments of multi-site tests with site-specific, albeit consistently applied, straightness scales, suggests that site-specific scales are quite appropriate for the purposes of cross-site genetic analyses. Results of this study where the standard assessment scale was used for assessment show the difficulties of using the standard scale and a site-specific scale is recommended for future assessment of stem straightness.

The magnitude of the efficiencies of selection reflect not only the correlation between sites, but also the magnitudes of heritabilities at different sites (Equations 2.19, 2.20 and 2.21). In other words, they will be determined by the heritability of particular traits at particular sites, as well as by the correlation

between traits across sites. The genetic correlation between traits across sites is probably the most useful estimator of the significance of genotype-environment interaction *per se*, whereas efficiencies of selection are probably of more relevance to selection decisions. In the case of these tests, genotype-environment interaction appears to be of little practical significance, with most genetic correlations greater than Robertson's (1959) suggested threshold of 0.8; however, the most efficient selection would have been effected by using different tests for selection of different traits at different times. In this case the results obtained from all four methods used to test the importance of the statistically significant genotype-environment interaction found by the ANOVA, were consistent in that genotype-environment interaction was not biologically important, suggesting that in future a single method would be sufficient. Burdon's (1977) correlation is recommended, because, not only does it estimate the importance of the interaction but it can also be used in making selection decisions, through the estimation of efficiencies.

2.7 - Pooled parameter estimates

2.7.1 - Introduction

Regardless of the breeding strategy employed, successful selection depends on reliable estimates of genetic parameters (Baker 1986). Estimation of variance components and genetic parameters usually assumes homogeneity of variance in each group of individuals being tested. This assumption is often invalid in

forest tree data sets, resulting in inaccurate estimates of parameters (White and Hodge 1989). The assumption is more likely to be violated if the data set is unbalanced and small. One means of avoiding this problem is to develop and use standard or pooled parameter estimates, *ie*, those estimated variously from a cross-site analysis. The case for the use of standard parameter estimates has been made by Cotterill and Dean (1990), who pointed out that parameters estimated from particular sites may be poorly estimated for the reasons discussed above, and that indices constructed from them will be sensitive to the varying parameters estimated at different sites. Standard parameters, derived from estimates made at individual sites, address these deficiencies by drawing from a larger data set and representing a wider range of environments. However, as Cotterill and Dean (1990) note, the use of standard parameters may reduce the efficiency of selection at any one site if estimates fluctuate markedly across sites.

Standard parameters have been estimated variously; for example, Dean (1990) summed parameters across sites and divided the total by the number of sites from which the parameters were estimated. This simple methodology averages across the number of sites tested, but if the parameters at individual sites differ markedly, the pooled estimates will be inappropriate and this will reduce the efficiency of selection. Cunningham *et al* (1977), Woolaston *et al* (1990) and Borralho (1991) weighted each parameter estimate by the inverse of its variance, such that estimates with higher variance were weighted less than those with lower variance. This method has the advantage of accounting

for estimates of varying quality but is dependent on accurate estimation of the standard errors of each of the individual parameter estimates.

A second alternative is that demonstrated by White and Hodge (1989), the use of BLUP (Best Linear Unbiased Prediction) for the derivation of pooled estimates. BLUP was developed by Henderson (1963) specifically to deal with unbalanced data in dairy cattle breeding, and is widely used by animal breeders. BLUP "incorporates best linear unbiased prediction estimates of the fixed effects through generalised least squares with best linear unbiased prediction of the random (ie. genetic) effects" (White and Hodge 1989).

The need to use large sample sizes for the estimation of variances and covariances has been emphasised by several authors, for example, Baker (1986), Sales and Hill (1976a and b), and White and Hodge (1989). White and Hodge (1989) suggest that analysis based on data pooled from several small sites will give a more reliable estimate than that based on a separate analysis of each site. Large samples are important because variances and covariances are second order statistics, and are thus subject to relatively large sample errors (Baker 1986). An increase in the number of crosses represented in a test will also tend to decrease inaccuracies in the estimates (Baker 1986). Baker (1986) found that a minimum of 45 genotypic groups are needed to calculate reliable index coefficients, but also that the number of observations per genotypic group was important. Sample sizes of 30-40 individuals per family have been suggested, for example, Cotterill and Dean (1990) and Magnussen

and Yanchuk (1993).

For these reasons, it seemed advantageous to develop a single set of genetic parameters representative of those sites on which commercial plantations of *P. elliottii* are established in the eastern Highlands of Zimbabwe. In this study, estimation of pooled parameters seemed preferable to derivation of standard parameter estimates involving only an averaging of individual estimates, as in the latter case there is little improvement in the quality of the estimates. The rationale for this is principally that argued by White and Hodge (1989), *viz*, that the more reliable estimates are likely to derive from the larger sample size.

A second decision required here was which data sets to pool for the estimation of pooled parameters. As discussed in section 2.3.1, test 23c differs in many ways from test 23a and 23b. It has fewer families and poorer development; it is established on a site atypical of those on which *P. elliottii* is established commercially; and parameter estimates and their pattern of change over time differed from those for test 23a and 23b.

Given that the purpose of this study was to estimate parameters applicable to the eastern highlands of Zimbabwe, and given the poorer estimates available for test 23c, it seemed sensible to exclude data from test 23c in the estimation of pooled parameters.

2.7.2 - Methods

The REML technique was used for a pooled analyses of variance, and to estimate variance components and heritabilities. Estimation of genetic parameters was based on all individuals in the two tests. The linear model used (Equation 2.21) was similar to that of Equation (2.3) with some modifications. The assumptions of this model are those that applied to Equation (2.3); the model is:-

$$Y_{ijklm}=\mu+F_i+M_j+FM_{ij}+FS_{il}+MS_{jl}+FMS_{ijl}+FMSR_{ijlk}+S_l+SR_{lk}+e_{ijklm} \qquad (2.21)$$

where μ = population mean;

F_i = random effect of the i^{th} female parent;

M_j = random effect of the j^{th} male parent;

FM_{ij} = random effect of the ij^{th} family (female x male interaction);

FS_{il} = random effect of the i^{th} female x l^{th} site interaction;

MS_{jl} = random effect of the j^{th} male x l^{th} site interaction;

FMS_{ijl} = random effect of the ij^{th} family x l^{th} site interaction;

$FMSR_{ijlk}$ = random effect of the ij^{th} family x fixed effect of the k^{th} replicate within the l^{th} site interaction;

S_l = fixed effect of the l^{th} site;

SR_{lk} = fixed effect of the k^{th} replicate within the l^{th} site interaction;

e_{ijklm} = residual error.

A generalised least-square program (Harvey 1987) was used to estimate phenotypic and additive genetic correlations. Analysis followed the simplified linear model (Equation 2.22) similar to that of Equation (2.15), with minor modifications. Assumptions correspond to those of Equation (2.15).

$$Y_{ijklm} = \mu + F_i + M_j + FM_{ij} + S_l + R_k:S_l + e_{ijkl} \quad (2.22)$$

where Y_{ijklm} = individual tree observation;

μ = population mean;

F_i = random effect of the i^{th} female;

M_j = fixed effect of the j^{th} male;

FM_{ij} = random effect of the ij^{th} family;

S_l = fixed effect of the l^{th} site;

$R_l:S_k$ = fixed effect of the k^{th} replicate within the l^{th} site;

e_{ijklm} = residual error.

2.7.3 - Results and discussion

Tables 2.31 - 2.34 summarise the mean squares, overall means and their standard deviations, variance components and their standard errors, relative proportions of total variance, additive and dominance genetic variances, ratios of additive to dominance variances, narrow-sense heritabilities and additive genetic correlations from the pooled analysis of all traits at ages five, eight and 15 years. Resin yield was not included in the pooled analysis as it was assessed in one test only (23a).

The magnitude of the parameters estimated from the pooled analyses were generally intermediate or lower than those from the individual tests, although there are some exceptions. All sources of variation had significant effects on all traits at all ages. As with the individual analyses, the residual error was the most important source of variation for all traits, generally followed by the male and female effects. Branch diameters and stem straightness were exceptions, for which the family x site x replicate interaction was the next most important source of variation at all ages.

The ratio of female to male genetic variance and of additive to dominance variances were also similar to those from individual site analyses. In the case of branching characteristics, ratios from the pooled analysis were not consistent with those from individual site analyses.

Both additive and dominance genetic variances increased with age, although the latter did so at a lower rate. The ratios of additive to dominance genetic variance decreased with age. Heritabilities were generally lower than those estimated in the individual tests, and associated standard errors were lower, especially when compared to those estimated from test 23b. Heritabilities estimated from paternal variances were higher than those estimated from maternal variances, and were also associated with much larger standard errors. Heritabilities generally decreased with age.

Additive genetic correlations were intermediate between those from the

individual test analyses. Correlations between BRCT5 and other traits were generally positive for both individual test analyses, but were generally negative when estimated from the pooled analysis. The individual site analyses were associated with high standard errors, whereas those from the pooled analyses had much lower standard errors. The higher precision in the genetic parameters estimated from the pooled analysis, as indicated by the lower standard errors, demonstrates the advantage of deriving these parameters.

2.8 - Conclusions

The results from this study show that test 23a is located on the most productive and test 23c on the least productive site. The analyses of variance demonstrated that differences in all traits between both female and male parents were almost always significant (P>0.05) in all tests at all ages. The within plot error (residual) was the most important source of variation for all traits at all ages. All traits but branch diameter were under moderate to strong additive genetic control.

The additive genetic correlations between growth traits in all tests were high at all ages and the correlations between stem straightness and growth traits were low to moderate. The additive genetic correlations between wood density and growth traits ranged from negative (*vs* diameter or volume) to slightly positive (*vs* height) in all tests.

Table 2.31 Mean squares and significance levels for all traits at ages five, eight and 15 years for pooled analysis of the three progeny tests.

	Mean Squares															
Source	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	STR15
Female	56.5	261.7	9119.1	88.8	264.7	0.3	16.3	64.4	277.1	57311.0	9.58	134.5	873.3	1070900.0	35765.0	7.5
Male	208.9	1015.2	35798.0	336.2	1459.0	1.4	54.6	193.8	1264.0	236120.0	25.6	373.3	3720.7	3990600.0	128500.0	31.5
FemxMale	4.3	17.0	619.2	6.4	27.6	0.03	1.5	6.8	27.4	5462.2	1.4	19.2	93.0	114750.0	3214.1	1.3
FemxSite	7.7	23.3	845.7	17.2	104.8	0.10	5.0	15.3	33.6	6433.2	5.5	51.0	169.2	179340.0	2992.1	5.6
MalexSite	19.5	68.6	2390.0	116.7	234.2	0.2	10.4	56.3	168.8	34654.0	15.3	308.5	1457.2	1690600.0	5351.1	34.4
FamxSite	1.9	7.1	206.9	5.7	23.3	0.01	1.0	2.8	10.6	1922.9	0.7	9.3	32.2	38103.0	2214.0	1.3
FamxSitexRep	1.0	5.5	155.6	3.8	16.4	0.01	1.0	2.0	8.6	1577.6	0.7	4.6	22.0	27294.0	2016.3	0.7
Residual	0.6	2.7	81.9	3.0	9.3	0.01	0.4	1.5	6.8	1225.1	0.5	3.6	19.1	22915.0	1947.1	0.6

All sources of variation had significant effects ($P<0.05$) on all traits at all ages.

Table 2.32 Variance components, standard errors, and proportions of total variance (bracketed) for all traits from the pooled analysis at five, eight and 15 years.

Trait	Age	Source							
		Female	Male	Fem x Male	Fem x Site	Male x Site	Fam x site	Fam x Site x Rep	Residual
HT	5	0.08±0.02 (8.6)	0.10±0.06 (10.8)	0.02±0.01 (2.2)	0.02±0.01 (2.2)	0.02±0.01 (2.2)	0.02±0.003 (2.2)	0.04±0.003 (4.3)	0.63±0.01 (67.7)
	8	0.15±0.05 (6.9)	0.14±0.11 (6.4)	0.07±0.02 (3.2)	0.07±0.02 (3.2)	0.10±0.06 (4.6)	0.03±0.01 (1.4)	0.09±0.01 (4.1)	1.54±0.02 (70.3)
	15	0.21±0.12 (4.0)	0.07±0.25 (1.3)	0.18±0.04 (3.4)	0.30±0.09 (5.7)	0.59±0.31 (11.1)	0.16±0.04 (3.0)	0.20±0.03 (3.8)	3.59±0.05 (67.7)
DBH	5	0.38±0.11 (9.4)	0.50±0.27 (12.3)	0.09±0.02 (2.2)	0.05±0.02 (1.2)	0.06±0.03 (1.5)	0.03±0.01 (0.7)	0.28±0.02 (6.9)	2.67±0.03 (65.8)
	8	0.75±0.23 (7.6)	1.16±0.68 (11.7)	0.30±0.06 (3.0)	0.13±0.05 (1.3)	0.30±0.16 (3.0)	0.07±0.04 (0.7)	0.36±0.06 (3.6)	6.83±0.10 (69.0)
	15	2.16±0.73 (7.3)	2.37±2.14 (8.1)	1.11±0.20 (3.8)	0.83±0.26 (2.8)	2.95±1.52 (10.0)	0.35±0.13 (1.2)	0.58±0.15 (2.0)	19.09±0.28 (64.8)
VOL	5	13.38±3.8 (10.4)	17.87±9.60 (13.9)	3.74±0.64 (2.9)	1.83±0.62 (1.4)	1.98±1.12 (1.5)	0.86±0.41 (0.7)	7.46±0.50 (5.8)	81.92±0.79 (63.5)
	8	158.1±47.63 (8.6)	211.0±127.3 (11.5)	64.4±11.5 (3.5)	27.2±9.50 (1.5)	61.88±33.55 (3.4)	11.5±7.68 (0.6)	71.8±10.8 (3.9)	1225.1±17.81 (66.9)
	15	2676.8±897.5 (7.7)	2403.8±2313.0 (6.9)	1402.7±240.8 (4.0)	870.2±269.4 (2.5)	3459.0±1762.4 (9.9)	372.5±152.1 (1.1)	901.9±189.0 (2.6)	22915.0±334.0 (65.5)
BRCT	5	0.11±0.04 (3.1)	0.13±0.09 (3.7)	0.01±0.01 (0.3)	0.03±0.01 (0.9)	0.10±0.05 (2.9)	0.03±0.01 (0.9)	0.08±0.01 (2.3)	3.01±0.03 (86.0)
BRDM	5	0.25±0.11 (2.2)	0.65±0.38 (5.7)	0.04±0.04 (0.4)	0.22±0.07 (1.9)	0.18±0.10 (1.6)	0.11±0.05 (1.0)	0.72±0.05 (6.3)	9.30±0.09 (81.1)
AIL	5	0.0004±0.0001 (3.2)	0.001±0.0004 (8.1)	0.0001±0.00003 (0.8)	0.0003±0.0001 (2.4)	0.0002±0.0001 (1.6)	0.0001±0.00003 (0.8)	0.0003±0.00003 (2.4)	0.01±0.0001 (80.7)
STR	5	0.02±0.01 (3.5)	0.02±0.01 (3.5)	0.004±0.002 (0.7)	0.01±0.004 (1.8)	0.01±0.01 (1.8)	0.0004±0.002 (0.1)	0.06±0.003 (10.6)	0.44±0.004 (80.0)
	8	0.01±0.01 (1.6)	0.01±0.02 (1.6)	0.01±0.003 (1.6)	0.03±0.01 (4.9)	0.03±0.02 (4.9)	0.0001±0.003 (0.02)	0.04±0.01 (6.6)	0.48±0.01 (78.7)
	15	0.01±0.01 (1.4)	0.0001±0.02 (0.01)	0.001±0.004 (0.1)	0.02±0.01 (2.9)	0.06±0.03 (8.6)	0.02±0.01 (2.9)	0.03±0.01 (4.3)	0.56±0.01 (79.9)
DENS	15	204.88±58.05 (8.2)	252.20±133.50 (10.1)	36.27±15.36 (1.5)	7.83±8.70 (0.32)	10.37±8.25 (0.42)	13.93±18.53 (0.56)	14.67±22.34 (0.59)	1947.1±40.34 (78.3)

Table 2.33 Trait means, standard deviations, additive and dominance genetic variances, ratios of additive to dominance variances and heritabilities for all traits from the pooled analysis at ages five, eight and 15 years.

Trait	Source										
	Age	Mean	$4\sigma^2_f$	$4\sigma^2_m$	σ^2_f/σ^2_m	$4\sigma^2_{fm}$	σ^2_f/σ^2_{fm}	σ^2_m/σ^2_{fm}	h^2_f	h^2_m	h^2_{fm}
HT	5	5.72±0.96	0.32	0.40	0.80	0.08	4.00	5.00	0.34±0.10	0.43±0.22	0.39±0.11
	8	9.71±1.63	0.60	0.57	1.06	0.29	2.06	1.94	0.27±0.09	0.26±0.18	0.27±0.10
	15	17.63±2.73	0.85	0.26	3.23	0.71	1.19	0.37	0.16±0.08	0.05±0.19	0.10±0.10
DBH	5	10.45±2.02	1.52	2.00	0.76	0.36	4.20	5.60	0.38±0.10	0.50±0.23	0.44±0.11
	8	15.61±3.17	3.01	4.63	0.65	1.22	2.47	3.81	0.30±0.09	0.47±0.24	0.39±0.12
	15	23.81±5.43	8.62	9.48	0.91	4.46	1.94	2.13	0.29±0.10	0.32±0.27	0.31±0.14
VOL	5	23.95±11.42	53.50	71.50	0.75	15.00	3.60	4.80	0.42±0.11	0.55±0.26	0.48±0.12
	8	91.28±43.79	632.8	844.08	0.75	257.44	2.46	3.28	0.35±0.10	0.46±0.25	0.40±0.12
	15	387.09±189.77	10709.6	9613.6	1.11	5611.6	1.90	1.71	0.31±0.10	0.27±0.25	0.29±0.13
BRCT	5	7.50±2.05	0.44	0.52	0.85	0.04	11.00	13.00	0.13±0.04	0.14±0.10	0.14±0.05
BRDM	5	13.90±3.55	1.00	2.60	0.39	0.16	6.30	16.30	0.09±0.04	0.23±0.13	0.16±0.06
AIL	5	0.35±0.10	0.08	0.08	1.00	0.02	5.00	5.00	0.17±0.06	0.27±0.15	0.22±0.08
STR	5	3.95±0.79	0.11	0.11	1.04	0.08	1.31	1.26	0.12±0.05	0.16±0.10	0.14±0.05
	8	3.80±0.84	0.04	0.04	1.10	0.05	0.89	0.81	0.07±0.06	0.07±0.10	0.07±0.06
	15	4.04±0.84	0.03	0.0002	124.3	0.002	11.7	0.09	0.04±0.04	0.0003±0.13	0.02±0.07
DENS	15	399.84±51.26	819.50	1008.80	0.81	145.08	5.65	6.95	0.36±0.09	0.43±0.20	0.38±0.10

Table 2.34 **Genetic correlations (estimated from maternal components of variance) and associated standard errors (upper triangle), and phenotypic correlations (lower triangle), estimated from pooled analysis of all traits at five, eight and 15 years.**

Trait	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	STR15
HT5		0.80±0.07	0.88±0.04	-0.46±0.17	0.08±0.18	0.12±0.18	0.41±0.15					0.92±0.04	0.74±0.10	0.80±0.08	0.09±0.18	0.06±0.23
DBH5	0.71		0.99±0.01	-0.55±0.16	0.42±0.15	0.23±0.17	0.32±0.16					0.64±0.13	0.87±0.05	0.88±0.05	-0.31±0.17	0.08±0.23
VOL5	0.85	0.94		-0.54±0.16	0.34±0.16	0.19±0.17	0.32±0.16					0.75±0.10	0.89±0.05	0.91±0.04	-0.21±0.18	0.07±0.23
BRCT5	-0.03	-0.05	-0.07		-0.21±0.21	-0.56±0.16	-0.09±0.21					0.42±0.15	0.45±0.15	0.43±0.15	-0.08±0.19	0.10±0.19
BRDM5	0.13	0.32	0.24	0.01		0.30±0.17	-0.03±0.18					0.05±0.19	0.33±0.17	0.27±0.17	-0.13±0.19	-0.03±0.19
AIL5	0.21	0.20	0.19	-0.002	0.24		0.05±0.18					0.21±0.18	0.17±0.18	0.15±0.18	0.07±0.19	0.13±0.19
STR5	0.31	0.23	0.24	0.02	-0.02	0.06						0.41±0.18	0.15±0.21	0.18±0.21	0.16±0.19	0.73±0.16
HT8									0.78±0.07	0.86±0.05	0.28±0.17	1.00	0.87	0.92	0.14	0.85
DBH8								0.82		0.98±0.01	0.12±0.18	0.64±0.13	0.95±0.02	0.94±0.03	-0.30±0.17	0.39±0.17
VOL8								0.84	0.95		0.10±0.18	0.88	1.00	1.00	-0.17	0.87
STR8								0.40	0.33	0.29		0.14±0.22	-0.09±0.22	-0.09±0.22	-0.06±0.20	0.88±0.06
HT15	0.65	0.54	0.56	0.14	0.12	0.416	0.24	0.92	0.66	0.77	0.34		0.75±0.10	0.81±0.08	0.18±0.18	0.21±0.22
DBH15	0.61	0.69	0.69	0.17	0.24	0.12	0.23	0.77	0.89	0.91	0.30	0.73		0.99±0.004	-0.22±0.18	0.19±0.22
VOL15	0.61	0.66	0.69	0.16	0.20	0.12	0.22	0.82	0.85	0.94	0.27	0.74	0.96		-0.19±0.18	0.19±0.22
DENS15	0.01	-0.13	-0.10	-0.07	-0.05	-0.02	0.002	0.13	-0.10	-0.16	0.003	0.08	-0.04	-0.04		-0.43±0.17
STR15	0.32	0.30	0.29	0.06	0.07	0.04	0.34	0.59	0.40	0.62	0.56	0.46	0.48	0.43		

Correlations between density and stem straightness were all moderately negative, suggesting that trees with good stem form had lower wood density. These correlations were not strongly negative and it may be possible to find individuals with a desirable combination of growth rate, stem straightness and wood density. The small positive correlation between height and wood density means that breeding for either one of these traits will likely lead to only a small change in the other. Additive genetic correlations between resin yield and growth traits were all moderate and positive, and those with stem straightness were high and positive. It seems likely, therefore, that timber and resin yield could be improved in the same population. These genetic parameters are comparable with those reported in literature for other industrial species.

Juvenile-mature correlations for growth traits were high in this study. Those for wood density and diameter or volume were generally negative, with the magnitude of the negative association decreasing with age. Genetic correlations between height and wood density were generally always positive, ranging from low to moderate, as were those between stem straightness and growth traits. The high juvenile-mature correlations between growth traits found in this study indicate good potential for early selection and the results of this study compare well with those reported for other *Pinus* species as detailed earlier.

Correlations between resin yield and growth traits or stem straightness were

positive and moderate, indicating the possibilities of selecting for resin yield at an early age.

In terms of assessment of the importance of genotype-environment interaction, the contrast between the results of the analysis of variance (ANOVA), which found genotype-environment interaction to be significant for all traits, and those of the other four methodologies, which suggested this interaction to be of little practical importance, demonstrates the advantage of using more than one approach for the analyses of genotype-environment interaction. The ANOVA is a sensitive test if assumptions are not violated, but it fails to show whether gei is of practical importance. In this case, the statistically significant result may have been caused by lack of homogeneity in the family variance resulting from a few highly interactive families, or confounding of the family and family x site interaction effects resulting from too limited a number of sites being used in the analysis (Johnson and Burdon 1990).

A variety of approaches has been proposed elsewhere to address the issue of genotype-environment interaction. The first approach illustrated by Matheson and Raymond (1984a) and advocated by Talbert[4] (pers. comm.) is the identification of good general performers and their use across a wide range of sites. A second approach is to regionalise breeding populations, an option considered by Kanowski and Nikles (1989) for *P. caribaea* in Queensland,

[4] Dr. C.B. Talbert, Weyerhaeuser Company, Biological Sciences Research Division, WTC - 2H5 Tacoma, Washington, 98477, US.

Australia. However, as Johnson and Burdon (1990) and Carson (1988) noted for the case of *P. radiata* in New Zealand, regionalisation is costly and the additional costs may not be recouped by additional gains.

A major difficulty in attempting to match families and sites more closely, to take advantage of gei, is the difficulty of classifying sites as suitable for particular genotypes. Matheson and Cotterill (1990) and Borralho (1991) both suggest that, in the case of most afforestation sites, small scale environmental variation limits our capacity to match genotypes to sites. The causes of most interactions in tropical and subtropical regions are not known (Matheson and Cotterill 1990), although major factors such as altitude or rainfall may be useful for broad-scale classification.

P. elliottii is planted in Zimbabwe across a range of sites, varying in altitude from 967 to 1760 m above sea level, annual rainfall from 885 to 2279 mm, and on soil types ranging from sandy loams to lower fertility sands. Test sites 23a and 23b are typical of the sites on which *P. elliottii* is planted, whereas test 23c is located at a drier, lower altitude site where commercial afforestation with *P. elliottii* would not take place. Within that range of sites types, within the afforestation zone, it appears from these results that there is no individual site which is likely to be more efficient for selecting at other sites (23a/23b) for all traits assessed. Testing should therefore continue across the range of site types. However, as indicated by the efficiencies of selection, if testing had to be restricted to one site, that selection at test 23b, where heritabilities were

highest and hence where there is a better resolution of genotypes, would be more efficient.

There is no evidence from these results which favours regionalisation of the breeding populations, if afforestation is limited to the zone of which sites 23a and 23b are typical. If afforestation were to be extended to other sites which differed from these as much as did 23c, the results obtained here suggest that regionalisation would be worth considering.

In either case, another option is to identify and exclude from the afforestation programme those families identified as being particulary interactive. In this case, families such as, 76 x 49, 174 x 23, 200 x 9 and 58 x 49, might be excluded. However some of the families which are highly interactive also rank highly for growth traits, stem straightness and wood density; for example, 76 x 49 and 58 x 49. It is therefore important to consider the implications of excluding such families from the breeding population. In the Zimbabwean *P. elliottii* breeding population, the number of interactive families is small, and there seems little reason to exclude any from the breeding population on this criterion.

The pooled estimates obtained here will be used in subsequent chapters in which the derivation of selection indices is intended to be generally applicable to *P. elliottii* in the eastern highlands of Zimbabwe. The use of the pooled estimates in this way parallels that in similar studies by Dean (1990) for

P. radiata in New Zealand, and Borralho (1991) for *Eucalyptus globulus* in Portugal.

Chapter 3 -

3 - Breeding objectives and gains expected from combined index selection

3.1 - Introduction

The tree breeding cycle consists of three major activities, *viz*, evaluation, selection and mating (White 1987), and the rate of genetic progress depends on both being conducted efficiently and effectively. Cotterill (1986a) and Dean (1990) have made the point that, historically, tree breeders have emphasised mating designs to the relative neglect of efficient selection. Selection, defined as the "choosing of individuals with desired qualities to serve as parents for the next generation" (Zobel and Talbert 1984), can be performed according to a number of criteria, and the choice of the best methodology is influenced by the expected genetic gains, the time and amount of genetic information available, and the costs involved (Wright 1976). Selection can be phenotypic, where genetic information is not available or not used; on a family/within family basis (Cotterill and Dean 1990), where family mean information is used

to determine those families in which individuals will be selected phenotypically; or on the basis of genetic information, through index selection. The use of family/within family selection and index selection is restricted to individuals of known pedigree, usually those planted in replicated trials; it is not, for example, applicable to selection in wild or typical plantation populations. Where it is feasible, index selection is always superior, in terms of genetic gain, to alternative methods (Falconer 1981). In the case of typical genetic parameters and generation intervals for populations of industrial trees, Cotterill (1986a and b) demonstrated that the use of index selection in conjunction with simple mating designs returned genetic gains per unit time comparable to those associated with more elaborate mating schemes, because of the additional time required to complete the latter.

Combined index selection, which takes account of both individual and family performance, is the most efficient form of index selection (Cotterill and Dean 1990). Use of a combined index allows individual superiority to compensate, to some extent, for poor family performance, and vice versa. As heritability decreases, individual phenotype becomes a less accurate guide to an individual's genetic worth; consequently, relatively more weight is placed on family mean performance. As the heritabilities of most traits of interest in tree breeding programmes are no more than moderately strong (Cotterill and Dean 1990), combined index selection is appropriate.

Selection may be direct, on the trait of interest, or indirect, where gain is

sought through selection on correlated traits (Wright 1976). The case of selection on juvenile traits to improve traits at maturity is a particular case of indirect selection of considerable relevance to tree breeding, as it shortens the generation interval, with consequences for the rate of genetic progress over time and, therefore, the returns from breeding activities (Borralho 1991, Cotterill 1986b, Cotterill and Dean 1990, Dean 1990). The duration of the performance testing[1] phase is one of the major determinants of the generation interval; to maximise the rate of genetic gain, the breeder must utilise genetic test results as soon as family or individual performance at maturity can be reasonably predicted (Gill 1987). Where juvenile-mature correlations are less than unity, as is almost invariably the case, selecting earlier than rotation age shortens the generation interval at the expense of gain per generation, but may lead to greater genetic gains per year (Matheson *et al* 1988). The success of early selection is dependent on trends over time in heritabilities and in genetic correlations of the juvenile and mature traits of interest (Cotterill and Dean 1988), so information describing these is essential for optimising selection procedures.

In the Zimbabwean *P. elliottii* breeding program, selection has historically been effected phenotypically, although a conscious effort has been made to maintain

---

[1] The term "performance testing" is widely used by animal breeders (Nicholas 1987) to refer to genetic tests where individuals are ranked and selected according to their own performance. Generally in tree breeding, individuals in progeny tests are also ranked and selected as parents for the next generation, with no backward selection of the parents. In these cases, the term "progeny testing" has become something of a misnomer, and performance testing is preferred here.

broad family representation in successive generations; there has, therefore, been an element of family/within family selection. Selection traits have been stem height, diameter and straightness, usually at around eight years, which is a third of the rotation age.

3.1.1 - Index selection

3.1.1.1 - Evolution of index theory

The theory of index selection has a long history, originating with the derivation of conditional means and variances by Pearson in 1903, and being formalised by Smith in 1936 and Hazel in 1943 (Henderson 1990). Smith and Hazel formulated the selection index to maximise the mean of breeding values of individuals selected (Henderson 1990). Henderson (1963) demonstrated that economic weights could be included in the indices, thereby permitting the breeder to nominate economic weights relevant to the traits of interest. The genotypic worth of an individual, which is defined as a linear function of the genotypic values of each trait weighted by known relative economic values, is thus expressed as a linear function of the genotypic values of several traits (Baker 1986). In the case of multi-trait selection, Hazel and Lush (1942) proved that index selection, where traits are properly weighted and information from relatives included, was more efficient than either tandem selection or independent culling levels.

There is difficulty in the application of index selection where other traits of interest are adversely correlated with the breeding objective or with others in the index, resulting in low genetic gains in individual traits and the breeding objective. This difficulty can be addressed by the use of restrictions. Kempthorne and Nordskog (1959) introduced the concept of placing restrictions on changes in certain traits on selection; their formulation maintained the value of specific traits (Cotterill and Jackson 1981), to prevent deterioration in those traits that were adversely correlated with others in the index, while maximising possible gains in the latter (Baker 1986). Tallis (1962) introduced restrictions in the index that limited the magnitude of changes in certain traits, and Binet (1965) formulated restrictions that maximised gains in traits which were not included in the index, for example, in the case of juvenile-mature correlations. However, by definition, placing restrictions on traits in the index generally results in lower gains in the traits under improvement in comparison to those which would result from use of an unrestricted index.

3.1.1.2 - Application to animal and tree breeding

The efficiency of index selection has resulted in relevant methodologies being well-developed by animal breeders (*eg* Henderson 1990, James 1972, Turner and Young 1969) and long recommended by tree breeders (*eg* Baradat 1976, Burdon 1979, Dean *et al* 1983). The genetic gain from multi-trait selection within a population is dependent on selection intensity, correlations between

aggregate breeding values and the selection index, and the level of genetic variability (Hazel and Lush 1942). The predicted response to selection is sensitive to sampling errors and, to obtain the optimum response to selection, genetic parameter estimates should be precise (Sales and Hill 1976a and b). In populations of trees, index selection has been shown - as theory suggests - to be more efficient, in terms of genetic gain per unit time, than alternative methods of selection (*eg* Christophe and Birot 1983, Cotterill 1986b, Cotterill and Dean 1990, Cotterill and Jackson 1989, Magnussen and Yeatman 1989). The Binet restriction, which maximises gains in traits not included in the index, is of particular relevance to tree breeding where it is used primarily to achieve gain in important mature traits from selection on juvenile traits. Burdon (in press) has discussed some of the limitations which apply to the use of index selection in tree breeding. The following are usually assumed, the candidate material has equal evaluation times and costs; the amount of candidate material is not a limiting factor; sufficient knowledge of economic weights and that genetic parameters included in the index are well estimated. These assumptions often do not hold. Despite these limitations, Burdon (in press) suggests that the construction of indices is nevertheless instructive, because it allows sensitivity analyses through the gains predicted from indices with using varying economic weights and genetic parameters.

Several programs have been written to calculate selection indices (summarised by Cotterill and Dean 1990). They include SELIND (Cunningham 1970), SELECT (Talbert 1986, Talbert and Welty 1987) and RESI (Jackson 1978,

Cotterill and Jackson 1981). RESI has advantages of flexibility in terms of genetic and phenotypic information required, and was used in this study. However, the precision of indices estimated is limited because of the simplifying assumptions and amount of information it is able to accept. The required omission of the plot mean variance (σ^2_{fmr}), from the input files is a likely source of error where these effects are other than negligible. The assumption that the plot mean variance was smaller than either the family and error variance was also necessary to enable the use of the program; this assumption is justified here, as this source of variation was smaller than the error and family variances for some of the traits considered (see Tables 2.13-2.15).

The aims of this Chapter are two-fold. The first is the calculation of genetic gains resulting from the use of combined index selection to achieve specified breeding objectives for *P. elliottii* in Zimbabwe. The indices are evaluated in terms of genetic gain per unit time, efficiency and accuracy. Efficiency of early selection, estimated as a ratio between gains from indirect selection to those from direct selection, indicates the possibility of early selection. The accuracy of selection, defined as the correlation between the selection criteria and the breeding objective, is an indicator of how much response to selection can be expected from the offspring of selected individuals (Nicholas 1987). If those individuals with the best breeding values can be clearly identified, that is, if the accuracy is high, then the response to selection will be maximised, but if accuracy is low then the response to selection is small or negligible. The

accuracy of selection will also be an important criterion for choosing an index, where several alternative indices are available (Nicholas 1987). The correlation of breeding values for different objectives was estimated as a measure of the degree of similarity among breeding objectives derived for the different production systems (Borralho 1991). This parameter describes the measure of agreement between the individual breeding values selected under each of the breeding objectives; the higher the correlation, the more the breeding objectives in question favour the selection of similar genotypes.

The second objective is to use the results of these analyses to estimate the optimum age for selection, again in terms of genetic gains per unit time and efficiencies and accuracies of selection. The study considers selection for improvement at maturity, taken to be approximated by 15 year data, from selection at each of the two juvenile ages for which data was available; five and eight years. This will allow recommendations to be made on the best index or indices to achieve optimal genetic gains in the specified breeding objectives.

3.2 - Specification of breeding objectives

The purpose of selection is defined by the "breeding objective", described by Ponzoni and Newman (1989) as "the combination of economically important traits in the production system". The choice of breeding objective should, therefore, be influenced by the economics of the production system (Miller and

Pearson 1979, James 1987). Ponzoni and Newman (1989) listed four requirements for determination of the breeding objective:

1 - specification of the production system;

2 - identification of the sources of income and expense;

3 - identification of biological traits influencing income and expense;

4 - calculation of the economic weights.

There are presently two production systems of relevance in Zimbabwean *P. elliottii* plantations. The first is the production of saw-timber alone; the second is the production of both saw-timber and resin. The sources of income and expense for both are assumed here to be represented by the market value of the products and the costs of genetic improvement, respectively; the latter are assumed to be equivalent for either production system. The biological traits and the derivation of economic weights relevant to each of these production systems are discussed below.

3.2.1 - Saw-timber production

As noted in Chapter 1, *P. elliottii* plantations in Zimbabwe are grown principally for saw-timber production, which is determined primarily by log volume; stem straightness, wood density and branching traits also have an impact on saw-wood recovery (Ehrenberg 1970, Blair *et al* 1975). In this case, stem straightness is generally favourably correlated with growth *ie* height,

diameter and volume (see Table 2.34); hence, improvement in growth will also improve stem straightness and saw-wood recovery, as discussed by Dean *et al* (1988) for the case of *Araucaria cunninghamii* Sweet. in Queensland, Australia. Wood quality is a complex trait, integrating the influence of physical (*eg* branch size and frequency) and anatomical (*eg* density) features (Barbour and Kellogg 1990). In this case, branch traits are not considered to be important in the determination of saw-timber quality; the basal six meters of tropical pines is responsible for most of their value (Barnes and Gibson 1986), and the bottom third of each residual tree in Zimbabwean *P. elliottii* plantations is pruned by about age eight years, when the non-commercial thinning is performed. Density is generally considered to be the single most useful index of wood quality (Kellogg 1982, Zobel and van Buijtenen 1989), but is of little relevance in the present Zimbabwe saw-timber market because no premium is placed on it (Barnes[2] pers. comm.). At an average of 400 kg/m^3 at 15 years (Table 2.34), wood density in this population of Zimbabwean *P. elliottii* is at the lower end of the range reported by Zobel and van Buitjtenen (1989) for older *P. elliottii*, of 400-600 kg/m^3, but is nevertheless considered adequate by local industries (Barnes pers. comm).

There are, however, two reasons for considering density, either in terms of improvement or simply maintenance at around its present level. The first is the relatively lower density of *P. elliottii* at higher altitudes, where much of the

[2] Dr. R.D. Barnes, Department of Plant Sciences, University of Oxford, South Parks Road, OX1 3RB, UK.

plantation estate is located, and the possibility that gains achieved in growth could, through their negative correlation with density (r_a with either diameter or volume = -0.31 to 0.09 at age 15 years; Table 2.34), decrease density to a level such that saw-timber quality was affected. The second is the potential of *P. elliottii* as a species for pulp production (Zimbabwe Forestry Commission[3] pers. comm.), for which improvement in density could be important; Borralho *et al* (1993), for example, demonstrated the crucial importance of including density in the breeding objectives for pulp production in *Eucalyptus globulus*. As wood density is favourably correlated with height in this population of *P. elliottii* (see Table 2.34), improvement in wood density would follow as a correlated response to selection on height alone.

3.2.2. - Resin production

The production system for saw-timber and resin is dependent on obtaining saw-timber of good quality and large quantities of resin at low cost. Resin production is not economically viable without the associated production of saw-timber (Border Timbers[4] pers. comm.).

The level of resin production is determined primarily by the basal diameter of the tree (Coppen *et al* 1984, Greenhalgh 1982), although the size of live crown

---

[3] Commercial Division, Zimbabwe Forestry Commission, P.O. Box 8111, Causeway, Harare, Zimbabwe.

[4] Border Timbers, Mutare Division, Mutare, Zimbabwe.

will also influence the amount of resin produced (Coppen *et al* 1984). Studies carried out in the USA have shown that trees tapped for resin tend to be less vigorous than untapped trees; for example, a reduction of 26 per cent in volume increment followed two years of tapping of 20 - year old *P. elliottii* (Greenhalgh 1982). Tapping may also have adverse consequences for wood quality: Zobel and van Buijtenen (1989) reported that stem wood is generally resin soaked after tapping, rendering it more difficult to use. However, Hurley *et al* (1976) found no effect on either pulping characteristics of the wood or physical properties of the paper from resin tapped trees. There have been no reports of adverse effects on saw-timber quality from resin tapping in Zimbabwean *P. elliottii* plantations (Border Timber pers. comm.).

3.2.3 - Derivation of economic weights

Economic weights for traits X and Y may be defined as the "additional profit that may be expected from a one unit increase in trait X relative to that from a one unit increase in trait Y" (Cotterill and Dean 1990). As no economic information was available for the relative importance of different traits of *P. elliottii* in Zimbabwe, a baseline index was constructed following the equal emphasis method of Cotterill and Dean (1990) and Dean *et al* (1986).

Under the equal emphasis method, weights are calculated as the inverse of the phenotypic standard deviation of the trait:-

$$w_i = \frac{1}{\sigma_j} \quad (3.1)$$

where w_i = weight for trait j;

σ_j = phenotypic standard deviation of trait j.

When economic weights are calculated in this manner, equal importance is given to each trait, such that a change of one standard deviation (s.d.) in any trait is assumed to be as important as a corresponding one standard deviation change in another trait. The method is simple and offers some sort of base level protection against determining extremely erroneous weights for index selection (Cotterill and Jackson 1985, Cotterill and Dean 1990). In practice, traits are seldom of equal importance, so the primary purpose of the equal emphasis method is as a baseline for the development of other weights, as demonstrated by Dean *et al* (1986) in their study of *P. caribaea*. The ad hoc variation of the weighting accorded different traits gives some idea of the relative importance of each trait (Cotterill and Dean 1990) and allows, in essence, the conduct of sensitivity analyses.

Thus, in this study, economic weights were varied by differentially weighting each trait in turn, in order to explore the consequences for expected genetic gains in the breeding objectives and in individual traits.

3.3 - Breeding objectives

The generalised breeding objective considered in this study reflect the present market for *P. elliottii* in Zimbabwe, *viz*, saw-timber and joint saw-timber and resin production. On the basis of the arguments advanced in section 3.2.1, saw-timber production was assumed to correspond simply to volume production. Resin production was assumed to correspond to resin yield.

The generalised breeding objective for the two production systems can be expressed as:

$$H_i = w_j A_{j15} \qquad (3.2)$$

where H_i = breeding objective i;

w_j = economic weight for trait j;

A_{j15} = the tree's true breeding value for trait j at age 15 years, assumed here to approximate maturity.

Four breeding objectives were considered. Breeding objective H_1 reflects simply the objective of maximum saw-timber production; objective H_2 places twice as much weight on gains in saw-timber production as on those in resin yield; objective H_3 accords equal emphasis to gains in saw-timber production and resin yield, and objective H_4 places twice as much emphasis on gains in resin yield as on saw-timber production. Varying weights for the traits in the breeding objectives in this manner reflects varying assumptions about their

relative importance.

Stem straightness is not included as a trait in any breeding objective for two reasons. Firstly, in this population, it is generally highly rated, with an average score of four; on the scale defined in Table 2.5, this equates to saw-timber quality. Secondly, stem straightness and growth traits are positively correlated at ages five and 15, so that gains in stem straightness will follow those in volume. The slight negative correlations between stem straightness at age eight and growth traits at age 15 years (see Table 2.34) are probably more an artifact of the straightness scoring system than of reality. The merits and limitations of the absolute stem straightness assessment scale used in this study were discussed in section 2.6.4.

The criteria against which the results of selection on the four breeding objectives are judged are discussed below.

3.4 - Expected genetic gains

Genetic gains were estimated for both direct and indirect selection. In direct selection, at the mature age of 15 years, the selection traits used in the index were those in the breeding objectives. For indirect selection, at all three ages, the selection traits were different from those in the breeding objectives. The general combined selection index on which selection was effected is that given by Cotterill and Dean (1990, Chapter 9):-

$$I = b_1P_1 + b_2F_1 + b_3P_2 + b_4F_2 + \ldots + b_jP_j + b_{j+1}F_j \quad (3.3)$$

where P_j and F_j represent individual phenotypic and family mean values, respectively, for the j^{th} trait, and b_j's represents the index coefficients. The index coefficients were calculated assuming a constant 60 progeny per family at five years, and 30 progeny per family at ages eight and 15 years, due to the 50% thinning effected at eight years. It has been shown that 30 progeny per family will provide a reliable estimate of the family mean (Cotterill and James 1984). The b coefficients were calculated following Cotterill and Dean (1990), according to Equation (3.4):-

$$b = P^{-1}Aw \quad (3.4)$$

where b = vector of index coefficients;

P^{-1} = inverse of the phenotypic variance-covariance matrix;

A = matrix of additive genetic variances and covariances;

w = vector of economic weights.

The objective of the combined index is to maximise gain in the breeding objective (H) (Cotterill and Dean 1990, Chapter 8). Individual and family mean data were available for all but two traits. Resin yield was assessed only in test 23a; consequently, only family data could be used in the estimation of gains. The measurement of felled trees only, at eight years meant that there were no corresponding measurements for those trees left standing at 15 years.

This lack of individual tree height at eight years which matched that at 15 years necessitated that genetic correlations between HT8 and traits at 15 years were estimated using Burdon's (1977) method rather than by generalised least squares; there were no estimates of phenotypic correlations corresponding to the genetic correlations. It was assumed that phenotypic correlations approximated the corresponding family mean correlations in these cases. Therefore, only family mean data was used in the gain calculations.

3.4.1 - Genetic gains from direct selection

Genetic gains per year from direct (mature) selection were estimated by the programme RESI (Cotterill and Dean 1990), as in Equation (3.5):-

$$G_1 = i_m \frac{\frac{w'Gw}{b'Pb}}{T_m} \qquad (3.5)$$

where G_1 = annual gain from direct selection;

i_m = selection intensity at m (15 years), here estimated as 2.421 (1:50), due to the 50% thinning at eight years;

w' = transpose of the vector of economic weights;

G = genotypic variance-covariance matrix of traits in the breeding objective;

w = vector of economic weights;

b' = transpose of the vector of the index coefficients;

P = phenotypic variance-covariance matrix of traits in the index;

b = a vector of the index coefficients;

T_m = m+y; the generation interval for mature selection;

where m = the time to selection, here 15 years;

y = the breeding interval, that is, the estimated time between selection of parents and establishment of the next generation, here estimated as eight years.

3.4.2 - Genetic gains from indirect selection

Gains per year from indirect selection were estimated by the program RESI (Cotterill and Dean 1990), as in Equation (3.6):-

$$G_2 = i_j \frac{w'Gw}{\sqrt{b'Pb}} \frac{1}{T_j} \qquad (3.6)$$

where G_2 = annual gains from indirect selection;

i_j = selection intensity at age j, here five and eight years, estimated as 2.665 (1:100) at five years and 2.421 (1:50) at eight years and 15 years;

T_j = the generation interval for juvenile selection;

where j = the time to selection, here five or eight years;

y = as defined above, here estimated as eight years;

and w', G, w, b', P and b are as defined above.

Gains in individual traits, at both mature and juvenile ages, were calculated

according to Equation (3.7), following Cotterill and Dean (1990):-

$$\Delta A_j = i\beta_{A_jI}\sigma_I \tag{3.7}$$

where ΔA_j = represents the gain expected in the breeding value of the j^{th} trait in the index;

β_{AjI} = the regression of A_j on the index value I;

σ_I = phenotypic variance of the index, and;

i = the standardised selection differential as defined above.

3.5 - Efficiency of index selection

The efficiency of index selection was estimated, following Lambeth (1980), according to Equation (3.8):-

$$E = \frac{G_i}{G_j} \tag{3.8}$$

where E = efficiency of index selection;

G_i = gains per year from indirect selection at age i, here five, eight or 15 years;

G_j = gains per year based on direct selection at age j, here 15 years.

3.6 - Accuracy of selection

The accuracy of selection was estimated for all indices used in the estimation of gains, following Falconer (1981):-

$$\rho A = \sqrt{\frac{C' V^{-1} C}{\sigma_a^2}} \qquad (3.9)$$

where ρA = accuracy of selection;

C' = transpose of the covariance matrix;

V^{-1} = inverse of the variance-covariance matrix;

C = covariance matrix;

σ^2_a = additive genetic variance for volume.

3.7 - Correlations among breeding objectives

The methodology outlined by James (1982) was used to estimate the correlations of breeding values for different objectives, as in Equation 3.10:-

$$r_{H_i, H_j} = \frac{w_i' G w_j}{\sqrt{(w_i' G w_i)\ (w_j' G w_j)}} \qquad (3.10)$$

where $r_{Hi,Hj,}$ = correlation between breeding objectives H_i and H_j;

w'_i, w'_j = vector of economic weights of the traits in the breeding objective (H_i, H_j) respectively;

G = genotypic variance-covariance matrix of traits in the breeding objective.

3.8 - Application

Genetic parameters used in these calculations were those estimated on a pooled basis in Chapter 2 (Tables 2.32 - 2.34). The economic weights derived

for breeding objectives H_1 to H_4, according to Equation 3.1, are shown in Table 3.1.

Table 3.1 Economic weights for traits in the breeding objectives.

Breeding Objective	Description	Relative emphasis per s.d.		W_i	
		VOL15	RESQ15	VOL15	RESQ15
H_1	**Saw-timber only**	1	0	0.01	0.00
H_2	**Saw-timber emphasis**	2	1	0.02	0.07
H_3	**Equal emphasis**	1	1	0.01	0.07
H_4	**Resin emphasis**	1	2	0.01	0.14

3.8.1 - Inclusion of traits in the index

Conceptually, the most self-evident case is that where all traits assessed are included in the index. However, the inclusion of all available information in an index has several drawbacks. Genetic gains expected in individual traits diminish as the number of traits under selection is increased; for example, an index combining three, four or five traits may produce only 60%, 50% or 45%, respectively as much gain in each trait as would result from single trait selection (Cotterill and Dean 1990; see also Appendix II).Secondly, high correlations between any two traits used in the index renders one superfluous, as it does not necessarily result in extra gains (Baker 1986, Cotterill and Dean 1990, see also Appendix II); discarding one of these traits from the index may result in an improved response to selection. In the case of trees, for example,

Cotterill and Dean (1990) suggest using only one of height and diameter, as they are highly correlated, or calculating and using a composite trait such as volume. In the latter case, Baker (1986) noted that traits derived mathematically from measurements on primary traits are subject to error, which may lead to poorer genetic gains.

The decision as to which traits should be included in the index is influenced by a number of factors; traits may be of high economic value, degree of difficulty in measuring the traits (Cotterill and Dean 1990), offer important information that other traits in the index do not provide, or may be highly correlated with the breeding objective (Baker 1986).

The correlation between any pair of traits is an important criterion in determining whether a trait should be included. In certain cases, favourable (not necessarily high) correlations between two traits would result in indirect gains in one from selection on the other, suggesting exclusion of the correlated trait which is less important in achieving the breeding objective. Alternatively, either may be excluded on the basis of availability of measurement data, assessment costs, or ease and reliability of assessment.

Resource constraints may not allow measurement and assessment of all traits which the breeder may wish to include in the index. In this case, information about these traits may be obtained from other traits through correlated responses, or a sub-sample may be measured or assessed and information only

included in the index as family means. Traits of low heritability may also be included in the index in the form of family means, and selection on this basis has been found to produce improved gains (Cotterill and Dean 1990).

3.8.1.1 - Direct selection

The generalised selection index used in the estimation of gains for the breeding objectives is summarised in Table 3.2. The results from direct selection provide a bench-mark against which genetic gains from indirect selection can be compared, and allow estimation of efficiencies of selection. Direct selection was based on volume (VOL15) for breeding objective H_1 and on volume and resin yield (RESQ15) for breeding objectives H_2 - H_4.

Table 3.2 Traits included in selection indices for the estimation of gains from direct (mature) selection in the four breeding objectives.

Breeding objective	Index No	Traits in index	
		VOL15	RESQ15
H1	I1.i	I,F	-
H_2 - H_4	$I_{2.i}$ to $I_{4.i}$	I,F	I,F

I and F indicate where individual or family information have been used, respectively, and i refers to the number of the breeding objective.

3.8.1.2 - Indirect selection

Two criteria were used to select traits for inclusion in the indices. Firstly, the correlations between individual traits were examined so that one of each pair

of highly correlated traits could be excluded as discussed above. In this case, height and diameter were highly correlated; the calculation of a composite trait in the form of volume from height and diameter was not attractive, because mathematically derived traits are subject to errors (Baker 1986). It was also not clear that the use of a composite trait would offer any advantage, in terms of gain, compared to those from height or diameter alone, as the heritability of volume and its correlations with other traits were similar to those for height and diameter (Tables 2.33 and 2.34).

Secondly, the correlations between potential selection traits and those in the breeding objectives were examined. The correlations between the breeding objective, saw-timber (volume) and each of diameter and height were high. Correlations between each of diameter and height with resin yield were low. Correlations between stem straightness and volume were low (Table 2.34), and although, those between stem straightness and resin yield were relatively high, stem straightness was not included in the selection criteria because it is not of direct relevance to resin production. It was important for traits used in the calculation of gains to have been estimated at all three ages as the results would be used to estimate the optimal age for selection. Resin yield and wood density could not be used for selection at the earlier ages as they were assessed only at 15 years.

Consequently, selection was based on the two indices listed in Table 3.3. The first index ($I_{5.i}$) included only diameter and the second ($I_{6.i}$) only height. The

index based only on diameter will result in higher genetic gains than that based on height because diameter is better correlated with traits in the breeding objectives, and because heritability of diameter is higher than that of height. However, it will also result in losses of gain in wood density, because these two traits are adversely correlated. Height was positively correlated with wood density at all ages. This correlation, although low, implies that gains in wood density should follow from selection for height. It therefore provides a means of recognising wood quality considerations, and the potential for pulp production, in selection. However, periodic monitoring of wood density should also be considered to ensure that the mean of wood density is kept above the minimum levels.

Table 3.3 Traits included in the selection indices for the estimation of genetic gains from indirect selection in the four breeding objectives.

	Traits in the index	
Index No	HT_x	DBH_x
$I_{5.i}$	-	I,F
$I_{6.i}$	I,F	-

HT_x and DBH_x refer to the traits height, diameter and respectively at age x, where x = five, eight and 15 years. I, F and i are as defined in Table 3.2.

3.9 - Results

3.9.1 - Correlations among breeding objectives

Table 3.4 shows the correlations of breeding values for different breeding objectives H_1 to H_4. Correlations of breeding values for the most closely associated pairs of objectives (H_1 *vs* H_2, H_2 *vs* H_3, H_3 *vs* H_4) were uniformly high, about 0.94. Those between less closely related pairs of objectives (H_1 *vs* H_3, H_2 *vs* H_4) were of lesser but nevertheless high magnitude (0.81); the correlation between the least closely related objectives (H_1 *vs* H_4) was least (0.58), but still relatively high.

Table 3.4 Correlations between breeding objectives.

Breeding objective	H_2	H_3	H_4
H_1	0.95	0.81	0.58
H_2		0.96	0.81
H_3			0.94

3.9.2 - Genetic gains from direct selection

Expected genetic gains per year from index selection, for the four breeding objectives and for each individual trait, are listed in Table 3.5, for a selection intensity of 2.421 (1:50).

Genetic gains per year in H across breeding objectives are not comparable as

each is expressed in arbitrary units (Cotterill and Dean 1990, p69). However, the genetic gains per generation are expressed in common units (*ie* percentage genetic gains per generation), and may be compared. The gain per generation in H was greater for the breeding objective of timber only (47.6%); gains for the breeding objectives which included resin production were less and approximately 36 to 39% (see Figure 3.1). The results demonstrate that increasing emphasis on resin production lowered the overall responses in the breeding objectives.

Differences in the weighting of traits in the breeding objectives caused changes in gains in individual traits. Breeding objective H_1, which was solely concerned with maximizing timber production, resulted in the highest responses in VOL15 and the lowest gains in RESQ15. As more weight was assigned to resin, responses in growth traits were somewhat reduced, with VOL15 being the most affected. VOL15 dropped from 8.58 dm^3 for H_1 (a gain of 51% per generation) to 6.07 dm^3 for H_4 (or 36% per generation). Table 3.5 also presents correlated responses in height, diameter, density and stem straightness from selection based on VOL15 and RESQ15. Diameter follows a similar trend to VOL15, but responses in HT15 did not change across the range of breeding objectives.

Table 3.5 Genetic gains expected per year (absolute units) and per generation (percentage, in brackets) in the four breeding objectives and in individual traits from direct selection at 15 years at an intensity of in 1:50 (2.421), on Index $I_{1.i}$ (volume) or $I_{2.i}$ to $I_{4.i}$ (integrating volume and resin yield). Accuracies of selection are also listed.

		Gains in individual traits						Accuracy of selection
Breeding Objective (H) Selection Index (I)	Gains in H	HT15 (m)	DBH15 (cm)	STR15 (rating)	VOL15 (dm^3)	DENS15 (kg/m^3)	RESQ15 (kg/wk)	(r_{IH})
H_1 = 0.01VOL								
$I_{1.1}$	0.08 (47.6)	0.07 (9.1)	0.22 (21.3)	0.003 (1.7)	8.58 (51.0)	-0.45 (-2.6)	0.06 (4.4)	0.77
H_2 = 0.02VOL+0.07RES								
$I_{2.2}$	0.17 (39.3)	0.07 (9.1)	0.22 (21.3)	0.004 (2.3)	8.30 (49.3)	-0.67 (-3.9)	0.23 (16.8)	0.76
H_3 = 0.01VOL+0.07RES								
$I_{3.3}$	0.10 (37.9)	0.07 (9.1)	0.20 (19.3)	0.01 (5.7)	7.62 (45.3)	-0.82 (-4.7)	0.36 (26.3)	0.75
H_4 = 0.01VOL+0.14RES								
$I_{4.4}$	0.13 (36.1)	0.07 (9.1)	0.16 (15.5)	0.01 (5.7)	6.07 (36.1)	-1.95 (-11.2)	0.50 (36.5)	0.73

In contrast to the decline in VOL15, gains in resin yield (RESQ15) improved dramatically as more weight was assigned to RESQ15 in the breeding objective, ranging from 0.06 kg/wk for H_1 (a 4% response per generation) to 0.50 kg/wk for H_4 (a 37% response per generation). Including RESQ15 as a selection criterion resulted in a substantial improvement in RESQ15, at relatively little expense to VOL15; this is particularly obvious for H_2 and H_3. Even for H_4, where resin was considered twice as important as timber, gains in VOL15 dropped only from 51% to 36%, whereas RESQ15 improved from 4% to 37%.

As higher weights were assigned to RESQ15, a greater decline in wood density was observed (ranging from -0.45 kg/m^3 per year for H_1 to -1.95 kg/m^3 per

year for H_4). No substantial correlated changes in stem straightness were observed for the range of indices considered (approximately two percent for objectives H_1 and H_2 and six percent for H_3 and H_4).

Despite the marked differences in emphasis given to resin and volume, accuracies of selection from direct selection were remarkably constant, with r_{IH} between 0.74 and 0.71, decreasing as more emphasis was put on resin (Figure 3.1).

3.9.3 - Genetic Gains from Indirect Selection

Expected genetic gains per year from indirect selection based only on height ($I_{5.i}$), or diameter ($I_{6.i}$) are presented in Tables 3.6, 3.7 and 3.8 for five, eight and 15 years respectively. Due to thinning, selection intensity changed from 2.665 (1:100) at five years to 2.421 (1:50) at eight and 15 years.

As was found for direct selection, the rate of response in H, as given by the percentage change per generation, decreased from H_1 to H_4 (Figure 3.2). Percentage gains per generation were lowest for selection at five years and were highest at 15 years. It is also apparent from Tables 3.6 to 3.8 that gains in individual traits were not sensitive to changes in the breeding objectives when selection was based on either DBH ($I_{5.i}$) or HT ($I_{6.i}$) since individuals would be selected on the same trait for all breeding objectives.

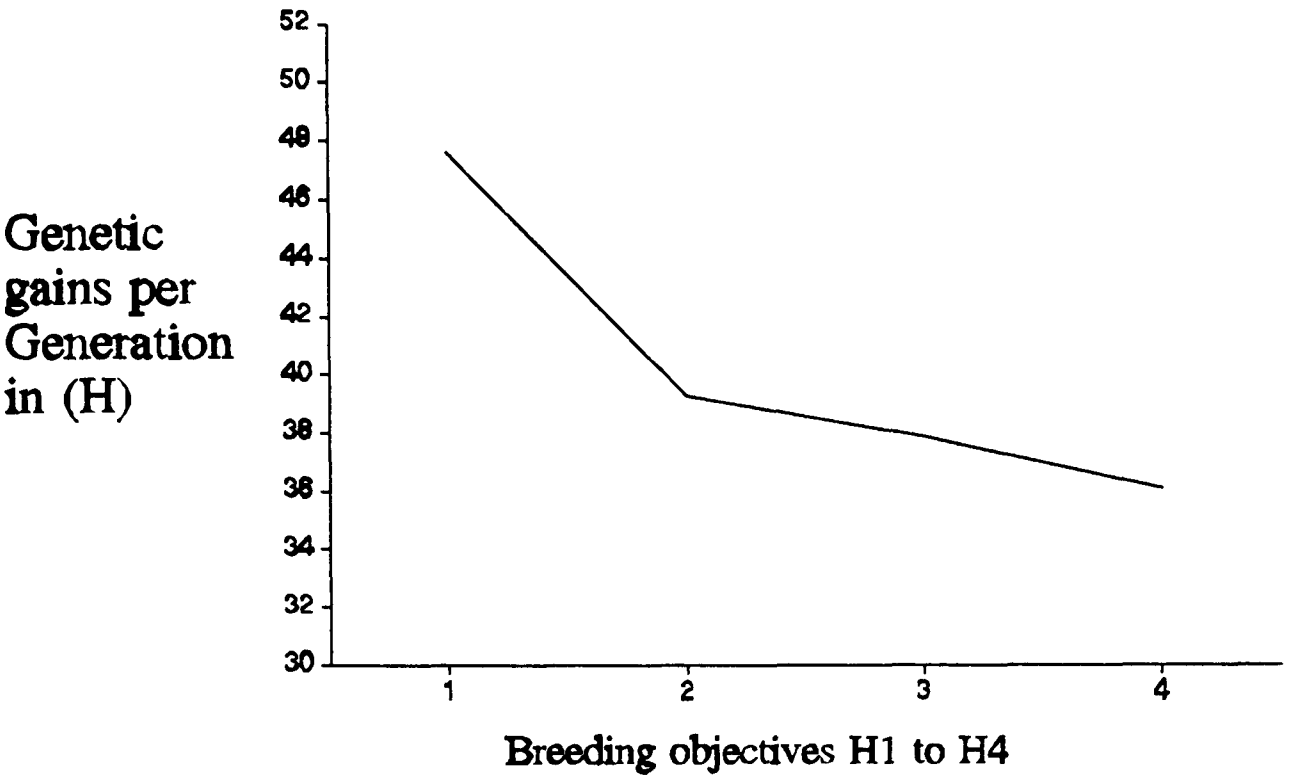


Figure 3.1. Expected genetic gain per generation and accuracies of selection for the four breeding objectives from direct selection.

Table 3.6 **Genetic gains expected per year (absolute units) and per generation (percentage, in brackets) in the four breeding objectives and in individual traits from indirect selection at five years at an intensity of in 1:100 (2.665), on Index $I_{5.i}$ (diameter) or $I_{6.i}$ (height). Accuracies of selection are also listed.**

Breeding Objective (H) Selection Index (I)	Gains in H	Gains in individual traits: HT15 (m)	DBH15 (cm)	STR15 (rating)	VOL15 (dm^3)	DENS15 (kg/m^3)	RESQ15 (kg/wk)	Accuracy (r_{IH})	Efficiency of selection: H	VOL15	RESQ15
H_1 = 0.01VOL											
$I_{5.1}$	0.15 (50.4)	0.07 (5.2)	0.20 (10.9)	0.01 (3.2)	12.8 (43.0)	-1.51 (-4.9)	0.09 (3.7)	0.68	1.88	1.49	1.50
$I_{6.1}$	0.13 (43.7)	0.09 (6.6)	0.16 (8.7)	0.02 (6.4)	11.3 (38.0)	0.43 (1.4)	0.10 (4.1)	0.61	1.63	1.32	1.67
H_2 = 0.02VOL+0.07RES											
$I_{5.2}$	0.30 (39.2)	0.07 (5.2)	0.20 (10.9)	0.01 (3.2)	12.8 (43.0)	-1.51 (-4.9)	0.09 (3.7)	0.65	1.77	1.54	0.39
$I_{6.2}$	0.27 (35.2)	0.09 (6.6)	0.16 (8.7)	0.02 (6.4)	11.3 (38.0)	0.43 (1.4)	0.10 (4.1)	0.53	1.59	1.36	0.44
H_3 = 0.01VOL+0.07RES											
$I_{5.3}$	0.15 (32.1)	0.07 (5.2)	0.20 (10.9)	0.01 (3.2)	12.8 (43.0)	-1.51 (-4.9)	0.09 (3.7)	0.59	1.50	1.68	0.25
$I_{6.3}$	0.14 (30.0)	0.09 (6.6)	0.16 (8.7)	0.02 (6.4)	11.3 (38.0)	0.43 (1.4)	0.10 (4.1)	0.53	1.40	1.48	0.28
H_4 = 0.01VOL+0.14RES											
$I_{5.4}$	0.16 (25.1)	0.07 (5.2)	0.20 (10.9)	0.01 (3.2)	12.8 (43.0)	-1.51 (-4.9)	0.09 (3.7)	0.45	1.23	2.11	0.18
$I_{6.4}$	0.15 (23.6)	0.09 (6.6)	0.16 (8.7)	0.02 (6.4)	11.3 (38.0)	0.43 (1.4)	0.10 (4.1)	0.41	1.15	1.86	0.20

Table 3.7 **Genetic gains expected per year (in absolute units) and per generation (percentage, in brackets) in the four breeding objectives and in individual traits from indirect selection at eight years at an intensity of in 1:50 (2.421), on Index $I_{5.i}$ (diameter) or $I_{6.i}$ (height). Accuracies of selection are also listed.**

Breeding Objective (H) Selection Index (I)	Gains in H	Gains in individual traits: HT15 (m)	DBH15 (cm)	STR15 (rating)	VOL15 (dm^3)	DENS15 (kg/m^3)	RESQ15 (kg/wk)	Accuracy (r_{IH})	Efficiency of selection: H	VOL15	RESQ15
H_1 = 0.01VOL											
$I_{5.1}$	0.11 (45.5)	0.07 (6.4)	0.19 (12.8)	0.003 (1.2)	11.0 (45.5)	-1.02 (-4.1)	0.08 (4.1)	0.69	1.38	1.28	1.33
$I_{6.1}$	0.11 (45.5)	0.09 (8.2)	0.15 (10.1)	0.01 (4.0)	10.6 (43.8)	0.47 (1.9)	0.10 (5.1)	0.66	1.38	1.24	1.67
H_2 = 0.02VOL+0.07RES											
$I_{5.2}$	0.23 (37.0)	0.07 (6.4)	0.19 (12.8)	0.003 (1.2)	11.0 (45.5)	-1.02 (-4.1)	0.08 (4.1)	0.66	1.35	1.33	0.35
$I_{6.2}$	0.22 (35.4)	0.09 (8.2)	0.15 (10.1)	0.01 (4.0)	10.6 (43.8)	0.47 (1.9)	0.10 (5.1)	0.64	1.29	1.28	0.44
H_3 = 0.01VOL+0.07RES											
$I_{5.3}$	0.12 (31.6)	0.07 (6.4)	0.19 (12.8)	0.003 (1.2)	11.0 (45.5)	-1.02 (-4.1)	0.08 (4.1)	0.60	1.20	1.44	0.22
$I_{6.3}$	0.11 (29.0)	0.09 (8.2)	0.15 (10.1)	0.01 (4.0)	10.6 (43.8)	0.47 (1.9)	0.10 (5.1)	0.58	1.10	1.39	0.28
H_4 = 0.01VOL+0.14RES											
$I_{5.4}$	0.12 (33.3)	0.07 (6.4)	0.19 (12.8)	0.003 (1.2)	11.0 (45.5)	-1.02 (-4.1)	0.08 (4.1)	0.47	0.92	1.81	0.16
$I_{6.4}$	0.12 (23.2)	0.09 (8.2)	0.15 (12.8)	0.01 (1.2)	10.6 (43.8)	0.47 (1.9)	0.10 (5.1)	0.46	0.92	1.75	0.20

Table 3.8 Genetic gains expected per year (in absolute units) and per generation (percentage, in brackets) in the four breeding objectives and in individual traits from indirect selection at 15 years at an intensity of in 1:50 (2.421), on Index $I_{5.i}$ (diameter) or $I_{6.i}$ (height). Accuracies of selection are also listed.

	Gains in individual traits							Accuracy	Efficiency of selection		
Breeding Objective (H) Selection Index (I)	Gains in H	HT15 (m)	DBH15 (cm)	STR15 (rating)	VOL15 (dm^3)	DENS15 (kg/m^3)	RESQ15 (kg/wk)	(r_{IH})	H	VOL15	RESQ15
H_1 = 0.01VOL											
$I_{5.1}$	0.08 (47.5)	0.06 (5.2)	0.22 (21.3)	0.002 (1.1)	8.0 (47.5)	-0.52 (-3.0)	0.07 (5.1)	0.72	1.00	0.93	1.17
$I_{6.1}$	0.06 (35.7)	0.08 (10.4)	0.15 (14.5)	0.002 (1.1)	5.89 (35.0)	0.38 (2.2)	0.15 (11.0)	0.53	0.75	0.69	2.50
H_2 = 0.02VOL+0.07RES											
$I_{5.2}$	0.17 (39.3)	0.04 (5.2)	0.22 (21.3)	0.002 (1.1)	8.0 (47.5)	-0.52 (-3.0)	0.07 (5.1)	0.69	1.00	0.96	0.30
$I_{6.2}$	0.13 (30.1)	0.08 (10.4)	0.15 (14.5)	0.002 (1.1)	5.89 (35.0)	0.38 (2.2)	0.15 (11.0)	0.54	0.76	0.71	0.65
H_3 = 0.01VOL+0.07RES											
$I_{5.3}$	0.09 (34.1)	0.06 (5.2)	0.22 (21.3)	0.002 (1.1)	8.0 (47.5)	-0.52 (-3.0)	0.07 (5.1)	0.63	0.90	1.05	0.19
$I_{6.3}$	0.07 (26.5)	0.08 (10.4)	0.15 (14.5)	0.002 (1.1)	5.89 (35.0)	0.38 (2.2)	0.15 (11.0)	0.52	0.70	0.77	0.42
H_4 = 0.01VOL+0.14RES											
$I_{5.4}$	0.09 (25.0)	0.04 (5.2)	0.22 (21.3)	0.002 (1.1)	8.0 (47.5)	-0.52 (-3.0)	0.07 (5.1)	0.63	0.69	1.32	0.14
$I_{6.4}$	0.08 (22.2)	0.08 (10.4)	0.15 (14.5)	0.002 (1.1)	5.89 (35.0)	0.38 (2.2)	0.15 (11.0)	0.44	0.62	0.97	0.30

Thus, gains in individual traits were constant across the four breeding objectives. It was also observed that indices $I_{5.i}$ and $I_{6.i}$ were ineffective at improving RESQ15, even when great emphasis was assigned to it, as in H_4. Overall, indices based on height or diameter were very effective in improving timber production (*i.e.* H_1), and substantial gains were obtained in VOL15, but there were only marginal responses in RESQ15.

Efficiencies of selection were highest at five years, regardless of the breeding objective considered. For example, yearly gains in VOL15 from indirect selection at five years were 12.8 dm^3, compared to 8.58 dm^3 from direct selection, a difference of almost 50%. The most efficient selection was that from index $I_{5.i}$ to improve breeding objective H_1, with E = 1.88 (*i.e.* 88% better gains in terms of H than direct selection, see Figure 3.3).

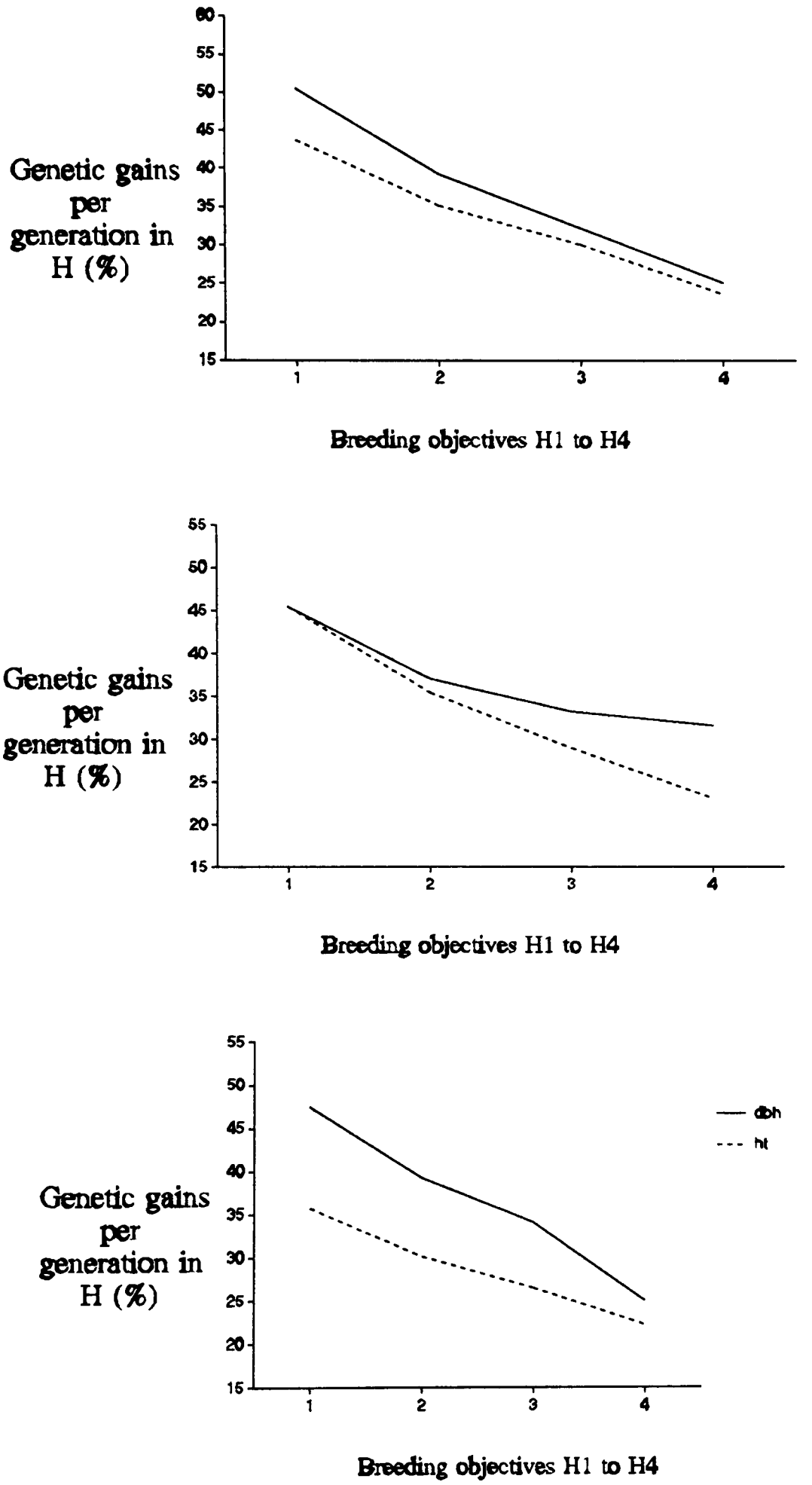
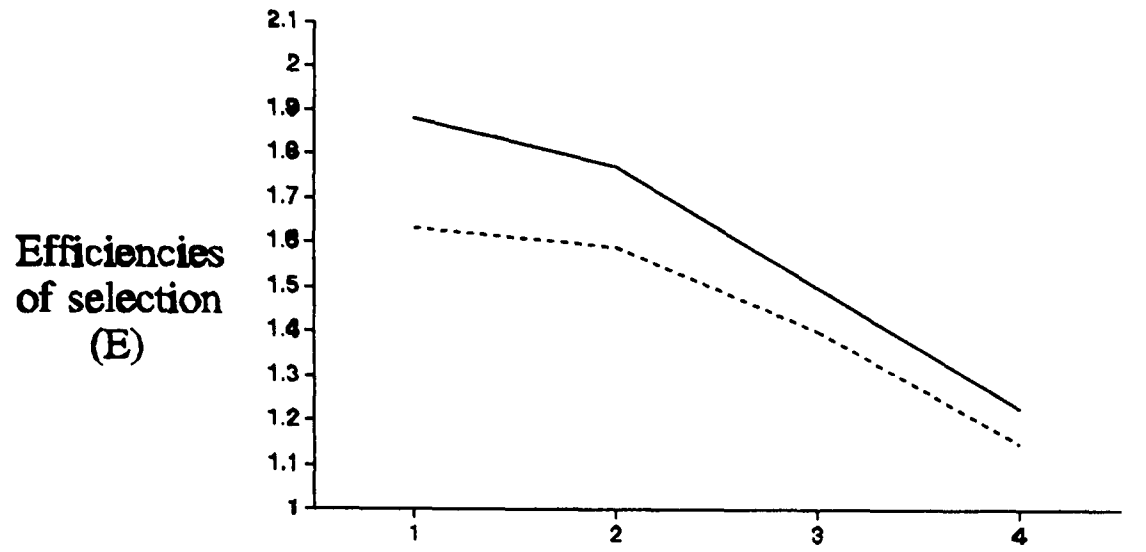
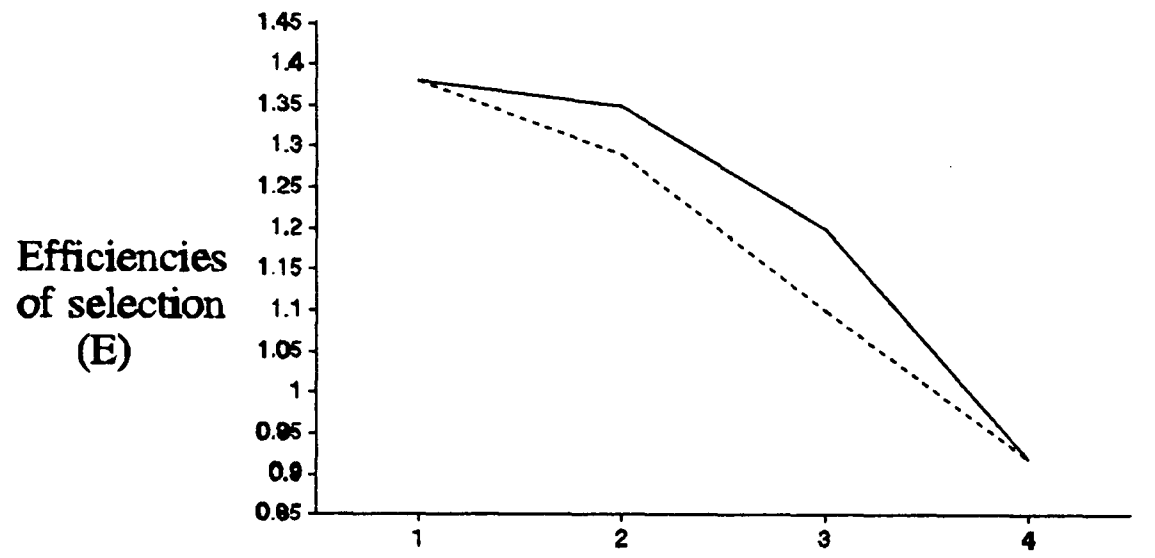


Figure 3.2. Expected genetic gains for H1-H4 at 5, 8 and 15 years (top to bottom), from selection based on diameter (Ii.5) or height (Ii.6).

However, even for H_4, where RESQ15 was the most important trait, the greatest gains per year were obtained at five years, although with lower efficiencies (E = 1.23 for Index $I_{5.i}$). This decline in efficiency from early selection for RESQ15 results from the incapacity of indices $I_{5.i}$ or $I_{6.i}$ to improve resin production. Nevertheless, efficiencies remain above 1.00 at five years (Table 3.6), because selection results in higher responses in VOL15 and in much shorter generation intervals. These high genetic gains in volume can compensate for the marginal responses in RESQ15 itself.

Accuracies of selection from selection based on $I_{5.i}$ increased with an increase in age but those from selection based on $I_{6.i}$ increased between five and eight years and then decreased. However, the difference in accuracies at the different ages was small, with the exception of that from selection based on height between eight and 15 years. The results reflect the overall good correlations between early growth and volume at 15 years. There were small differences in gains and accuracies between indices using height and diameter (Figure 3.4). Indices including DBH resulted in greater gains and efficiencies of early selection, and in higher accuracies of selection. Gains in RESQ15 were similar for the two indices. When selection was based on $I_{6.i}$, accuracies increased between five and eight years, but decreased at age 15 to values similar to those at five years.





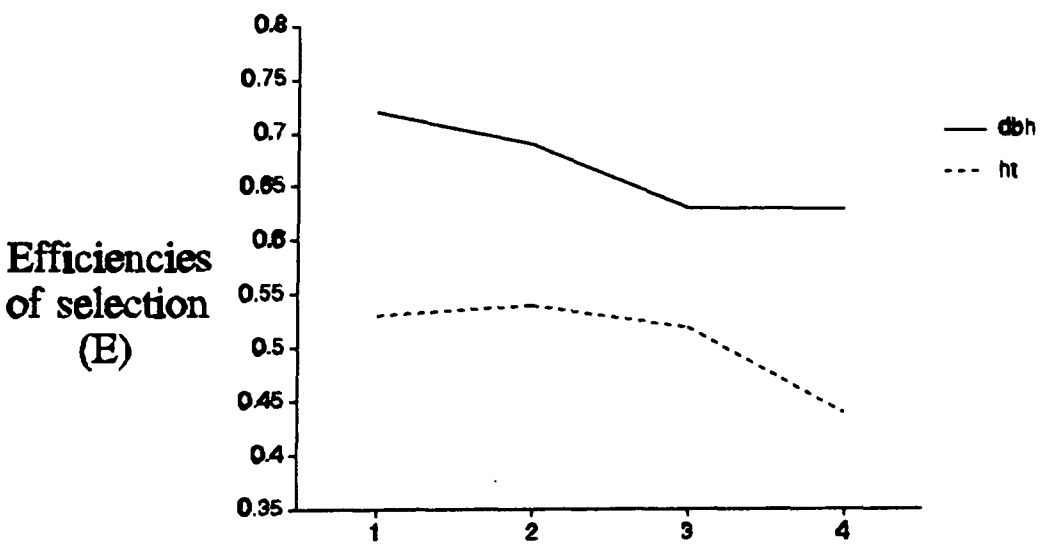
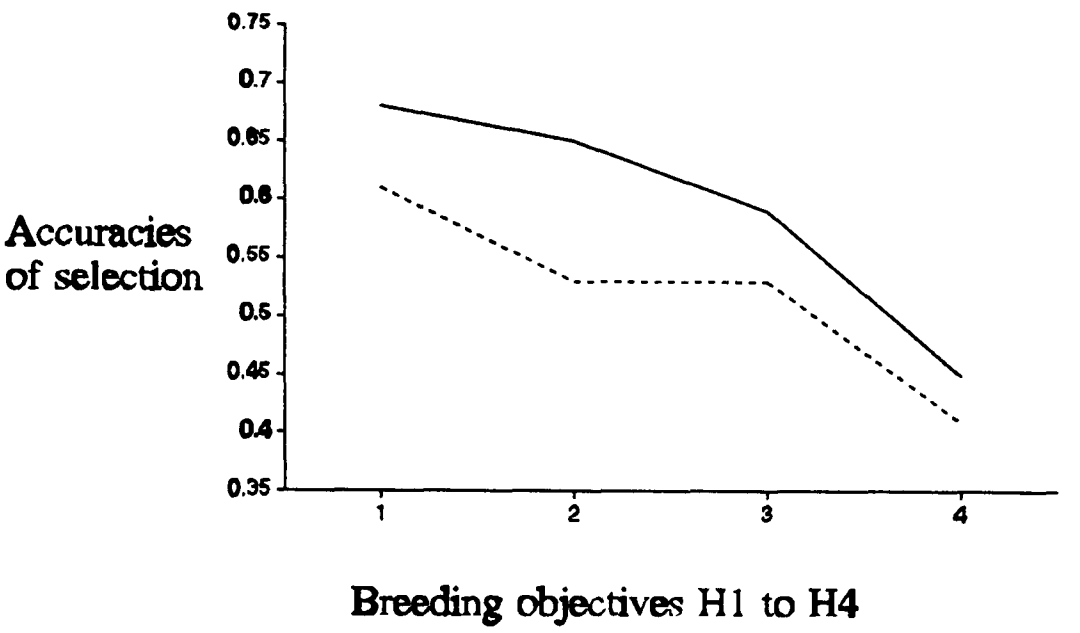


Figure 3.3. Efficiencies of selection for H1-H4 at 5, 8 and 15 years (top to bottom), from selection based on diameter (Ii.5) or height (Ii.6).



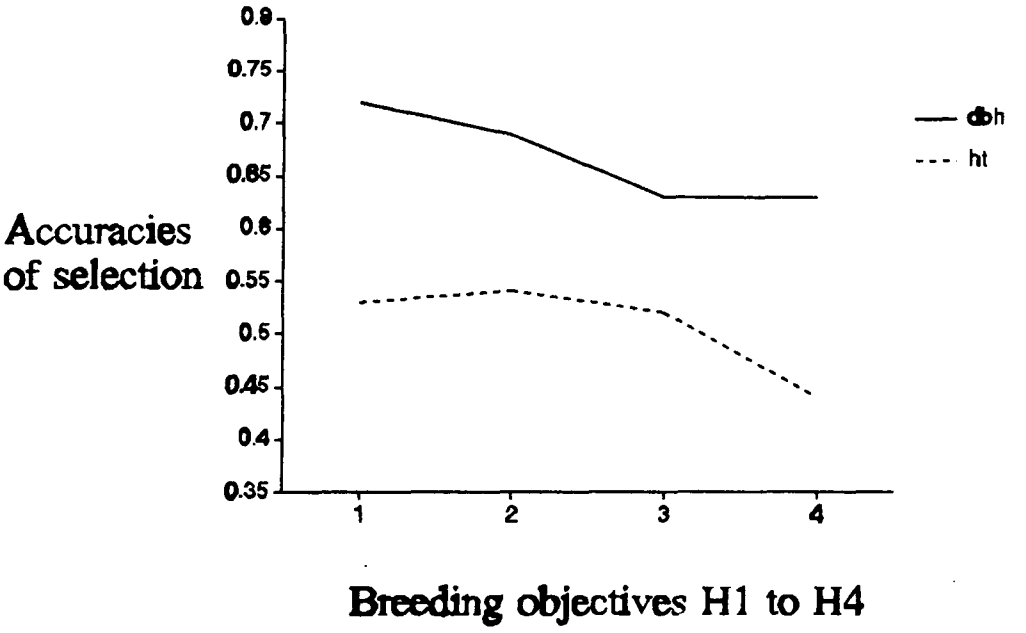


Figure 3.4. Accuracies of selection for H1-H4 at 5, 8 and 15 years (top to bottom), from selection based on diameter (Ii.5) or height (Ii.6).

It is apparent from Tables 3.6 to 3.8 that correlated responses in other traits did not differ from those found under direct selection. There was a minimal correlated response in STR15 from selection on $I_{5.i}$ (3.2% per generation) and $I_{6.i}$ (6.4% per generation). For DENS15, correlated responses were also small, but they were in opposite directions, depending on whether selection was based on height or diameter. The index including DBH resulted in a decrease in density whereas that including HT resulted in a slight improvement (Tables 3.6 to 3.8), a consequence of the genetic correlations between each of diameter and height with density (Table 2.34). In the case of $I_{5.i}$, losses in DENS15 were highest when selection was at five years (-5% per generation), and lowest at 15 years (-3% per generation). A similar trend was found for selection based on $I_{6.i}$, with the lowest gains at five years (1.4% per generation) and the highest gains at 15 years (2.2%).

Comparing accuracies from direct selection (Table 3.5) with those from indirect selection (Tables 3.6 to 3.8), it is apparent that differences were small for H_1, with accuracies between 0.68, at age five, and 0.72, at age 15, for index $I_{5.i}$. These values were close to the value of 0.74 for direct selection on VOL15. However, when RESQ15 was also included in the breeding objective (H_2 to H_4), accuracies from indirect selection using indices $I_{5.i}$ or $I_{6.i}$ decreased considerably, and differences between direct and indirect selection became more pronounced. As expected, accuracies declined as more weight was put on RESQ15, since indices $I_{5.i}$ and $I_{6.i}$ were well correlated with VOL15, but poorly correlated with RESQ15.

3.10 - Discussion

3.10.1 - Correlations between breeding objectives

Correlations between most of the breeding objectives were close to unity, implying that there would be a reasonable flexibility in breeding for these objectives, as selection of similar genotypes is favoured by all objectives (Table 3.4). The lowest correlation (r=0.58) occurred between the two most contrasting breeding objectives, H_1 and H_4, a consequence of the low correlations between resin and volume production.

3.10.2 - Direct selection

It is apparent from the results that varying the weights of traits in the breeding objective influences the genetic gains in traits of economic importance, but had little effect on the other traits considered, namely, stem straightness and wood density. Consequently, as more weight was placed on resin in the breeding objective, there was a decrease in gains per year in volume from 8.6 to 6.1 dm^3, in diameter from 0.22 to 0.16 cm, and in density from 0.45 to 1.95 kg/m^3. Selection for timber production based on direct selection on volume at 15 years (H_1) had the highest rate of genetic gain per generation in H. These high genetic gains are a function of the high genetic correlation between diameter and volume. This result demonstrates that increasing the weight on a trait in the breeding objective that is well correlated with the selection trait/s will

result in higher gains. Placing twice as much emphasis on resin yield did not result in as large an increase in genetic gains compared to placing equal emphasis on both resin and volume, a consequence of the lower genetic correlations between resin and diameter.

The results demonstrate the importance of correctly assigning economic weights, given their influence on the genetic gains in the traits of economic importance. Variation in gains associated with the different breeding objectives highlights the importance of obtaining correct economic data before results from sensitivity analyses, such as these, are used in practice. In order to make the index optimal and selection efficient, it is important that appropriate economic weights are known, particularly when traits are negatively correlated (Burdon in press). This requires long-term planning, in terms of the quality and quantity of the wood required (Magnussen and Keith 1990). When economic weights are known, monetary gains associated with the breeding objectives can be determined, as demonstrated by, for example, Borralho *et al* (1993).

3.10.3 - Indirect selection

Comparison of the gains from indirect selection allows the definition of the optimum selection age in terms of genetic gains and efficiencies of selection. The highest genetic gains per year and efficiencies of selection in all breeding objectives resulted from selection at five years, indicating the potential for

early selection. However, this advantage from early selection is entirely due to gains in volume production and not to gains in resin yield. This is particularly apparent for the case of H_4 and selection based on $I_{5.i}$ at five years, where genetic gains in volume were 53% greater than direct selection, but gains in resin were 82% less than direct selection for resin yield. The high genetic gains at this early age are a function of the higher selection intensity used, higher heritabilities of early traits and high genetic correlations between the traits at age five and traits in the breeding objective at age 15 years. In Chapter 2, it was found that additive genetic correlations between juvenile height and diameter *vs* mature volume were high. Another reason for the high efficiencies of selection is that early selection is associated with shorter generation intervals. As a consequence, efficiencies of selection were also highest at five years and the results suggest that early selection for timber is highly efficient. Unlike the result observed for genetic gains under indirect selection, there was relatively little difference in efficiencies of selection of breeding objectives with contrasting economic weights. This result demonstrates that putting more emphasis on volume may result in higher genetic gains but will not necessarily increase the efficiency of selection by the same magnitude.

When early index selection was based on diameter, wood density declined for all breeding objectives at all ages, with the losses being least at 15 years and greatest at five years. This trend in losses of wood density is a consequence of negative genetic correlations between wood density and diameter

decreasing with age. One of the means of limiting the decline in wood density would be to place a restriction on that trait; this was not done as restricted indices would, by definition, result in large reductions in genetic gains in the traits under improvement, as found by, for example, Dean *et al* (1986) and Dean (1990).

Another way of minimising losses in wood density would be to use a selection trait which was favourably correlated with both wood density and growth traits. In this study, it was found that changes in wood density when selection was based on height ($I_{6.i}$) were small but positive at all ages, a consequence of the small positive genetic correlations between height and wood density. As a consequence, selection based on height should maintain the mean of the population at about the present level, thus preserving timber quality. The consequent losses of gains in the traits in breeding objectives, were not large, 2 - 7%.

Overall, indices based on height or diameter were very effective in improving timber production (*i.e.* H_1), as indicated by the substantial gains obtained in VOL15. It was clear also that both height and diameter did not produce the optimal response in breeding objectives H_3 and H_4. It seems, therefore, that in cases where resin yield is an important breeding objective, resin yield itself or a correlated trait should be included in the selection criteria.

Accuracies of indirect selection were highest for H_1, a result of the high genetic

correlations between the selection traits, diameter and height, and the trait in the breeding objective, volume. Accuracies decreased as more emphasis was placed on resin, a result which reflects the poor genetic correlations between early growth traits and mature resin yield.

As expected, accuracies were lower for all breeding objectives when selection was based on $I_{6.i}$, because of the lower correlation between height and traits in the breeding objectives. Accuracies of selection were least at age five; however, the difference in accuracies between selection at different ages were small, and unlikely to be of great practical consequence.

In summary, the results of this study suggest that five years of age, when trees on sites 23a and 23b are around five to six metres in height, is the optimum of those considered for selection of *P. elliottii* in Zimbabwe. These results are not inconsistent with those reported in the literature, in terms of stage of development, as discussed in section 2.1.3.

3.11 - Conclusions

The lack of real economic information for traits in the breeding objective means that these results are contingent on the assumptions made about relative economic importance. Ideally, before these results are used, economic weights should be estimated and used in the generation of genetic gains.

The correlations of breeding values for different objectives were generally high, indicating that selection decisions for each of them would be largely similar. Consequently, each of these breeding objectives could be realised by the same breeding populations comprising mostly the same individuals.

Genetic gains per year from indirect selection for all breeding objectives and for individual traits were highest at five years, intermediate at eight years and lowest at 15 years, showing that five years is the optimal time for selection. Varying weights on the traits in the breeding objective under both direct and indirect selection influenced gains in the breeding objectives and accuracies and efficiencies of selection. Increasing emphasis on resin yield had the effect of decreasing the genetic gains, accuracies and efficiencies of selection in the breeding objectives, for both direct and indirect selection. In the case of direct selection, increased emphasis on resin yield also resulted in decreased genetic gains in individual traits, particularly, diameter and volume. However, genetic gains in individual traits from indirect selection did not respond to variation of the weights for the traits in the breeding objectives.

It can be concluded from the results that the selection traits used are optimal for the improvement of saw-timber but, in order to obtain substantial genetic gains in resin yield, the latter or a correlated trait must be included in the selection criteria. As resin is tapped commercially only from the age of 15 years (Border Timbers, pers. comm.), early selection for this trait itself is not possible. This difficulty could be circumvented by including stem straightness

at age 5, with which resin production is favourably correlated (r_a = 0.59), as a selection criterion.

The deterioration in wood density following selection based on diameter may eventually present problems for saw-timber quality, even though density is not currently valued by the market. However, the marginal gains in wood density following selection based on height would be adequate to maintain wood density at the present level. In this population of *P. elliottii*, it seems that the use of height as a selection trait may be more desirable than the use of diameter if maintenance of wood quality is of concern. Increasing the emphasis on resin yield had the effect of increasing the losses in wood density, indicating that it would be difficult to breed for resin production and maintain wood quality in the same population.

The use of pooled parameters in this study allows the genetic gains obtained to be interpreted more generally for *P. elliottii* in Zimbabwe, particularly because the sites from which the pooled parameters were estimated are typical of the areas commercially afforested with this species in Zimbabwe. However, the lack of real economic information for traits in the breeding objective remains a real limitation to the derivation of appropriate breeding objectives and selection criteria.

Chapter 4 -

4 - Genetic gains expected from indices including more complete information from relatives

4.1 - Introduction

In advanced-generation breeding programmes, information is generally available on individuals, their parents and relatives (White 1987). This information, if used in a combined index, will result in efficient and effective selection; the amount and quality of information available will determine the accuracy of the index (Burdon in press, Nicholas 1987). Information for an individual of interest may be available from a number of different sources, *eg*, relatives across sites or generations; the greatest response to selection will follow the best use of this data. As the proportion of genes expected to be common between individuals increases with degree of their relationship, the record of a close relative is more significant in influencing the accuracy of selection than is that of a distant relative; for example, accuracy of selection based on a single full-sib is 0.5h and that based on a single half-sib is 0.25h

(where h = heritability) (Nicholas 1987). As the number of individuals measured, and the amount of information and degree of relationship with their relatives increases, the accuracy of selection also increases.

In Chapter 3, genetic gains, accuracies and efficiencies of selection were calculated using the simplest application of combined indices. The factorial mating design, from which the individuals in these tests originate, generates full-sib families, and the most direct derivation of a combined index is to use information describing individuals and their full-sibs. However, as with the diallel mating design, use of a factorial design also generates half-sib relatives (Huber *et al* 1992), thereby offering an additional source of information with which to guide selection.

As the response to selection is dependent on the accuracy of selection, which in turn is dependent on the amount of information included in the index, one objective of this Chapter is to investigate the increase in the response and the accuracy of selection through the additional incorporation of half-sib information.

However, high genetic gains from selection are obtained at the expense of genetic diversity in the selected population (White in press). Selection will alter gene frequencies, which may in turn permanently change the genetic variance; genetic variability will eventually become exhausted under continued directional selection. When all genes have been fixed in the population, the

population will no longer respond to selection (Bulmer 1980). Because of the emphasis it places on family mean performance when the trait under selection is of low heritability, combined index selection is particularly effective in reducing diversity in the selected population (Namkoong *et al* 1988, White in press). This loss of diversity is apparent in the increased relatedness of individuals selected in advanced generations of both tree (*eg* Namkoong *et al* 1988, van Buijtenen and Burdon 1990) and animal (*eg*, James 1972, Woolliams 1989) breeding populations.

The potential for future breeding efforts will be determined by selection of the founders and establishment of the base breeding population; any mistakes made in sampling at this stage may be costly to correct at a later stage (Namkoong 1984). Most of the breeding stock currently represented in tree improvement programmes was sampled with short-term breeding in mind, and the loss of alleles in subsequent generations was not considered important (Kang and Nienstaedt 1987). This means that the genetic base on which selections are being made is likely to be relatively small. Working with a limited base population will yield high genetic gains over two or three generations, but gains will then decrease or plateau as inbreeding increases (Kang and Nienstaedt 1987). The completion of the first generation of breeding for most tree improvement programmes, and the subsequent development of advanced generation breeding populations, emphasize the need to ensure a broad genetic base to safeguard long-term genetic gains (White in press).

In this study, genetic gains expected per generation and per year, and accuracies of selection, are used as criteria to compare selection indices based on information from different sets of relatives. The study also considers the effect of selection on diversity of the breeding population by estimating the loss of variance in the breeding population after one generation of selection. The results of these analyses should provide some guidance on how best to compromise between obtaining high genetic gains and maintaining genetic diversity in the breeding population. Genetic gains and accuracies of selection were calculated for one breeding objective only; maximisation of saw-timber production. The objective of saw-timber production was chosen because it closely approximates, in practice, the most important breeding objective of the Zimbabwean *P. elliottii* breeding programme, as discussed in Chapters 1 and 3.

4.2 - Materials and Methods

Genetic gains were calculated for one progeny test, 23a, the largest and most complete of the three tests (see Table 2.2).

The generalised breeding objective studied, of saw-timber production, is that which was specified by Equation (3.2), repeated here as Equation (4.1) below:-

$$H = w_1 A_{j15} \tag{4.1}$$

where H = breeding objective;

w_1 = economic weight for trait j, here, volume;

A_{j15} = the tree's true breeding value for trait j at 15 years, assumed here to approximate maturity.

The factorial mating design from which individuals originated is part of a larger design represented in Table 2.2, and summarised here in Table 4.1.

Table 4.1 Families represented in progeny test 23a.

	Males								
Females	22	23	45	49	129	137	177	9	130
58	5151	5177	5208	6088	5263	5298	5322	4997	
76	6025	6044	6069	6089	6108	6131	5323	4998	
87	6026	6045	6070	6090	6109	6132	5324	4999	
126	6029	6048	6072	6092	5266	5302	5326	6003	
128	5159	5184	5215	5241	5267	5303	5327	6004	
174	6034	6055	5222	6098	6115	6139	5334	6012	
175	6035	6056	6078	6099	6116	6140	6150	6013	
200	6037	6059	6081	5251	5276	6142	5338	6016	5287
28	5146	5716		5722		6123	5749	4990	
43	6021	6041		6085	6103			4991	
57	6024	6043	6068		6107	6130	5321	4996	
125	5157	5182		5725	5735		5753	6002	
132	6031	6051	6075	6094	6113	6137	5330	6007	
138	6032	6052	6076	6095	6114		5337	6009	6119
172	6033	6053		6096			5754	6010	
173		6054	6077	6097		6138	6149	6011	5285
176	6036	6057			6117	6141	5336		5286
86			5210	5724			5751	5123	
88	6027	6046	5212	5238	5734	6133		6000	
89	6028	6047		6091	6110	6134	6146		
178				5727			5755		
203		5719		5728			5736	6017	
224	5713	5720		5729	5738		5757	5708	
234	5714	5721		5730	5739			5709	

The numbers in the body of the table are the codes for families derived from crossing the corresponding parents.

It is apparent from Table 4.1 that each individual in each full-sib family also has a substantial set of half-sib relatives - an average of 9 paternal half-sib families across the rows and 21 maternal half-sib families down the columns

of Table 4.1. Therefore, indices comprising various combinations of individual, full-sib and half-sib information can be constructed. The simplest index considered here included individual information only (phenotypic selection), and the most comprehensive included individual, full and half-sib information.

The indices on which comparisons were based are specified in Table 4.2.

Table 4.2 Combinations of individual, full-sib and half-sib information used in the estimation of genetic gains and accuracies of selection for H.

	Information included in the index		
Index No	Individual	Full-sib	Half-sib
I_1	✓	-	-
I_2	✓	✓	-
I_3	✓	✓	✓

✓ shows information included in the index.

The index including individual and half-sib information only was not considered as it does not represent a likely scenario where full-sib information is available.

The program RESI (Jackson 1978, Cotterill and Jackson 1981), which would have been the preferred means of estimating genetic gains and accuracies of selection, was found not to be accurate for this purpose under certain conditions. There are a number of reasons for this. The RESI algorithm calculates a simplified form of an index which is a good approximation only

under certain circumstances: in particular, the plot variance components must be of negligible magnitude. If these components are other than negligible there will be errors in the estimates (Birks[1] pers. comm.). RESI also makes the assumption that there are equal numbers of half-sib families for each individual. This assumption, if violated, affects the covariances in which effects of the half-sib families are included. It would have been possible to run the program for each of the different numbers of half-sibs but this would be difficult in practice, as each of the full-sib families have varying numbers of half-sib families associated with them. The structure of the program is also problematic in this regard; the program input files restrict the amount and nature of information which the program is able to accept, making it difficult to adjust for the circumstances outlined above. RESI is useful for the calculation and comparison of a large number of alternative indices, as was done in Chapter 3, but it is not sufficiently exact for accurate evaluations such as that needed here.

This meant that it was necessary to perform calculations mainly by hand; consequently, pragmatism restricted calculation of genetic gains and accuracies of selection to one breeding objective and one site. Test 23a was chosen as it represented the largest number of families from which selection could be effected, and it was also the single most complete test. The methodology used is described in the following sections.

---

[1] Mrs J.S. Birks, Oxford Forestry Institute, Department of Plant Sciences, South Parks Road, OX1 3RB, UK.

The economic weight for the trait in the breeding objective (volume) was set to unity, so that the breeding objective corresponded to volume production. Selection in this study was based on diameter at five years, which was found in Chapter 3 to be the optimal age for selection. Diameter was used as the selection trait because it was found to result in the highest genetic gains in the breeding objective (see Chapter 3).

The genetic parameters used in this study are those estimated in Chapter 2 (Tables 2.12, 2.14, 2.16 and 2.17). The relevant parameters are summarised below, in Tables 4.3 and 4.4.

Table 4.3 Variance components (± standard errors) for diameter (DBH5) at five years and volume at 15 years (VOL15), estimated from progeny test 23a.

Source	DBH5	VOL15
Female	0.25±0.08	2514.1±708.3
Male	0.34±0.18	3057.5±1588.0
Fem x Male	0.06±0.02	1220.6±225.23
Fam x Rep	0.39±0.03	1098.5±379.7
Residual	1.94±0.03	18828.0±379.70

Table 4.4 Heritabilities and associated standard errors (bold on diagonal) of diameter at five years and volume at 15 years, and genetic (± se) and phenotypic correlations (above and below diagonal, respectively) between diameter at five years and volume at 15 years, estimated for test 23a from maternal components of variance.

Trait	DBH5	VOL15
DBH5	**0.33±0.10**	0.92±0.04
VOL15	0.61	**0.38±0.10**

4.3.1 - Genetic gains from selection based on individual information alone

Genetic gains from selection based on individual information alone were estimated following Falconer (1981) as in Equation (4.2):-

$$G = ih_x h_y r_{xy} \sigma_{ay} \tag{4.2}$$

where i = selection intensity, assumed to be 2.665 (1:100);

h_x, h_y = square root of the heritability for diameter and volume, respectively;

r_{xy} = correlation between diameter and volume;

σ_{ay} = square root of the additive genetic variance for volume.

4.3.2 - Genetic gains from selection based on both individual and sibling information

Genetic gains from indices including information from both individuals and siblings (either full-sibs alone, or both full and half-sibs) were calculated following White and Hodge (1989). In summary, their estimation requires derivation of variance and covariance matrices for the traits of interest, as described below.

The **V** matrix (matrix of variances for the selection trait, diameter) when individual and full-sib family information are used, was constructed and calculated as follows:-

$$V = \begin{bmatrix} var(y_{ijkl}) & cov(y_{ijkl}, \bar{y}_{ijk}) \\ cov(y_{ijkl}, \bar{y}_{ijk} & var(\bar{y}_{ijk}) \end{bmatrix} \tag{4.3}$$

The **V** matrix for individual, half-sib and full-sib family information was constructed and calculated as follows:-

$$V = \begin{bmatrix} var(y_{ijkl}) & cov(y_{ijkl}, \bar{y}_{ijk}) & cov(y_{ijkl}, \bar{y}_{ik}) \\ cov(y_{ijkl}, \bar{y}_{ijk} & var(\bar{y}_{ijk}) & cov(\bar{y}_{ijk}, \bar{y}_{ik} \\ cov(y_{ijkl}, \bar{y}_{ik}) & cov(\bar{y}_{ijk}, \bar{y}_{ik} & var(\bar{y}_{ik}) \end{bmatrix} \quad (4.4)$$

where $var(y_{ijkl})$ = phenotypic variance of diameter;

$var(\bar{y}_{ijk})$ = full-sib family variance = $\sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_{fmr}/b + \sigma^2_e/nb$

= $cov(y_{ijkl}, \bar{y}_{ijk})$;

where σ^2_f = variance due to the female parent;

σ^2_m = variance due to the male parent;

σ^2_{fm} = variance due to the female x male interaction (family);

σ^2_{fmr} = family-block interaction variance;

b = number of blocks, here = 6;

σ^2_e = error variance or within plot variance;

n = number of individuals per block, here = 10;

$var(\bar{y}_{ik})$ = half-sib family variance;

$cov(y_{ijkl}, \bar{y}_{ijk})$ = covariance between the individual and full-sib family means;

$cov(y_{ijkl}, \bar{y}_{ik})$ = covariance between the individual and half-sib family variance;

$cov(\bar{y}_{ijk}, \bar{y}_{ik})$ = covariance between the full-sib and the half-sib family means.

The mean of the half-sib families was estimated as follows:-

$$\bar{y}_{ik} = \frac{(m-1)\bar{y}_m + (f-1)\bar{y}_f}{(m+f-2)} \quad (4.5)$$

where $\bar{y}_{ik}$ = mean of the mean of half-sib families;

$\bar{y}_m$ = mean of the mean for diameter based on male parents;

$\bar{y}_f$ = mean of the mean for diameter based on female parents;

m = number of male parents;

f = number of female parents.

In this case, there are (m+f-2) half-sib families with (f-1) common females and (m-1) common males. As the number of half-sibs related to each female and male parent was variable, the average number was used here, (30 per full-sib family, that is, 9 related through the male parent and 21 through the female parent). The variances due to the half-sib families related through the female parent and the half-sib families related through the male parents were estimated as in Equation (4.6):-

$$var(\bar{y}_f) = \sigma^2_f + \frac{(\sigma^2_m + \sigma^2_{fm} + \sigma^2_w)}{(m-1)} + \frac{\sigma^2_e}{nb(m-1)} \qquad (4.6)$$

where σ^2_w = the remainder of the genetic variance plus all the environmental variance.

$$var(\bar{y}_m) = \sigma^2_m + \frac{(\sigma^2_f + \sigma^2_{fm} + \sigma^2_w)}{(f-1)} + \frac{\sigma^2_e}{nb(f-1)} \qquad (4.7)$$

Therefore, the variances of the half-sib families were estimated as follows:-

$$var(\bar{y}_{ik}) = \frac{(m-1)^2\ var(\bar{y}_f) + (f-1)^2\ var(\bar{y}_m)}{(m+f-2)^2} \qquad (4.8)$$

The covariances between the full-sib family means, and half-sib families with the male parent or female parent in common, were estimated as:-

$$cov(\bar{y}_{ijk}, \bar{y}_f) = \sigma_f^2 \quad (4.9)$$

$$cov(\bar{y}_{ijk}, \bar{y}_m) = \sigma_m^2 \quad (4.10)$$

$$cov(\bar{y}_{ijk}, \bar{y}_{ik}) = \frac{(m-1)\,\sigma_f^2 + (f-1)\,\sigma_m^2}{(m+f-2)} \quad (4.11)$$

Covariances between the individual phenotypes, and the half-sib families with the female parent in common or the male parent in common, were expressed and calculated as follows:-

$$cov(y_{ijkl}, \bar{y}_f) = \sigma_f^2 \quad (4.12)$$

$$cov(y_{ijkl}, \bar{y}_m) = \sigma_m^2 \quad (4.13)$$

$$cov(y_{ijkl}, \bar{y}_{ik}) = \frac{(m-1)\,\sigma_f^2 + (f-1)\,\sigma_m^2}{(m+f-2)} \quad (4.14)$$

$$cov(y_{ijkl}, \bar{y}_{ijk}) = var(\bar{y}_{ijk}) = \sigma_f^2+\sigma_m^2+\sigma_{fm}^2+\sigma_{fmr}^2/b+\sigma_e^2/nb \quad (4.15)$$

The second matrix constructed, **C**, consisted of the covariances between the selection trait, diameter at 5 years, and the breeding objective, volume at 15 years. The **C** matrix including individual and full-sib family means was

constructed and calculated as follows:-

$$C = \begin{bmatrix} cov(H, y_{ijkl}) \\ cov(H, \bar{y}_{ijk}) \end{bmatrix} = \begin{bmatrix} 2\,(cov_f + cov_m) \\ \frac{nb-1}{nb}\,(cov_f + cov_m) \end{bmatrix} \quad (4.16)$$

The **C** matrix including individual, full-sib and half-sib family means was constructed and calculated as follows:-

$$C = \begin{bmatrix} cov(H, y_{ijkl}) \\ cov(H, \bar{y}_{ijk}) \\ cov(H, \bar{y}_{ik}) \end{bmatrix} = \begin{bmatrix} 2\,(cov_f + cov_m) \\ \frac{nb-1}{nb}\,(cov_f + cov_m) \\ \frac{(m-1)\,cov_f + (f-1)\,cov_m}{(m+f-2)} \end{bmatrix} \quad (4.17)$$

The b coefficients were calculated as in Equation (4.18):-

$$\beta = P^{-1}Aw = V^{-1}Cw \quad (4.18)$$

where β = vector of index coefficients;

P^{-1} = inverse of the phenotypic variance-covariance matrix;

A = matrix of additive genetic variances and covariances;

$\mathbf{V}^{-1}$ = the inverse variance-covariance matrices;

C = the covariance matrix defined above;

w = vector of economic weights.

The accuracy of selection was estimated as in Equation (4.19), following Falconer (1981) :-

$$\rho A = \sqrt{\frac{C' V^{-1} C}{\sigma_a^2}} \quad (4.19)$$

where ρA = accuracy of selection;

$\mathbf{C}'$ = transpose of the covariance matrix;

V^{-1} = inverse of the variance-covariance matrix;

C = covariance matrix;

σ^2_a = additive genetic variance for volume.

Genetic gains per year in the breeding objective were estimated as follows:-

$$\Delta H = \frac{i \,.\, C' \boldsymbol{\beta} \,.\, \sigma_I / \sigma_I^2}{T} \quad (4.20)$$

where $\mathbf{C}'$ = transpose of the C matrix;

β = vector of weights;

σ_I = phenotypic standard deviation of the index I;

σ^2_I = variance of the index;

i = selection intensity, here assumed to be 2.665 (1:100);

T = generation interval for selection, here estimated as 13, *ie*, allowing five years to the time of selection and eight years from the time of parent selection to establishment of the next generation.

The variance of the index was estimated as follows:-

$$\sigma_I^2 = C' V^{-1} C \quad (4.21)$$

and the standard deviation of the index as:-

$$\sigma_I = \sqrt{C' V^{-1} C} \tag{4.22}$$

4.3.3 - Construction of indices

Trees were selected for breeding objective H based on all three indices. Data were first block-adjusted, following Cotterill and Dean (1990), as in Equation (4.23):-

$$P^* = P + (\boldsymbol{P} - \boldsymbol{B}_x) \tag{4.23}$$

where P^* = the block adjusted diameter;

$\mathbf{P}$ = each tree's measured diameter;

$\mathbf{P}$ = overall trial mean;

$\mathbf{B}_x$ = mean of block in question.

The index value of each tree from selection based on the index including individual information only was calculated as follows:-

$$I_1 = P^* \tag{4.24}$$

The index value of each tree from selection based on individual and full-sib family information was calculated as follows:-

$$I_2 = b_1 P^* + b_2 F \tag{4.25}$$

The index value of each tree from selection based on individual and full-sib and half-sib family information was calculated as follows:-

$$I_3 = b_1 P^* + b_2 F + b_3 HF \tag{4.26}$$

where b_i = the index coefficient;

P^* = the adjusted phenotypic value of each tree;

F = full-sib family mean value;

HF = half-sib family mean value.

The index values for all trees were ranked and the 60 highest ranking individuals were selected.

4.3.4 - Effect of selection on the family variance

The methodology outlined by Bulmer (1980, Chapter 9) was used to estimate the effect of selection on the additive genetic family variance after one generation of selection. The methodology is briefly outlined below.

Several assumptions must be made in order to calculate the changes in genetic variance. Any departures from normality before selection are unimportant and are therefore ignored. It is assumed that the character under study "is

determined by a large number of loci with individually small and additive effects" (Bulmer 1980). From the above, the normal distribution theory can justifiably be assumed, *ie*, "the joint distribution of genotypic (or phenotypic) values among relatives is multivariate normal" (Bulmer 1980).

The additive variance after one generation of phenotypic selection in the progeny may then be estimated as:-

$$Var(A^*) = (1-\frac{1}{2}h^2k)\,Var(A) \qquad (4.27)$$

where Var(A*) = additive genetic variance after one generation of selection;

h^2 = heritability;

k = i(i-x);

i = selection intensity;

x = truncation point (1%);

Var(A) = the genetic variance before selection.

The additive variance after one generation of index selection in the progeny may then be estimated as:-

$$Var(A^*) = (1-\frac{1}{2}r^2k)\,Var(A) \qquad (4.28)$$

where r = accuracy of selection, and Var (A*), h^2 and k are as defined above.

Changes in the genetic variance for varying selection intensities and hence varying k values, were estimated in order to investigate the effect of increasing

or decreasing the intensity of selection on genetic variance after one generation of selection. The varying selection intensities and corresponding k values are listed in Table 4.5.

Table 4.5 The selection intensities and corresponding k values used to study the effect of selection intensity on the family variance.

Selection intensity	k
2.421 (1:50)	0.889
2.665 (1:100)	0.903
2.800 (1:150)	0.910
2.892 (1:200)	0.914
2.962 (1:250)	0.918

4.4 - Results

Expected genetic gains and accuracies of selection for H, for a selection intensity of 2.665 (1:100), from selection based on I_1 - including individual information only, I_2 - individual and full-sib information, and I_3 - individual, full and half-sib information - are presented in Table 4.6.

Table 4.6 Genetic gains expected per year in dm^3 and percentage gain per generation (bracketed) from selection based on I_1, I_2 and I_3 at an intensity of 1:100 (2.665). The table also shows the accuracies of selection (r_{IH}).

Index No	Gains in H	Accuracy of selection (r_{IH})
I_1	0.148 (46.3)	0.72
I_2	0.165 (51.6)	0.80
I_3	0.168 (52.5)	0.83

Differences in the amount of information included in the index resulted in differences in the response to selection. The selection index including all available information, I_3, resulted in the highest genetic gains and accuracies of selection. The difference between genetic gains obtained from selection based on I_2 *vs* I_3 was small (approximately 2%); differences between I_1 *vs* I_2 and I_1 *vs* I_3 were greater, at 10.3 and 11.9%, respectively. Genetic gains per generation followed the same trend. Differences between accuracies of selection followed a similar pattern, with little difference (4%) between I_2 *vs* I_3, but larger differences between I_1 *vs* I_2, (27.3%) and between I_1 *vs* I_3 (30.7%).

Table 4.7 lists the 60 highest ranking individuals from selection based on each of the three indices, and their corresponding ranks.

Table 4.7 A comparison of trees selected for breeding objective H from selection based on I_1, I_2 and I_3 at an intensity of 1:100 (2.665).

I_1				I_2				I_3			
Family	Replicate	Tree	Rank	Family	Replicate	Tree	Rank	Family	Replicate	Tree	Rank
5302	1	9	1	6095	2	2	1	6010	5	3	1
6132	3	9	2	6132	3	9	2	6010	6	10	2
6096	2	2	3	6010	5	3	3	6132	3	9	3
6033	4	9	4	6010	6	10	4	6096	2	2	4
6010	5	3	5	6095	1	1	5	5302	1	9	5
6010	6	10	6	5302	1	9	6	6095	1	1	6
6029	1	3	7.5	4990	4	1	7	6010	1	5	7
6095	1	1	7.5	6010	1	5	8	6010	2	5	8
6029	4	5	9	6010	2	5	9	4990	4	1	9
5241	6	1	10	5293	1	10	10	4990	1	7	10
4990	4	1	11.5	4990	1	7	11	5298	1	10	11
4997	4	7	11.5	5298	2	1	12	5298	2	1	12
6090	2	6	13	5238	3	10	13	6010	5	9	13
6139	3	2	14	6033	4	9	14	6123	2	2	14
4990	1	7	15	6096	1	3	15	6139	3	2	15
5238	3	10	16	6029	1	3	16	6010	4	5	16
5212	2	6	17	6123	2	2	17	5238	3	10	17
5298	1	10	18	6010	5	9	18	4990	3	3	18
5293	2	1	19	6029	4	5	19	6132	1	2	19
6010	1	5	21	5298	6	8	20	5298	6	15	20
6051	1	8	21	6139	3	2	21	6096	1	3	21
6132	1	2	21	6010	4	5	22	6123	1	4	22
6010	2	5	23.5	4990	3	3	23	4997	4	7	23
6123	2	2	23.5	6090	2	6	24	6132	3	1	24
5325	1	7	25	6132	1	2	25	5298	5	8	25
4990	3	3	27	4997	4	7	26	6132	3	3	26
6053	3	6	27	5212	2	6	27	6090	2	6	27
6132	3	1	27	5298	5	8	28	6096	3	9	28
5298	6	8	29	6095	3	9	29	6123	2	8	29
6095	1	3	30	6123	1	4	30	6132	1	10	30
6034	5	1	31	6132	3	1	31	5298	5	7	31.5
6132	3	3	32	5241	6	1	32	6010	6	2	31.5
5302	1	7	33.5	6132	3	3	33	6000	5	6	33
6123	1	4	33.5	5238	1	6	34	5302	1	7	34
6010	5	9	35	5298	5	7	35	6010	5	6	35
4999	4	4	36	6132	1	10	36	5241	6	1	36
5754	1	4	37.5	5293	3	6	37	6123	2	6	37
6132	1	10	37.5	6123	2	8	38	5238	1	6	38
5298	5	8	40	6000	5	6	39	5298	3	6	39
5302	5	4	40	6010	6	2	40	6010	5	5	40
5303	5	4	40	6123	2	6	41	6010	4	4	41
6010	4	5	42.5	6010	5	6	42	5302	5	4	42
6054	4	2	42.5	5303	5	4	43	6000	1	3	43
6090	2	7	44	6096	5	7	44	5303	5	4	44
5238	1	6	45	6096	3	1	45.5	5212	2	6	45
5302	5	8	46.5	6096	3	7	45.5	5302	5	8	46
6095	5	7	46.5	5302	1	7	47	6132	3	5	47
6095	3	9	48	5238	1	4	48.5	6010	4	8	48.5
5722	6	9	49	5238	1	10	48.5	6010	4	10	48.5
6072	1	8	50	6132	3	5	50	6123	4	3	50
6113	4	5	51	5298	5	10	51	6139	1	3	51
5212	2	4	53.5	6000	1	3	52	5298	5	10	52
5728	2	10	53.5	6010	5	5	53	4990	2	5	53
6004	2	7	53.5	6010	4	4	54	6095	5	7	54
6123	2	8	53.5	5238	6	2	55	6096	3	1	55.5
5724	6	3	56	6090	2	7	56	6096	3	7	55.5
5298	5	7	57.5	5302	5	4	57	6000	3	3	57
6000	5	6	57.5	5238	5	4	58	6033	4	9	58
6132	3	5	59	6096	2	6	59	5238	1	4	59.5
6090	2	9	60	4990	2	5	60	5238	1	10	59.5

Table 4.8 shows the number of families from which individuals were selected for each of the three indices and the proportion of common families and individuals selected by the three indices at an intensity of 2.665 (1:100).

As might be expected, the index which used only individual information, I_1, selected individuals across the greatest number of families (32); conversely, the index which used all available family information, I_3, selected individuals in only 15 families, 53% fewer than I_1. The commonality between individuals selected and families represented was greatest between the two indices incorporating family information, I_2 and I_3, and least between indices with least information in common (I_1 and I_3).

Table 4.8 The number of families represented in the population selected by each of the three indices (bold on diagonal) and the percentage of common families (above diagonal) and trees (below diagonal) selected for H based on I_1, I_2 and I_3.

Index number	I_1	I_2	I_3
I_1	**32**	59	50
I_2	72	**19**	84
I_3	67	92	**15**

As might also be expected, selection based on the index which incorporated all available family information (I_3) led to the greatest number of selections within families (up to 12), whereas use of the index (I_1) based only on individual information led to selection of the fewest individuals per family (a

maximum of 6).

The phenotypic (k) and the additive family variances remaining after one generation of selection on either I_1, I_2 and I_3, at varying selection intensities, are presented in Table 4.9. Additive family variances are expressed both in absolute terms and as a percentage of the variance prior to selection.

As expected, losses in additive variance were highest for selection based on the most complete index (I_3) and lowest for selection based on the index with individual information only (I_1). Only 50% of the initial additive variance remained after one generation of selection on I_3, whereas 83% remained after one generation of phenotypic selection. Increasing the intensity of selection increased losses of genetic variance from selection on all three indices.

Table 4.9 The phenotypic (k) and the additive family variances remaining after one generation of selection on either I_1, I_2 and I_3, at varying selection intensities.

		Additive genetic variance after one generation of selection					
		In absolute units			As a percentage		
		Index number			Index number		
Selection intensity	k	I_1	I_2	I_3	I_1	I_2	I_3
2.421	0.889	8357.8	7739.1	5027.6	83.1	77.0	50.0
2.665	0.903	8331.0	7702.6	4948.4	82.8	76.6	49.2
2.800	0.910	8317.7	7684.4	4908.8	82.7	76.4	48.8
2.892	0.914	8310.0	7674.0	4886.1	82.6	76.3	48.6
2.962	0.918	8302.4	7663.5	4863.5	82.6	76.2	48.4

Additive genetic variance before selection was estimated at 10056.4.

4.5 - Discussion

4.5.1 - Response to and accuracy of selection

As expected, phenotypic selection yielded the lowest genetic gains and accuracies of selection, a consequence of selection being based only on the phenotypic value of the individual. Although many of the control-pollinated mating designs commonly used in tree breeding programmes generate both full and half-sibs families, information from both types of relatives is seldom included in the analyses. This results in lower genetic gains and accuracies of selection than would follow from the use of all available information. Including both full and half-sib information in the index resulted in the highest genetic gains and accuracies of selection. At the low heritabilities evident here, and typical of many traits of interest to tree breeders, information from relatives contributes greatly to the selection decision, much more so than for evaluation of individuals for traits of high heritability (Nicholas 1987). In this case, the increase in genetic gains and accuracies of selection from the inclusion of half-sibs in the index was small. This may be because the number and size of full-sib families analysed was large and the inclusion of half-sib information added relatively little additional information. It has been estimated that for a trait with a heritability of 0.1, information from at least 5 full-sibs or 26 half-sibs are needed for sib selection to be as accurate as selection based on a single measurement of a candidate's own performance (Nicholas 1987). Although the difference in genetic gains obtained from the

index including individual, full and half-sib information over that including individual and full-sib information was small, it has been reported that gains of between two and a half to four percent have been used to justify entire breeding programmes (Davis 1967). These additional genetic gains do not involve any extra costs, other than those associated with the construction of more sophisticated indices; there seems, therefore, no reason to forgo them. The use of this additional information also improves the efficiency of selection in terms of genetic gain per unit cost.

It has been noted that as well as incorporating a large amount of information on relatives, the accuracy of selection may also be increased by achieving greater control of the environment (Woolliams 1990). This results in a lower environmental variance leading to a greater accuracy of selection. However, forest environments are difficult to control and, instead, increased accuracy is usually achieved by increasing the number of replications on a site and across sites, thereby sampling as many environments as possible. Reducing measurement errors and having an efficient field design that facilitates testing of a large number of individuals to be tested will similarly improve accuracy (Woolliams 1990).

The mating design used will influence the genetic gains made in each generation through the type of data it makes available for analyses as well as through the breeding population it generates. Poor mating designs, with respect to the number of crosses completed and the degree of balance, result

in poor estimates of genetic parameters (Namkoong and Roberds 1974) and, hence, sub-optimal responses to selection. Different mating designs are optimal for different purposes. Although the factorial design is not the most efficient design with regard to the estimation of genetic parameters and generation of genetic gains, the design is reliable for the provision of both (Namkoong and Roberds 1974, van Buijtenen 1976). The factorial mating design used to generate the individuals analysed in this study was originally selected to emphasise progeny testing and estimation of reliable genetic parameters. As selection in the Zimbabwean tree breeding programme has mainly been on a family/within family basis, where family mean information is used to determine those families in which individuals will be selected phenotypically, the factorial scheme was adequate for fulfilling these objectives. The efficiency of the mating design, in terms of generating expected genetic gains, was only a subsidiary consideration.

The extra information given by the factorial design, in the form of half-sibs, means that the efficiency of the mating design with respect to generating genetic gains can be further enhanced, as evident from this study. Further, van Buijtenen and Burdon (1990) found little difference between balanced factorial and diallel mating designs in terms of efficiency of estimation of genetic parameters and generation of genetic gains; they demonstrated that the latter design was marginally more efficient. The results of this study show that efficiency of generating genetic gains and accuracies of selection can be increased by the use of information from relatives, even when data are

obtained from a mating design which is not optimal for these purposes.

4.5.2 - Consequences of selection for levels of genetic variance

When individuals that do not meet the required criteria are discarded from breeding populations, there are permanent changes in gene frequencies, which cannot be returned to the original state even when selection is relaxed. As Bulmer (1971) demonstrated, recurrent selection in a population, will reduce the genetic variance to a level beyond which the population no longer responds to selection. For this reason, the effect of selection on genetic variance is of particular interest. However, the rate at which the additive variance is decreased depends on the method and intensity of selection, as was observed in this study.

Reductions in variance under phenotypic selection are due solely to changes in heritability (Bulmer 1980, Dekkers 1992), and will therefore be at a lower rate than in index-selected populations. Under phenotypic selection, the reduction in variance increases with heritability, on which the accuracy of selection is solely dependent. Under index selection, the reduction is influenced by both heritability and the accuracy of selection. Accuracies of selection from index selection are generally higher than those from phenotypic selection because of the emphasis placed on family information (Dekkers 1992); hence, losses of genetic variance are greater. For a trait of high heritability, therefore, the reduction in genetic variance due to selection will be larger

(Bulmer 1971), whether under phenotypic or index selection.

The loss of genetic variance increases the importance of differentiating between an individual and its relatives (as opposed to using information from relatives to help differentiate between the individual's family and other families) (Woolliams[2] pers. comm.). The loss of variance means also that those genes that occur in low frequencies may be lost from the population. When selection is from a large unselected population, it is the first generation of selection that is critical with regard to losing or retaining genes of low frequencies. After a generation of selection, the frequencies of the favoured genes are expected to increase, and their chances of being lost decreases. For the maintenance of genotypes, therefore, the numbers that are retained depends on the number of generations through which the population of interest has passed. If selection has been effected over many generations, then the numbers that need to be retained are small, as most genes of interest will be present in sufficiently high frequencies. However, if the population has not undergone any selection, or is in its early generations of selection, more individuals should be retained as most genes will still be in low frequencies (Robertson 1960). This highlights the importance of maintaining large population sizes in tree improvement programmes; as most have only been through one generation of selection, it is therefore likely that some genes of interest are still at low frequencies and therefore in danger of being lost forever.

---

[2] Mr. J. Woolliams, AFRC Institute of Animal Physiology and Genetics Research, Roslin, Midlothian EH25 9PS, UK.

The lower numbers of families from which individuals originated under index selection further illustrate the rate at which family genetic variance is reduced through intensive selection, as a function of the emphasis placed on family information in index selection. The dilemma which the breeder faces between obtaining high genetic gains and maintaining high genetic variance (diversity), on which further selection is to be based, is well illustrated by Robertson's (1960) comment: "individuals of one generation are the parents of the next - if they are accurately evaluated and selected in the first generation, the variation between families will be reduced in the next. You cannot have your cake and eat it".

Lower levels of additive genetic variance lead to inbreeding (Nicholas 1987), the potential for which increases with each generation of selection. The rate at which inbreeding sets in is dependent on the frequency with which relatives are chosen (Woolliams 1989). In tree populations, a generally high level of heterozygosity has been reported as necessary for vigorous growth (Ledig *et al* 1983). Inbreeding depression has been reported in Pinaceae (Geburek 1986), where it has been found to affect both germination and survival (Franklin 1970, Libby *et al* 1981) and subsequent growth (Geburek 1986). The effects of self-pollination on *P. radiata* reported by Wilcox (1983) are probably typical; the inbred progeny were shorter and thinner, and had more crooked stems and poorer branching than did outcrossed progenies. Similar effects have been reported for *P. elliottii* (Gansel 1971, Layton and Goddard 1983). Inbreeding effects may not be adverse for all traits: in Wilcox's study, for example, wood

density was not affected by inbreeding. These empirical results suggest that the loss of variance in breeding populations are likely to cause serious problems for the breeder, and the level of variation in the population must be monitored and maintained at a sufficiently high level.

4.5.3 - Addressing the dilemma

One of the reasons that maintenance of diversity in the breeding population is important is because trees have relatively long generation intervals, and the variation of breeding objectives is only possible in the long run if the alleles that are needed for future breeding are retained in the population (Namkoong and Roberds 1982). However, intensive tree improvement programmes will be working to maximise short-term genetic gains in both the breeding and production population because it is these gains that determine the economic value of the programme, for example, as estimated by discounted cash flow analyses (White in press). The consequent reductions in the effective population size[3] (N_e) and the genetic variance will, however, prejudice maintenance of gain in the longer term. Thus, as both short and long-term breeding are essential to most tree breeding programmes, compromises must be made between the maintenance of diversity and achievement of high genetic gains. In terms of this discussion, there is a contrast between index

[3] Effective population size is the "theoretical number that reflects relatedness among numbers of the breeding population", in contrast to the census number which is the "mean total number of selections retained in the breeding population in any given generation" (White in press).

selection - the genetic accuracy of which returns higher genetic gains in the short-term, and more quickly reduces the additive genetic variance - and phenotypic selection which returns lower genetic gains in the short-term but maintains high levels of diversity in the breeding population. As stated by King and Johnson (1993) "There is no single solution to the trade-off between maintaining genetic diversity and maximising gain within the framework of a fixed resource". Various suggestions have been made by both animal and tree breeders as to how to obtain both high genetic gains and to maintain diversity.

The type of mating design used will influence the degree of relationship between individuals, and hence the effective population size. Namkoong and Roberds (1974) reported that factorial designs are not sufficiently robust to develop breeding populations, because they generally act to decrease the effective population size through the mating of a few male parents to a larger number of female parents. Increasing the number of parents means that the number of crosses that must be completed become much larger, resulting in longer generation intervals and reduced genetic gains. Using a combination of designs as suggested by Burdon (in press), will allow both the generation of a large number of unrelated individuals through designs such as, the open-pollinated and single-pair mating schemes and intensive mating of those individuals with high breeding values through designs such as positive assortative mating (Lindgren 1986). King and Johnson (1993) found that greater genetic gains per generation followed use of a positive assortative

mating design, but that this strategy substantially reduced the effective population size. They recommended the use of a mating design which produced large numbers of crosses for selection as this afforded more flexibility in terms of achieving both short and long-term genetic gains.

Generally, maintaining a base population of no less than 300 individuals has been recommended for advanced generation breeding (Namkoong 1984, Namkoong *et al* 1988, Namkoong and Roberds 1982, White in press). A large population size will allow both intensive breeding for high genetic gains and maintenance of genetic variance, as the effective population size will be large and, therefore, reductions in genetic variance low. In cases where it is not feasible to manage a large population due to financial and/or management constraints, infusions from other breeding programmes or from related populations may be introduced into the programme. This will increase the genetic variance but, depending on the level of improvement of the infused material, it may lower genetic gains in the short-term. To avoid this problem, infusions could be improved before they are incorporated into the breeding population (Cotterill *et al* 1989).

Lower selection intensities have been recommended as a way of preserving genetic diversity; for example, a selection intensity of 0.8 (1:2) was recommended as optimal for maintaining diversity to ensure long-term genetic gains (Dempster 1955, Smith 1969, Askew and Burrows 1983). However, this selection intensity is much lower than that used by most tree improvement

programmes (White in press); such a low selection intensity would compromise short-term genetic gains and is therefore not an economically feasible option.

To lessen reductions in genetic variance it is necessary to restrict the number of individuals selected per family (Cotterill and Dean 1990) and, hence, for a given population size, increase the number of families selected. As index selection emphasises family mean performance for a trait of low heritability, decreasing the weighting on the family mean should result in fewer individuals being selected from the same families. However, using a combination of lower selection intensities and reduced emphasis on the family mean will lead to lower genetic gains. Thus, a combination of working with a large population size, restricting the number of individuals selected per family, and reducing the family weighting in the index is seen to be a better option than using any of these solutions alone (White in press).

The results of this study have shown the significant benefits of using index selection in terms of increasing genetic gains and accuracies of selection, but also the disadvantage in terms of high losses of genetic variance sustained. In practice, however, a breeding programme is only tenable if it returns near maximum gains in the short-term. This result suggests that the most complete index, delivering the greatest genetic gains, should be used. The problem, therefore, is how to maintain diversity.

Maintenance of genetic diversity should be achieved by retaining not only a large census number but by also ensuring a large effective population size. In the population studied, although the number of families from which selection was effected was large, the parental population was relatively small, comprising only 33 individuals. In this case, a large census number, in the region of 300 to 400 as suggested by, for example, White (in press) is necessary to address this problem.

Use of a combination of mating designs can be achieved through the use of a breeding strategy which allows differential breeding in different sections of the population. Structures such as the multiple-population breeding strategy and the nucleus breeding strategy are appropriate. Detailed development of these structures is beyond the scope of this thesis, but relevant issues will be discussed briefly in Chapter 5.

It is also evident that the numbers selected per family for the next generation of breeding must be restricted to limit the number of relatives in the next generation. White *et al* (in press) recommend selection of a maximum of seven individuals per family for the Florida breeding population of *P. elliottii*. For a given number of parents, this will have the effect of increasing the number of families from which selections are made.

4.6 - Conclusions

Efficient selection is not only a matter of early selection as discussed in Chapter 3, but also of efficient use of information from relatives. The index including all available information - from individuals, half-sibs and full-sibs - resulted in the highest genetic gains, although these were only marginally greater than those from the index including only individual and full-sib information. However, the difference between the accuracies of selection of the two indices was greater. As half-sib information is generated as a consequence of the mating design, its use does not incur any extra cost, and its incorporation in the index is therefore recommended.

The index including the largest amount of information also resulted in the largest reduction in additive genetic variance, the lowest number of families from which individuals were selected, and the highest number of individuals selected per family. Regardless of selection methodology, increasing the selection intensity always resulted in larger losses of genetic variance. The results show that increasing the response to selection and accuracy of selection is at the expense of genetic diversity.

The implications of these results could be substantial in terms of the response to selection in later generations. If additive variance were reduced greatly, then long-term genetic gains would be prejudiced. Loss of additive variance will limit the flexibility of the breeding programme responding to changing

breeding goals in the future, as alleles for the future traits of interest may no longer be available. With most forestry breeding programmes now entering their second generation of selection, selection within the parental population for advanced breeding will have to be performed with care to preserve genes that may be needed in the future. A combination of a large breeding population size and a structure that allows for differential breeding methods would allow for the attainment of both objectives. Restriction of the number of individuals selected per family would also be desirable. The results reported here should apply generally to other tree breeding programmes.

Chapter 5 -

5 - Conclusions

The aims of this thesis have been to estimate genetic parameters and use these in selection indices to optimise selection for a Zimbabwean breeding population of *P. elliottii*. This Chapter summarises the major results of the study and discusses their implications.

5.1 - Genetic parameter estimates

Of the three sites established as part of the trial series on which analyses were based, only two tests, 23a and 23b, yielded useful information. Test 23c was planted off-site to facilitate the study of genotype-environment interaction; however, the relatively small number of families represented, the unbalanced design from which they originated, and the poor development of trees at the site, limited analysis and interpretation of data from this test site. Genetic parameters estimated from test 23c were imprecise in comparison to those estimated from sites 23a and 23b. It is apparent with hindsight that a greater number of families from a more balanced design would have been desirable

were a test at site 23c to yield much useful information. Conversely, tests 23a and 23b could have been planted with fewer individuals per family without prejudicing the estimates of genetic parameters. It has been reported elsewhere in the literature (Cotterill and James 1984) that half the number of individuals per family as those used in these tests is adequate for estimation of genetic parameters, although the constraints imposed on selection by limited sample size (Magnussen and Yanchuk 1993) should also be borne in mind. Thus, a more balanced distribution of the experimental material would have yielded information of equal reliability in all tests.

High genetic variability, as judged by the magnitude of genetic variances, was found to exist in the population studied. Growth traits, wood density and resin yield were found to be under moderate to strong additive genetic control; stem straightness and branching traits were under less additive genetic control, although the magnitude of the heritability estimates nevertheless suggests a substantial response to selection. The estimates are consistent with those reported elsewhere for corresponding traits of industrial species.

Additive genetic variances were found to be much greater than non-additive genetic variances for all traits but branch diameter; the ratios of additive to non-additive genetic variance for growth traits and stem straightness agreed well with other published estimates for pine species. The results suggest that additive genetic effects are the most important in the control of all traits measured, with the probable exception of branch diameter.

Generally, estimates of heritabilities derived from the male parents used in the factorial mating design were higher and were associated with larger standard errors than those derived from the female parents. The inflated standard errors of estimates associated with male parents are a result of the smaller number of male parents tested, and are a common problem where factorial mating designs are used; similar results have been reported in the literature. In this case, estimates from the female parents were assumed to be more accurate, and were used as the basis of subsequent analyses.

Genetic correlations between growth traits were found to be high, with low standard errors, while those between each of diameter and volume with wood density were negative. Those between height and wood density ranged from low negative to low positive values. Juvenile-mature correlations between growth traits, and between growth traits and wood density, followed the same pattern. Standard errors associated with these correlations, and those between branch traits *vs* growth traits, stem straightness and wood density, were generally high. These results are not inconsistent with those reported for *P. elliottii* and other industrial species in the literature. The high juvenile-mature correlations between growth traits indicated the possibility of early selection, at least for yield. This result is important in terms of reducing the generation interval and, therefore, increasing responses to selection on a per unit time basis. Genetic correlations between resin yield and each of height and diameter were low, but those between resin yield and stem straightness were high.

In this study, as in many breeding programmes, there was a need to estimate genetic parameters, and hence genetic gains, which could be widely applied. To this end, data were pooled from the two larger tests, 23a and 23b, and analysed as a single data set. A large pooled data set not only results in a representative set of genetic parameters but, as reported by Cotterill and Dean (1990), should also increase the precision with which genetic parameters are estimated. This is because a larger data set gives more complete information on variation, therefore, allowing a more accurate partitioning of that variation. However, in this study, the precision of genetic parameter estimates was not substantially increased by the pooled analysis. This is principally because the individual data sets were already sufficiently large to yield reasonable estimates. However, the advantages of a widely applicable set of parameter estimates nevertheless remain. Estimates of genetic parameters from the pooled analyses were generally intermediate in magnitude between those from the individual site analyses, with equivalent or lower standard errors.

The residual maximum likelihood technique (REML), which was used to estimate genetic parameters in this study, has been proved to be optimal for the estimation of genetic parameters from unbalanced data (Huber *et al* 1992). However, the program is not without its draw-backs. It is expensive in terms of computer memory and time, especially if the data set being analysed is large and has several factors and interaction levels, as was the case in this study. The program used is at present also unable to estimate genetic correlations, and it was necessary to use another program, Least Squares Maximum Likelihood (Harvey 1987), for this purpose. This program was

found not to be as powerful as REML; it was unable to handle a large degree of imbalance and it was restrictive with regard to the number of models that could be executed, requiring the analyst to make a number of assumptions (for example, about the magnitude of interaction effects) which were sub-optimal.

5.2 - Genotype-environment interaction

Although the analyses of variance identified statistically significant genotype-environment interaction, the other methods used to assess its importance did not find it to be biologically important in the population studied. This result shows the importance of investigating genotype-environment interaction from the perspective that is of most relevance to the breeder. Although genotype-environment interaction has been found to be present to varying degrees in many industrial species, most of these studies have reported its statistical significance rather than its practical importance. However, there have also been reports of practically important genotype-environment interaction for other coniferous species.

The lack of important genotype-environment interaction in this population of *P. elliottii* has implications for the Zimbabwe Forestry Commission (ZFC), for whom financial constraints necessitate rationalisation of the research programme. It is likely that the number of tests will be reduced, and that the

range of sites over which testing is effected will be limited (Barnes[1] pers. comm.). Consequently, selections may have to be effected on one site for planting on several sites. The results of this study suggest that this will result in some losses in the efficiency of selection, which may be minimised by selection at sites where heritabilities are highest and, therefore, where there is a better resolution of genotypes. In the case of this trial series, given the limitations of site 23c, selection would be best carried out in test 23b; consequent losses in efficiency for planting on sites such as 23a would be minimal.

5.3 - Genetic gains expected from combined index selection

The breeding objectives considered in this study comprised various combinations of saw-timber and resin production, for the reasons discussed in **3.2.1**. Variable weighting of the traits in the breeding objectives influenced the genetic gains, accuracies and efficiencies of selection. Emphasising a trait which was poorly correlated with the selection trait did not result in high genetic gains, or in accurate or efficient selection. These results demonstrate the importance of correctly assigning economic weights, and of using a selection trait that is well correlated with the breeding objective, to obtain maximal genetic gains.

---

[1] Dr R.D. Barnes, Oxford Forestry Institute, Department of Plant Sciences, South Parks Road, OX1 3RB, UK.

It was evident from the analyses that the selection criterion of diameter at five years was optimal for improving saw-timber production, but that increasing resin yield required that this trait also be included as a selection criterion. Resin is not tapped until about half the rotation age; delaying selection until this age, to allow the inclusion of resin yield as a selection trait, would increase the generation interval by about 10 years. A number of alternative approaches to this problem are possible. One alternative is to identify a juvenile trait that is well correlated with resin yield. In this study, stem straightness at five years was found to be highly correlated with resin yield (r_a = 0.59). If resin production were to assume greater economic importance than at present, indices which include stem straightness would need to be constructed and compared - in terms of genetic gains, accuracies and efficiencies of selection - to those constructed in Chapters 3 and 4, to determine the index or indices representing the best compromise between saw-timber production and resin yield.

A second alternative would be to select for the two objectives at different stages (2-stage selection; Borralho *et al* 1992, Cotterill and James 1981). Saw-timber production could be selected for at an early age, and resin yield at a later age; selection at the earlier age would have to be at a lower intensity to ensure that individuals which will be selected at the later ages for resin yield are represented in this first stage sample. Following this option would necessitate maintenance of a larger number of selections than the first alternative, and this may not be feasible in the Zimbabwean breeding

programme. On this basis, the former alternative would be the most suitable for the Zimbabwean programme.

Genetic gains from indirect selection were highest from the index which included diameter. These high genetic gains from selection based on diameter were associated with losses in wood density, a result of the negative genetic correlations between these traits. Eventually, this reduction in wood density could be expected to reduce both saw-timber quality and cellulose yield in pulping (Borralho *et al* 1993). Although *P. elliottii* is not presently pulped in Zimbabwe, maintaining both wood quality and the pulping option for *P. elliottii* requires that the mean value of wood density should not be allowed to fall further. One means by which this problem could be addressed is through the use of height, rather than diameter, as a selection criterion. Height was found to be positively correlated with wood density and, although this correlation was low, use of height as a selection criteria would usually, result in the maintenance of wood density above the assumed minimum critical level. The losses of gain in the breeding objectives incurred by using height rather than diameter as the selection criterion were in the order of 2-7%. However, there is no justification for further emphasising wood density, for example by maintaining a separate breeding population for wood density as has been done elsewhere, because this trait is not presently valued by the market.

Genetic gains and efficiencies from indirect selection were higher from

selection at age five than at age eight, the two juvenile ages considered. Selecting at this early age will significantly reduce the testing phase of the breeding cycle, resulting in a shorter generation interval. It is not possible to investigate whether selection could be brought still further forward as there are no data for earlier ages. Work on earlier selection has been carried out elsewhere for several species, and some of these studies have reported promising results. In some cases, for example with *P. elliottii* in Florida, traits have been found that correlate well with the mature traits. There, strong correlations have been reported between seed weight components and seedling growth traits; correlations between seed weight components and field breeding values at five and 15 years were low but significantly greater than zero, while correlations between the embryo weight and predicted field breeding values for volume at five and 15 years were moderately high (CFGRP 1993). These results suggest that it may be possible to select for growth before seed is sown, but further investigations are clearly needed as the risk of poor genetic gains due to low accuracies of selection will be high.

The results of Chapter 3 showed that selection could be brought forward, from the present 8-10 years to five years, which will increase gains per unit time by at least 20%. This would also result in a substantial cost saving, as operations such as weeding, pruning and measurements could be ended early. However, early selection also involves risk, in terms of losses of genetic gain that could be sustained if selection decisions are poor. It has been suggested by Magnussen and Yanchuk (1993) that, to reduce such risks, a larger number of

individuals per family and families than ultimately required should be selected, to allow some margin of error. In the case of the ZFC, the feasibility of selecting more individuals and families than ultimately necessary, as opposed to selecting fewer individuals at later ages, would have to be assessed in monetary terms. However, in the present circumstances, where human and financial resources are restricted, it is unlikely that the breeding programme will be able to support the maintenance of large numbers of selections which will eventually be discarded from the programme. The high age-age correlations for growth evident here suggest that the degree of risk relevant to saw-timber production is not particularly high and that, consequently, there is little need to select more individuals than eventually needed.

Another problem with estimating the best age for early selection is that progeny tests are rarely carried to mature age, because of the cost involved. As a result, the performance of individuals beyond the age at which measurements are terminated has to be extrapolated. Whilst these correlations with mature performance are generally assumed to be positive, Franklin (1979) and Namkoong *et al* (1972) report circumstances in which they may be negative. Franklin (1979) noted that the problem of extrapolation can not be easily solved because, even when data are available on age-age correlations up to rotation age, there would still be questions about inter-genotypic competition and repeatability of growth records. In the case of the ZFC, measurements should be carried out to rotation age in selected tests to provide information on correlations between juvenile and true mature performance.

Such data are not currently available, but could be acquired with relative ease because, even though measurements are terminated at 15 years, these tests are subsequently maintained as part of the commercial plantation estate.

Magnussen and Yanchuk (1993) have also suggested that genotype-environment interaction should be integrated into the decisions about the age of early selection. As they pointed out, establishment on sites at which the age-age correlation structure is unknown will, for a given level of risk, lead to selection at older ages. As genotype-environment interaction was not found to be of practical importance in this study, its influence on the decision about the age of early selection should be of minimal consequence here. However, if areas such as that where test 23c is located were to be afforested commercially, this issue would require further investigation.

5.4 - Index selection

The high returns from index selection observed in this study demonstrate its potential for use in the Zimbabwean *P. elliottii* breeding programme. Selection on the basis of an index has been demonstrated to be superior to that on a family/within family basis (Cotterill 1986b, Cotterill and Dean 1990), the method presently used by the ZFC.

The major limitation of index selection is the lack of economic and genetic information on some traits, which makes it difficult to include them in the

breeding objective. However, even where breeding objectives cannot be specified precisely, the strength of developing selection indices is that the process of doing so identifies those traits which are important in achieving the breeding objective, and indicates the relative emphasis that should be accorded each trait (Ponzoni and Newman 1989).

The major limitation in the calculation of genetic gains in this study was the lack of knowledge of the economic importance of traits included in the breeding objective. Consequently, weights were estimated following arbitrary assumptions about the relative importance of each trait, which neither reflects the true economic importance of traits nor their likely relativity. The lack of definition of economic weights is a common problem in forestry, and before the results of this study are used in practice, it would be prudent to investigate further the economic importance of traits represented in the breeding objectives. However, even in the absence of precisely estimated economic values, the high genetic correlations between breeding objectives, which imply that similar genotypes are favoured by the different objectives, suggest a reasonable robustness in selection of the breeding population.

Whilst the combined index is advantageous compared to family/within family or phenotypic selection, more sophisticated and precise methods are being developed, *eg*, BLUP, of which the index is a special case when the data are balanced. The BLUP method calculates an index for each individual in accordance with the amount and quality of information available (White and

Hodge 1989). As the quantity and quality on information describing individuals in the breeding programmes is usually variable, BLUP methods could be used to calculate breeding values with higher accuracy.

One other limitation of index selection is that trees selected on the basis of information included in the index may be undesirable in some other sense, *eg*, they may have defects such as forks or fox-tails. Data on traits such as these is difficult to include in the index because they are assessed on a categorical basis and although, it is theoretically possible to estimate genetic parameters from this data (McGuirk 1989), an alternative is to apply an independent culling level to such traits. In practice, this seldom presents difficulty as long as highly ranked individuals which exhibit a defect can be replaced by the next most highly ranked individual in that family in which the defect is not apparent. As evident from the results of Chapter 4, consequent losses in genetic gains should be minimal. If a defect were suspected to be under strong genetic control, the association of that defect with particular families could be assessed by testing the significance of differences between observed *vs* expected frequencies against the Chi-Squared distribution (Everitt 1977). Families thus identified as being prone to particular defects could be excluded from the breeding population.

There is also a practical problem with combined index selection in that the emphasis it places on family mean performance for traits of low heritability often results in a large number of individuals being selected in the better

families. To maintain diversity in the breeding population, the number of individuals selected per family needs to be limited, as suggested by Cotterill and Dean (1990) and White (in press). The decision is to some extent arbitrary and influenced by resource constraints and breeding strategy; White (in press) recommended a maximum of seven individuals per family for the Florida *P. elliottii* breeding programme. This would also be a reasonable maximum number for the ZFC, and selection could differentially favour families with higher breeding values (as suggested by, for example, Lindgren 1986). This approach will ensure high genetic gains and, if used in conjunction with a breeding strategy that allows differential breeding effort, long-term genetic gains can also be secured (Cotterill 1989).

It is desirable that genetic gains estimated in these and other studies be translated to meaningful estimates of realised gain, *ie*, in terms of yield. This is an important exercise if the breeder is to convince the commercial forester of the benefits of research, which is currently problematic in Zimbabwe as well as elsewhere. Part of the reason for the difficulty is that there is a lack of data which describes in monetary terms the results of research. Consequently, the estimation of economic gains should be one of the objectives for the next phase of work; Foster (1992) discusses the various ways by which this might be achieved.

5.5 - Maximal genetic gains and losses of genetic variance: the compromise

The results of this study demonstrate not only the significant benefits of using index selection in terms of increasing genetic gains and accuracies of selection, but also the potentially adverse consequence of large reductions in genetic variance. To achieve both long and short-term genetic gains, the breeding population (census number) and the effective population size must each be large; achieving the former does not guarantee the latter.

Population structures such as those inherent in the nucleus (Cotterill *et al* 1989) and multiple-population (Namkoong *et al* 1980, 1988) breeding strategies are appropriate for both facilitating high genetic gains and maintaining diversity. Nucleus breeding "involves concentrating the best breeding individuals, financial investment and breeding together in an elite nucleus population" (Cotterill *et al* 1989). The individuals which have lower breeding values than those in the nucleus are bred in the "main" population. With this structure, high genetic gains are obtained from the nucleus while diversity is maintained in the main breeding population. Diversity in the nucleus may be increased by infusions from the main population. Infusions from other populations may also be introduced into the main population, improved there and finally introduced into the nucleus, thereby avoiding the loss of gains that would be sustained in the nucleus from the introduction of less improved material. Under this structure, the population in which intensive breeding methods are used will yield high genetic gains, and that which is subject to less intensive

breeding will maintain diversity.

The multiple population breeding strategy has been adopted by the ZFC (Barnes 1981) as a way of maximising both short and long-term genetic gains. At present, 14 sub-populations are maintained for *P. elliottii*. A minimum of 50 individuals for each sub-population was recommended by Namkoong *et al* (1980), but this number has not been attained for most of the Zimbabwean sub-populations, mainly because there have not been enough individuals which satisfy the requirements for the respective populations. The smallest sub-population has four trees; Namkoong *et al* (1988) reported that a population of four or less has a low effective population size. The numbers of trees in the sub-populations should therefore be increased towards the recommended minimum of 50, to ensure a reasonably large effective population size within each sub-population. When numbers in the sub-populations are too small for their continued maintenance, crossing the sub-populations should restore a reasonable effective population size.

As in the nucleus breeding structure, different levels of breeding effort can be employed in the multiple-population strategy, thereby allowing both high genetic gains and the maintenance of diversity. Under the multiple-population strategy, populations are kept separate in order to develop populations with different gene complexes (Namkoong *et al* 1980); diversity between the populations is the main objective and will follow as a consequence of selection, as most traits are under multiple gene control. Crossing between the

sub-populations increases diversity and delays inbreeding depression in the population as a whole.

The Cooperative Forest Genetics Research Program (CFGRP) in Florida has adopted a relatively sophisticated breeding strategy for *P. elliottii*, as a way of ensuring both short and long-term genetic gains. The strategy uses a combination of the nucleus, multiple-population and subline breeding strategies (White *et al* in press, CFGRP 1993). The breeding population is arranged into three tiers. Firstly, the breeding population has been subdivided into 24 breeding groups of 39 selections per group. Selections within each of the breeding groups are unrelated, thereby controlling inbreeding in the production population, which is open-pollinated. Secondly, the population is split into two superlines, each containing half of the breeding population, *ie*, 12 breeding groups. Within each superline the population is split into a main population containing members of all 12 breeding groups and an elite population containing 30 of the best individuals from the 12 breeding groups. Thirdly, within the main populations, each of the breeding groups is stratified vertically into three strata of 13 selections, according to the individuals' breeding values. More breeding effort is concentrated on individuals with high breeding values and less on individuals at the lower end of the scale. Therefore, that part of the population with lower breeding values is used to maintain diversity, while that part with higher breeding values is used to produce high genetic gains.

The strategy adopted by the CFGRP cannot be readily adopted by the ZFC. It has been possible for the CFGRP to execute this complex and resource intensive strategy because the workload is shared among a cooperative group of 13 organisations. Consequently, no one organisation has to provide the resources on its own; breeding and testing of the material are shared out equally. Whilst the ZFC does not have the benefits of a cooperative structure such as the CFGRP's, some features of the strategy could be adopted and used by the ZFC.

The CFGRP breeding strategy restricts genetic interchange to allow maximum diversity to be maintained. Full-sib mating is allowed only among individuals within the same breeding group, with the exception of members of the elite population, which are restricted to the wider dimension of the superline. Restriction of movement of material in some planes of the breeding populations could be incorporated into the multiple-population strategy in Zimbabwe. At present, individuals which satisfy the criteria for more than one sub-population in the Zimbabwean programme are not restricted to any one sub-population. Relatedness is therefore being built up between the populations. A restriction that assumed that selected individuals were represented in only one of the sub-populations could be implemented; however, this would further restrict the census and the effective numbers in the sub-populations, some of which are already critically low. In this case, sub-populations may be divided into groups, depending on relatedness of selections between the populations. Crossing would be permitted between

related sub-populations but not between those that are unrelated, such that when individuals are selected from the respective groups for seed orchard establishment, related matings are minimised.

The CFGRP uses backward as well as forward selections to maintain a large census number. The strategy does not require that all selected individuals are progeny tested, as the breeding values of some of the backward selections are already well estimated, and do not require further verification. However, individuals with high breeding values are always progeny tested regardless of whether they are backward or forward selections. Individuals at the lower end of the scale may or may not be tested, depending on whether reliable estimates of breeding values already exist for them. This differential testing strategy could be adopted by the ZFC, and would reduce the number of individuals progeny tested at any one time, thereby reducing cost; alternatively, a greater number of new selections could be tested, leading to increases in both census and effective population numbers. Retention within the breeding population of earlier (backward) selections with high breeding values could also be used to increase the breeding population size in the ZFC programme.

5.6 - Implications for the Zimbabwean *P. elliottii* breeding population

The breeding population of *P. elliottii* in Zimbabwe is currently divided into 14 sub-populations, 11 of which have as their breeding objective saw-timber

production, pulpwood production, and resin yield, in decreasing order of importance. In the other three sub-populations, the order of importance of pulpwood production and resin yield is reversed. Selection criteria are variously volume (VOL), stem straightness (STR), branch diameter (BRD), wood density (DEN), resin *ie*, quantity (RESQ) and resin quality (RESQQ), which assesses the components of resin, such as terpenes. Six of the 14 sub-populations are related. Relevant details of the sub-populations are summarised in Table 5.1.

Table 5.1 Breeding objectives, selection criteria, census number and relationships of Zimbabwean *P. elliottii* sub-populations.

Sub-population No.	Breeding objective	Selection criteria	Census No.	Related populations
1	TPR	VOL,STR,BRD,DEN	36	5,12
2	TPR	VOL,STR,BRD,DEN	48	
3	TPR	VOL,STR,BRD,DEN	37	
4	TRP	VOL,RESQ,RESQQ, STR,BRD	35	
5	TPR	VOL,STR,BRD,DEN	25	13
6	TRP	VOL,RESQ,RESQQ, STR,BRD	16	14
7	TPR	VOL,STR,BRD,DEN	50	
8	TPR	VOL,BRD,STR,DEN	34	
9	TPR	VOL,STR,BRD,DEN	10	
10	TPR	VOL,STR,BRD,DEN	29	
11	TPR	VOL,STR,BRD,DEN	21	
12	TPR	VOL,STR,BRD,DEN	4	
13	TPR	VOL,STR,BRD,DEN	25	5
14	TRP	VOL,RESQ,RESQQ, STR,BRD	16	6

The letters, T, P and R represent the breeding objectives of saw-timber production, pulp production, and resin yield, respectively. Effective population numbers are not available.

Although, as discussed above, the multiple population strategy is intended to meet the dual objectives of maintaining diversity and achieving genetic gain, the small size of many of the sub-populations, their relatedness, the similarity of breeding objectives and selection criteria for many of the sub-populations, and the resource constraints within the ZFC, must limit progress towards these objectives. The results of this study, concerning breeding objectives and selection criteria, may be used to help rationalise the sub-population structure and the selection criteria used in each. In terms of breeding objectives, it is apparent from **3.2.1** that, for *P. elliottii* in Zimbabwe, the objective of saw-timber production can be equated to that of volume production, which is itself synonymous with pulpwood production. There is therefore little point, under current market circumstances and whilst current genetic parameters prevail, in retaining pulpwood production as a distinct breeding objective. Breeding objectives can therefore be limited to saw-timber production and resin yield.

It is evident from Table 5.1 that each sub-population has at least four selection criteria. Chapter 2 reported negative correlations between wood density and each of volume and branch diameter, and low correlations between volume and each of stem straightness and branch diameter. As discussed in **3.8.1**, using adversely or poorly correlated traits together in an index will have an adverse impact on genetic gains, accuracies and efficiencies of selection for the breeding objective. The use of traits that are poorly or adversely correlated with the breeding objective will also result in losses in genetic gains, accuracies and efficiencies of selection in the breeding objective. As evident from

Chapter 2, branch diameter is poorly correlated with both volume production and resin yield, and is therefore best excluded from the selection criteria. As also discussed in **3.8.1**, use of primary traits such as diameter or height is preferable to use of a mathematically derived secondary trait such as volume.

The results reported in Chapters 3 and 4 suggest that it would be advantageous to simplify selection criteria to diameter, for the breeding objective of saw-timber production, although height could be used instead, if losses in wood density from selection based on diameter were seen to be unacceptable. In the case of improving both resin yield and saw-timber production, stem straightness would be included as a selection criterion because of its favourable correlation with resin yield.

The existing sub-populations can be divided, on the basis of resin yield, into two groups: those including high resin-yielding individuals (sub-populations 4, 6 and 14), and those without these individuals (the other 11 sub-populations). Amalgamating the former group creates a sub-population with a census number of 67. The breeding objective for this group would be defined as saw-timber production and resin yield, and selection criteria would be height and stem straightness at five years.

The remaining 11 sub-populations could be amalgamated to ensure that the new sub-populations have census numbers of 50 and above. The first step would be to amalgamate related sub-populations, to reduce relatedness

between sub-populations. Amalgamations on this basis would merge the following sub-populations (the new census numbers are in brackets): 1, 5, 12 and 13 (90); 2 and 9 (58); 3 and 8 (71); 10 and 11 (50); sub-population 7 could be maintained separately, as it already has a census number of 50 and is not related to any other sub-population. These amalgamations result in a total of five sub-populations for which the breeding objective is saw-timber production, and the selection criteria would be either diameter or height, depending on the importance assigned to the maintenance of wood density.

The six populations resulting from this rationalisation would be unrelated, and each should have a reasonable effective population size, allowing maintenance of diversity over time. As the sub-populations are unrelated, selections from each could, if necessary, be represented in joint seed orchards without risk of related matings.

5.6 - Into the future

The relatively long generation intervals of industrial tree species present a number of challenges to breeders. Breeding strategies have to be sufficiently robust to accommodate both present and future needs (Namkoong *et al* 1988); this work has shown that such robustness is not necessarily difficult to achieve for particular breeding objectives. However, even for robust strategies, all decisions about the future involve a degree of uncertainty and risk; these can either be accepted (*ie* ignored) or, if deemed too great, decision-making can be

delayed until the availability of further information reduces them to acceptable levels (Friedman 1992). In terms of the selection decisions considered here, the high correlations between early and late performance suggest that uncertainty and risk are little inflated by bringing forward selection decisions. In addition, the increasing sophistication and availability of appropriate computer software and hardware will continue to improve the rigour and sophistication with which genetic analyses can be conducted. The enhanced quality of results from such analyses, of which those conducted here are a reasonable example, should also contribute to minimising uncertainty and risk in breeding programmes.

The results of this study also suggest that there is some future in the use of "standard" genetic parameter estimates, as advocated by Cotterill and Dean (1990). The reasonable degree of commonality between the estimates for *P. elliottii* reported here and those estimated from other studies confirms that breeding strategies for the species should also have a degree of robustness on this basis, and that cooperative breeding programmes, such as the CFGRP for *P. elliottii*, could be more widely developed. In the case of Zimbabwe, this might be achieved through closer cooperation with *P. elliottii* breeding programmes in other regions of the world: as Franklin (1989) observed, "the regional nature of needs and opportunities make obvious the opportunity for inter-agency cooperation". Nevertheless, genetic parameters should continue to be monitored, and breeding objectives and selection criteria refined, as the breeding of *P. elliottii* in Zimbabwe progresses into advanced generations.

The extensive series of trials which provided the basis for this study are typical of the substantial efforts which have characterised tree breeding in Zimbabwe. As the resources available for breeding activities diminish, precluding such comprehensive testing, the results of studies such as this can be used to guide breeders to the most efficient and effective use of the genetic resources available to them. The multiple population breeding strategy already implemented in Zimbabwe provides a sound framework for realising both short and long term objectives; the results of this work demonstrate how selection decisions can best be made within that framework.

Literature Cited

Allen, P.J., 1978. Genotypic and phenotypic correlations of wood and tree characteristics. In: *Proceedings of a joint workshop of IUFRO working parties*, Brisbane, Australia: 184-196.

Allen, P.J., 1985. *Estimation of genetic parameters for wood properties in slash pine in south east Queensland*. Department of Forestry, Queensland, Australia. Research Note 41: 15pp.

Askew, C.R. and Burrows, P.M., 1983. Minimum coancestry selection. I. A *P. taeda* population and its simulation. *Silvae Genetica* **32**: 125-131.

Baker, R.J., 1986. *Selection indices in plant breeding*. CRC Press, Inc. Boca Raton Florida: 218pp.

Baradat, P.H., 1976. Use of juvenile-mature relationships and information from relatives in combined multi-trait selection. In: *Proceedings of the IUFRO meeting on advanced generation breeding*, Bordeaux, INRA, Cestas, France: 121-138.

Barber, J.C., 1979. Tree improvement in the south: a promise fulfilled. In: *Proceedings of the 15th forest tree improvement conference*, Mississippi State University: 1-10.

Barbour, J.R. and Kellog, R.M., 1990. Forest management and end-product quality: a Canadian perspective. *Canadian Journal of Forestry Research* **20**: 405-414.

Barnes, R.D., 1973. *The genetic improvement of* P. patula *Schiede and Deppe in Rhodesia*. Unpublished DPhil thesis, University of London: 322pp.

Barnes, R.D., 1981. *A review of the tree breeding programme in Zimbabwe and recommendations for its development*. Technical Cooperation Scheme, Overseas Development Administration, UK: 68pp.

Barnes, R.D., 1982-1990. *The tree breeding programme in Zimbabwe. Plans for work for 1982/83, 1983/84, 1984/85, 1985/86, 1986/87, 1987/88, 1988/89, 1989/90.* Reports prepared under United Kingdom Overseas Development

Adminstration Technical Cooperation scheme: 56pp, 86pp, 178pp, 200pp, 303pp, 251pp.

Barnes, R.D., 1986. Multiple population tree breeding in Zimbabwe. In: *Proceedings of a joint workshop of IUFRO working parties*, Williamsburg, Virginia. North Carolina State University, Raleigh: 285-297.

Barnes, R.D., 1987. The breeding seedling orchard in a multiple population breeding strategy for tropical trees. In: *Simposio sobre silvicultura y genetico de especies forestales*, Tono II CIEF, Buenos Aires: 1-18.

Barnes, R.D. and Gibson, G.L., 1986. A method to assess stem straightness in tropical pines. *Commonwealth Forestry Review* **65**: 168-171.

Barnes, R.D. and Mullin, L.J., 1989. The multiple-population breeding strategy in Zimbabwe: five year results. In: *Proceedings of IUFRO conference on breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry*, Pattaya, Thailand. (Gibson, G.L. Griffin, A.R. and Matheson, A.C., eds.). Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA: 148-158.

Barnes, R.D., Mullin, L.J. and Battle, G., 1992a. Genetic control of fifth year traits in *Pinus patula* Schiede and Deppe. *Silvae Genetica* **41**: 242-248.

Barnes R.D., Mullin L.J. and Battle, G., 1992b. Genetic control of eight year traits in *Pinus patula* Schiede and Deppe. *Silvae Genetica* **41**: 318-326.

Barnes, R.D., Woodend, J.J., Schweppenhauser, M.A. and Mullin, L.J., 1977. Variation in diameter, growth and wood density in six-year-old provenance trials of *Pinus caribaea* Morelet on five sites in Rhodesia. *Silvae Genetica* **26**: 163-167.

Barrett, R.L. and Mullin, L.J., 1968. A review of introductions of forest trees in Rhodesia. *The Rhodesia Bulletin of Forestry Research* **1**: 227pp.

Becker, W.R. 1975. *Manual of quantitative genetics*. Washington State University Press, Washington: 170pp.

Bethune, J.E. and Langdon O.G., 1966. Seed source, seed size, and seedling grade relationships in South Florida slash pine. *Journal of Forestry* **64**: 120-124.

Binet, F.E., 1965. On the construction of an index for indirect selection. *Biometrics* **21**: 291-299.

Birks, J.S., 1990. *Efficiency of experimental design in the genetic improvement of*

tropical tree species. Overseas Development Agency Research Scheme R.4347. Oxford Forestry Institute. University of Oxford: 46pp.

Birks, J.S. and Barnes, R.D., 1991. Provenance variation in *Pinus caribaea, P. oocarpa,* and *P. patula* ssp. *tecunumanii*. Tropical Forestry Paper, Oxford Forestry Institute, University of Oxford. No. 21: 40pp.

Blair, R.L., 1975. Exploiting natural variation through genetic selection. In: *Forest tree improvement - the third decade*. Division of Continuing Education, Louisiana State University, Baton Rouge, La., USA: 35-45.

Borralho, N.M.G., 1991. *Genetic improvement of* Eucalyptus globulus *Labill. ssp.* globulus *for pulp production*. Unpublished DPhil Thesis. University of Oxford: 221pp.

Borralho, N.M.G., Cotterill, P.P. and Kanowski, P.J., 1992. Genetic control of growth of *Eucalyptus globulus* in Portugal II. Efficiency of early selection. *Silvae Genetica* **41**: 39-45.

Borralho, N.M.G., Cotterill, P.P. and Kanowski, P.J., 1993. Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. *Canadian Journal of Forest Research* **23**: 648-656.

Bridgewater F.E. 1992. *Mating designs*. In: *Handbook of quantitative forest genetics* (Fins, L., Friedman, S.T. and Brotschol, J.V., eds.). Kluwer Academic Publishers: 69-95.

Bulmer, M.G., 1971. The effect of selection on genetic variability. *American Naturalist* **105**: 201-211.

Bulmer, M.G., 1980. *The mathematical theory of quantitative genetics*. Clarendon Press, Oxford: 254pp.

Burdon, R.D., 1977. Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genetica* **26**: 168-175.

Burdon, R.D., 1979. Generalisation of multi-trait selection indices using information from several sites. *New Zealand Journal of Forestry Science* **9**: 145-152.

Burdon, R.D., in press. Testing and selection: strategies and tactics for the future. In: *Proceedings of the IUFRO Conference,* Cali, Colombia 1992.

Carson, S.D., 1986. Control-pollinated seed orchards of best general combiners: a new strategy for radiata pine improvement. Cited in: Dean, C.A., 1990. *Genetics of growth and wood density in radiata pine*. Unpublished

PhD Thesis. University of Queensland, Australia: 76pp.

Carson, S.D., 1988. Will a national seed orchard programme serve regional needs for radiata pine in New Zealand? Paper to Australian Plant Breeding Conference. Wagga Wagga, NSW, Australia: 2pp.

Carson, M.J. and Inglis, C.S., 1986. Genotype and location effects on internode length of *Pinus radiata* in New Zealand. In: *Proceedings of a joint workshop of IUFRO working parties*, Williamsburg, Virginia. North Carolina State University, Raleigh, USA: 527.

Christophe, C. and Birot, Y., 1983. Genetic structures and expected genetic gains from multi-trait selection in wild populations of Douglas fir and Sitka spruce. II. Practical application of index selection on several populations. *Silvae Genetica* **32**: 173-181.

Cooperative Forest Genetics Research Program, 1990. *Thirty-second progress report*. Department of Forestry, School of Forest Resources and Conservation, Institute of Food and Agricultural Sciences. University of Florida: 50pp.

Cooperative Forest Genetics Research Program, 1993. *Thirty-fifth progress report*. Department of Forestry, School of Forest Resources and Conservation, Institute of Food and Agricultural Sciences. University of Florida: 46pp.

Coppen, J.J.W., Greenhalgh, P. and Smith, A.E., 1984. *Gum naval stores: an industrial profile of turpentine and rosin production from pine resin*. Tropical Development and Research Institute. Report No. G187: 40pp.

Cotterill, P.P., 1984. A plan for breeding radiata pine. *Silvae Genetica* **33**: 84-90.

Cotterill, P.P., 1986a. Genetic gains expected from alternative breeding strategies including simple low cost options. *Silvae Genetica* **35**: 212-223.

Cotterill, P.P., 1986b. Breeding strategy: don't underestimate simplicity! In: *Proceedings of a joint workshop of IUFRO working parties*, Williamsburg, Virginia. North Carolina State University, Raleigh: 8-23.

Cotterill, P.P., 1987. Short Note: on estimating heritability according to practical applications. *Silvae Genetica* **36**: 46-48.

Cotterill, P.P. and Dean, C.A., 1988. Changes in genetic control of growth of radiata pine to 16 years and efficiencies of early selection. *Silvae Genetica* **37**: 138-146.

Cotterill, P.P. and Dean, C.A., 1990. *Successful tree breeding with index selection*. Division of Forestry and Forest Products. CSIRO, Australia: 80pp.

Cotterill, P.P., Dean, C.A., Cameron, J. and Brindbergs, M., 1989. Nucleus breeding: a new structure for rapid improvements under clonal forestry. In: *Proceedings of IUFRO conference on breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry*, Pattaya, Thailand. (Gibson, G.L. Griffin, A.R. and Matheson, A.C., eds.). Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA: 39-51.

Cotterill, P.P., Dean, C.A. and van Wyk, G., 1987. Additive and dominance genetic effects in *Pinus pinaster, P. radiata* and *P. elliottii* and some implications for breeding strategy. *Silvae Genetica* **36**: 221-232.

Cotterill, P.P. and Jackson, N., 1981. Index selection with restrictions in tree breeding. *Silvae Genetica* **30**: 106-108.

Cotterill, P.P. and Jackson, N., 1985. On index selection. I. Methods of determining economic weight. *Silvae Genetica* **34**: 56-63.

Cotterill, P.P. and Jackson, N., 1989. Gains expected from clonal orchards under alternative breeding strategies. *Forest Science* **35**: 183-196.

Cotterill, P.P. and James, J.W., 1984. Number of offspring and plot size required for progeny testing. *Silvae Genetica* **33**: 203-209.

Cunningham, E.P., 1970. SELIND. A Fortran program for genetic selection indices. Cited in: Cotterill, P.P. and Dean C.A. 1990. *Successful tree breeding with index selection*. CSIRO, Melbourne, Australia: 80pp.

Cunningham, E.P., O'Byrne, T. and Mescal, A.A., 1977. Genetic relationship between beef and dairy cattle traits in Friesian cattle. *Irish Journal of Agricultural Research* **16**: 243-249.

Davis, L.S., 1967. Investments in loblolly pine clonal seed orchards: production costs and economic potential. *Journal of Forestry* **65**: 882-887.

Dean, C.A., 1990. *Genetics of growth and wood density in radiata pine.* Unpublished PhD Thesis. University of Queensland, Australia: 76pp.

Dean, C.A., Cotterill, P.P. and Cameron, J.N., 1983. Genetic parameters and gains expected from multiple trait selection of radiata pine in eastern Victoria. *Australian Forest Research* **13**: 271-278.

Dean, C.A., Cotterill, P.P. and Eisemann, R.L., 1986. Genetic parameters and gains expected from selection in *P. caribaea* var *hondurensis* in northern Queensland, Australia. *Silvae Genetica* **35**: 229-236.

Dekkers, J.C.M., 1992. Asymptotic response to selection on best linear unbiased

predictors of breeding values. *Animal Production* **54**: 351-360.

Dempster, E.R., 1955. Genetic models in relation to animal breeding. *Biometrics* **11**: 535-536.

Department of Forestry, Queensland, Australia, 1990, 1983, 1979. *Report of Research Activities. Division of Technical Services*: 82, 80, 86pp.

Dorman, K.W., 1976. *The genetics and breeding of southern pines*. US Department of Agriculture Forest Service. Agriculture Handbook No. 471: 407pp.

Dorman, K.W. and Squillace, A.E., 1974. *Genetics of slash pine*. United States Department of Agriculture Forest Service. Research paper WO-20: 20pp.

Ehrenberg, C., 1970. Breeding for stem quality. *Unasylva* **24**: 23-31.

Eisen, E.J. and Saxton, A.M., 1983. Genotype by environment interactions and genetic correlations involving two environmental factors. *Theoretical and Applied Genetics* **67**: 75-86.

Everitt, P.S., 1977. *The analysis of contingency tables*. Chapman and Hall, London: 128pp.

Falconer, D.S., 1952. The problem of environment and selection. *American Naturalist* **86**: 293-298.

Falconer, D.S., 1981. *Introduction to quantitative genetics*. Second Edition. Longman: 340pp.

Finlay, K.W. and Wilkinson, G.N., 1963. The analysis of adaptation in a plant breeding programme. *Australian Journal of Agricultural Research* **14**: 742-754.

Foster, G.S., 1986. Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *Forest Science* **32**: 944-958.

Foster, G.S., 1992. Estimating yield. In: *Handbook of quantitative forest genetics* (Fins, L., Friedman, S.T. and Brotschol, J.V., eds.). Kluwer Academic Publishers: 229-269.

Franklin, E.C., 1970. *Survey of mutant forms and inbreeding depression in species of the family Pinaceae*. United States Department of Agriculture Forest Service. Southeast Forest Experimental Station. Research paper SE-61: 21pp.

Franklin, E.C, 1979. Model relating levels of genetic variance to stand

development of four North American Conifers. *Silvae Genetica* **28**: 207-212.

Franklin, E.C, 1989. Selection strategies for *Eucalyptus* tree improvement - four generations of selection in *Eucalyptus grandis* demonstrate valuable methodology. In: *Proceedings of IUFRO conference on breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry,* Pattaya, Thailand. (Gibson, G.L. Griffin, A.R. and Matheson, A.C., eds.). Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA: 197-209.

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

Friedman, S.T., 1992. Quantitative approaches to decision-making in forest genetics programmes. In: *Handbook of quantitative forest genetics* (Fins, L., Friedman, S.T. and Brotschol, J.V., eds.). Kluwer Academic Publishers: 270-312.

Gansel, R.C., 1971. Effects of several levels of inbreeding on growth and oleoresin yield in slash pine. In: *Proceedings of the 11th conference on southern forest tree improvement,* Atlanta, Georgia: 173-177.

Gaussen, H., 1960. *Les gymnospermes actualles et fossiles.* Cited in: Nikles, D.G., 1966. *Comparative variability and relationship of Caribbean pine* (Pinus caribaea *Morelet) and slash pine* (Pinus elliottii *Engelm.*). Unpublished PhD thesis, Department of Forest Management, North Carolina State University, Raleigh: 185pp.

Geburek, Th., 1986. Some results of inbreeding depression in Serbian spruce (*Picea omorika* (Panc.) Purk.). *Silvae Genetica* **35**: 169-172.

Gibson, G.L., 1982. *Genotype-environment interaction in Pinus caribaea.* Commonwealth Forestry Institute, Oxford: 112pp.

Gill, J.G.S., 1987. Juvenile-mature correlations and trends in genetic variances in Sitka spruce in Britain. *Silvae Genetica* **36**: 189-194.

Goddard, R.E. and Cole, D.E., 1966. Variation in wood production of 6 year old progenies of select slash pines. *TAPPI* **49**: 359-362.

Goddard, R.E. and Smith W.H., 1969. Progeny testing for intensive management. In: *Proceedings of the 10th southern forest tree improvement conference,* Houston, Texas: 76-83.

Greenhalgh, P., 1982. *The production, marketing and utilisation of naval stores.* Tropical Development and Research Institute. Report No. G170: 117pp.

Hamilton, J.R. and Harris, J.B., 1965. Influence of site on specific gravity and dimensions of tracheid in clones of *Pinus elliottii* and *P. taeda*. *TAPPI* **48**: 330-333.

Hans, A.S., 1972. Development of an instrument for the assessment of stem straightness. *Commonwealth Forestry Review* **51**: 336-345.

Harvey, W.R., 1987. *User's guide for LSMLMW and MIXMDL, PC-1 Version.* Mimeographed paper. Ohio State University, Ohio: 59pp.

Harville, D.A., 1977. Maximum likelihood approaches to variance component estimation and related problems. *Journal of the American Statistical Association* **72**: 320-340.

Hazel, L.N. and Lush, J.L., 1942. The efficiency of three methods of selection. *Journal of Heredity* **33**: 393-399.

Heinrichs, J.F. and Lassen, L.E., 1971. Improved technique for determining the volume of irregularly shaped wood blocks. *Forest Products Journal* **20**: 24.

Henderson, C.R., 1963. Selection index and expected genetic advance. In: *Statistical genetics and plant breeding*. (Hanson, W.D. and Robinson, H.F., eds.). NAS-NRC Publishers, Washington D.C.: 534pp.

Henderson, C.R., 1990. Statistical methods in animal improvement: historical overview. In: *Advances in statistical methods for genetic improvement of livestock.* (Gianola, D. and Hammond, K., eds.). Springer-Verlag: 2-14.

Huber, D.A., White, T.L. and Hodge, G.R., 1992. The efficiency of half-sib, half-diallel and circular mating designs in the estimation of genetic parameters in forestry: a simulation. *Forest Science* **38**: 757-776.

Hurley, D.W., Volkman, D.A., Andrews, R.S. and Scmidt, T.J., 1976. Pulping and by-product yield of paraquat treated slash pine. Cited in: Zobel, B.J. and van Buijtenen, P.J. 1989. *Wood variation: its causes and control.* Springer-verlag: 363pp.

Institute of Paper Chemistry, 1962. *Application of the pulp and paper making sciences to the genetic improvement of southern pulpwood. Base-line values for judging wood quality of slash-pine*. Program Report 7: 46pp.

Jackson, N., 1978. Fortran 77 programm (ANSI x3.9), Cited in: Cotterill, P.P. and Dean, C.A. 1990. *Successful tree breeding with index selection*. CSIRO Melbourne: 80pp.

James, J.W., 1972. Optimum selection intensity in breeding programs. *Animal Production* **14**: 1-9.

James, J.W., 1982. Construction, uses and problems of multi-trait selection indices. In: *Proceedings of the 2nd world congress of genetic and applied livestock production*, Madrid, Spain. V: 130-139.

James, J.W., 1987. Breeding objectives for the merino industry: an academic perspective. In: *Proceedings of the symposium on merino improvement programs in Australia.* (McGuirk, B.J., ed.). Laura, NSW: 19-24.

Johnson, G.R. and Burdon, R.D., 1990. Family-site interaction in *Pinus radiata*: implications for progeny testing strategy and regionalised breeding in New Zealand. *Silvae Genetica* **39**: 55-62.

Kang, H., 1979. Long-term tree breeding. In: *Proceedings of the 15th southern forest tree improvement conference*, Mississippi State University, MS, USA: 66-72.

Kang, H., 1985. Juvenile selection in tree breeding: some mathematical models. *Silvae Genetica* **34**: 75-90.

Kang, H. and Nienstaedt, H. 1987. Managing long-term breeding stock. *Silvae Genetica* **36**: 30-39.

Kanowski, P.J., Ferguson, G.B., Wood, D.G., Nikles, D.G. and Matheson, A.C., 1986. Variation of stem and crown characteristics between selected families of Hoop Pine (*Araucaria cunninghamii* Ait. ex D. Don). *Australian Forest Research* **15**: 449-461.

Kanowski, P.J. and Nikles, D.G., 1989. A plan for continuing genetic improvement of *Pinus caribaea* var *hondurensis* in Queensland. In: *Proceedings of IUFRO conference on breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry*, Pattaya, Thailand. (Gibson, G.L. Griffin, A.R. and Matheson, A.C., eds.). Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA: 236-249.

Kellog, R.M., 1982. Coming to grips with wood quality. *Forestry Chronicle* **58**: 254-257.

Kempthorne, O. and Nordskog, A.W., 1959. Restricted selection indices. *Biometrics* **15**: 10-19.

King, J.N., Yeh, F.C., Heaman, J.C. and Dancik, B.P., 1988. Selection of wood density and diameter in controlled crosses of coastal Douglas-fir. *Silvae Genetica* **37**: 152-157.

King, J.N. and Johnson, G.D., 1993. Monte Carlo simulation models of breeding-population advancement. *Silvae Genetica* **42**: 69-78.

Lambeth, C.C., 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. *Forest Science* **26**: 571-580.

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

Langdon, O.G., 1963. Range of South Florida slash pine. *Journal of Forestry* **61**: 384-385.

Layton, P.A. and Goddard, R.E., 1983. Low level inbreeding effects on germination, survival and early height growth of slash pine. In: *Proceedings of the 17th southern forest tree improvement conference*, Athens, GA: 106-115.

Ledig, F.T., Guries, R.P. and Bonefield, B.A., 1983. The relation of growth to heterozygosity in pitch pine. *Evolution* **37**: 1227-1238.

Libby, W.T., McCutchan, B.G. and Millar, C.I., 1981. Inbreeding depression in selfs of redwood. *Silvae Genetica* **30**: 15-25.

Lindgren, D. 1986. How should breeders respond to breeding values? In: *Proceedings of a joint workshop of IUFRO working parties*, Williamsburg, Virginia. North Carolina State University, Raleigh: 361-372.

Little, E. and Dorman, K.W., 1954. *Slash pine* (P. elliottii), *including South Florida slash pine, nomenclature and description*. United States Department of Agriculture Forest Service. South-eastern Forestry Experimental Station. Research paper 36: 82pp.

Magnussen, S. and Keith, C.T., 1990. Genetic improvement of volume and wood properties of jack-pine: selection strategies. *The Forestry Chronicle* **66**: 281-286.

Magnussen, S. and Yanchuk, A.D., 1993. Selection age and risk: finding the compromise. *Silvae Genetica* **42**: 25-40.

Magnussen, S. and Yeatmann, C.W., 1989. Predictions of genetic gain from various selection methods in open-pollinated *Pinus banksiana* progeny trials. *Silvae Genetica* **39**: 140-153.

Matheson, A.C. and Cotterill, P.P., 1990. Utility of genotype x environment interactions. *Forest Ecology and Management* **30**: 159-174.

Matheson, A.C. and Raymond, C.A., 1984a. Effects of thinning in progeny tests on estimates of genetic parameters in *P. radiata*. *Silvae Genetica* **33**: 125-128.

Matheson, A.C. and Raymond, C.A., 1984b. The impact of genotype x environment interactions on Australian *P. radiata* breeding programs. *Australian Forestry Research* **14**: 11-25.

Matheson, A.C., Spencer, D. J. and Magnussen, S., 1988. Optimum age for selection in *Pinus radiata* using basal area under bark for age-age correlations. In: *Proceedings of the 10th meeting of representatives*, Gympie, Queensland, Australia: 213-217.

McKeand, S.E., 1988. Optimum age for family selection for growth in genetic tests of loblolly pine. *Forest Science* **34**: 400-411.

McGuirk, B.J., 1989. The estimation of genetic parameters for all-or-none and categorical traits. In: *Evolution and animal breeding: reviews on molecular and quantitave approaches in honor of Alan Robertson*. (Hill, W.G. and Mackay, T.F.C., eds.). CAB International: 175-180.

Megraw, R.A., 1985. *Wood quality factors in loblolly pine*. TAPPI Press: 88pp.

Mergen, F., 1958. Genetic variation in needle characteristics of slash pine and in some of its hybrids. *Silvae Genetica* **7**: 1-9.

Miller, R.G., 1975. Visual assessment of stem straightness in radiata pine. *Australian Forestry* **19**: 8-12.

Miller, R.H. and Pearson, R.E., 1979. Economic aspects of selection. *Animal Breeding Abstracts* **47**: 281-290.

Mullin, L.J., Barnes, R.D. and Prevost, M.J., 1978. A review of the southern pines in Rhodesia. *The Rhodesia Bulletin of Forestry Research* **7**: 328pp.

Namkoong, G., 1984. A control concept of gene conservation. *Silvae Genetica* **33**: 160-163.

Namkoong, G., Barnes, R.D., Burley, J., 1980. *A philosophy of breeding strategy for tropical forest trees*. Tropical Forestry Papers 16. Commonwealth Forestry Institute. University of Oxford: 67pp.

Namkoong, G. and Conkle, M.T., 1976. Time trends in genetic control of height growth in Ponderosa pine. *Forest Science* **22**: 2-12.

Namkoong, G., Kang, H.C. and Brouard, J.S., 1988. *Tree breeding: principles and strategies*. Springer Verlag: 80pp.

Namkoong, G. and Roberds, J.H., 1974. Choosing mating designs to efficiently estimate genetic variance components for trees. *Silvae Genetica* **23**: 43-53.

Namkoong, G. and Roberds, J.H., 1982. Short-term loss of neutral alleles in small population breeding. *Silvae Genetica* **31**: 1-6.

Namkoong, G., Usanis, R.A. and Silen, R.R. 1972. Age-related variation in genetic control of height growth in Douglas-fir. *Theoretical and Applied Genetics* **42**: 151-159.

Nanson, A., 1976. Juvenile-mature relationships, mainly in provenance and progeny tests. In: *In: Proceedings of the IUFRO meeting on advanced generation breeding*, Bordeaux, INRA, Cestas, France: 99-120.

Neale, D.B., Wheeler, N.C. and Allard, R.W., 1986. Paternal inheritance of chloroplast DNA in Douglas-fir. *Canadian Journal of Forestry Research* **16**: 1152-1154.

Nicholas, F.W., 1987. *Veterinary genetics*. Clarendon Press, Oxford: 580pp.

Nikles, D.G., 1966. *Comparative variability and relationship of caribean pine* (Pinus caribaea *Morelet) and slash pine* (Pinus elliottii *Engelm*). Unpublished PhD thesis, Department of Forest Management, North Carolina State University, Raleigh: 185pp.

Nikles, D.G., 1970. Breeding for growth and yield. *Unasylva* **24**: 9-22.

Nikles, D.G., 1972. Progress in breeding *Pinus caribaea* Morelet in Queensland, Australia. In: *Selection and breeding to improve some tropical conifers.* (Burley, J. and Nikles, D.G., eds.). Commonwealth Forestry Institute, Oxford, and Department of Forestry, Queensland 1: 245-266.

Nikles, D.G. and Robinson, M.J., 1989. The development of *Pinus* hybrids for operational use in Queensland. In: *Proceedings of IUFRO conference on breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry*, Pattaya, Thailand. (Gibson, G.L. Griffin, A.R. and Matheson, A.C., eds.). Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA: 272-282.

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

Paschke, J.L., 1979. *Age-age relationships in loblolly pine* (Pinus taeda *L.*). Unpublished MSc thesis, Department of Forestry, North Carolina State University, Raleigh, N.C., USA.: 49pp.

Patterson, H.D. and Thompson, R., 1971. Recovery of inter-block information when block-sizes are unequal. *Biometrika* **58**: 445-554.

Patterson, H.D. and Thompson, R., 1975. Maximum likelihood estimation of components of variance. In: *Proceedings of the 8th international biometric conference,* Constanta, Romania: 197-207.

Pederick, L.A., 1990. Family x site interactions in *P. radiata* in Victoria, Australia and implications for breeding strategy. *Silvae Genetica* **39**: 134-140.

Pederson, D.G., 1974. The stability of varietal performance over years. 2. Analysing varietal trials. *Heredity* **33**: 217-228.

Ponzoni, R.W. and Newman, S., 1989. Developing breeding objectives for Australian beef cattle production. *Animal Production* **49**: 35-47.

Poynton, R.J., 1979. *The planting in southern Africa: the pines.* Department of Forestry, South Africa: 576pp.

Raymond, C.A. and Cotterill, P.P., 1990. Methods of assessing crown form of *Pinus radiata. Silvae Genetica* **39**: 67-71.

Riemenschneider, D.E., 1988. Heritability, age-age correlations and inferences regarding juvenile selection in jack-pine. *Forest Science* **34**: 1076-1082.

Robertson, A., 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* **15**: 469-485.

Robertson, A., 1960. A theory of limits in artificial selection. *Proceedings of the Royal Society,* **B153**: 234-249.

Robinson, D.L., 1987. Estimation and use of variance components. *The Statistician* **36**: 3-15.

Sales, J. and Hill, W.G., 1976a. Effect of sampling errors on efficiency of selection indices. 1. Use of information from relatives for single trait improvement. *Animal Production* **22**: 1-17.

Sales, J. and Hill, W.G., 1976b. Effect of sampling errors on efficiency of selection indices. 2. Use of information on associated traits for improvement of a single trait. *Animal Production* **23**: 1-14.

Searle, S.R., 1971. Topics in variance component estimation. *Biometrics* **27**: 1-76.

Searle, S.R., 1987. *Linear models for unbalanced data.* John Wiley and Sons: 536pp.

Shelbourne, C.J.A., 1972. Genotype-environment interactions: its study and its implications in forest tree improvement. In: *Proceedings of IUFRO Society for breeding research in Asia and Oceania joint symposia*, Tokyo, Japan B-1(I): 1-28.

Shelbourne, C.J.A. and Namkoong, G., 1966. Photogrammetric technique for measuring bole straightness., In: *Proceedings of the 8th southern forest tree improvement conference*, Gainesville, USA: 131-136.

Siegel, S. and Castellan, N.J. Jr., 1988. *Nonparametric statistics for the behavioral sciences*. Second edition. McGraw-Hill Book Company: 399pp.

Smith, F.H., 1969. Optimum selection procedures in animal breeding. *Animal Production* **11**: 433-442.

Snedecor, G.W. and Cochran, W.G., 1989. *Statistical methods*. Eighth edition, Iowa State University Press, Ames: 503pp.

Sohn, S.I. and Goddard, R.E., 1974. Genetic study of wood specific gravity in slash pine. In: *Proceedings of the 22nd northeastern forest tree improvement conference*, Syracuse, New York, USA: 61-72.

South African Department of Environmental Affairs, 1988. *Annual Report 1988*: 21-36.

Squillace, A.E., 1966. *Geographic variation in slash pine.* Forest Science Monograph, 10: 56pp.

Squillace, A.E., 1979. Progress and future needs of forest genetics research in the south. In: *15th southern forest tree improvement conference*. Mississippi State University, USA: 11-21.

Squillace, A.E., 1989. Tree improvement accomplishments in the south. In: *Proceedings of the 20th southern forest tree improvement conference*, Charleston, South Carolina: 9-20.

Squillace, A.E. and Gansel, C.R., 1974. Juvenile-mature correlations in slash pine. *Forest Science* **20**: 225-229.

Squillace, A.E. and Kraus, J.F., 1962. Effect of inbreeding on seed yield, germination, rate of germination and seedling growth in slash pine. In: *Proceedings of a forest genetics workshop*, Macon, Georgia: 59-63.

Talbert, C.B., 1986. Multi-criterion index selection as a tool for operational tree improvement. In: *Proceedings of a joint workshop of IUFRO working parties*, Williamsburg, Virginia. North Carolina State University, Raleigh, USA: 228-238.

Talbert, C.B. and Welty, J.J., 1987. A program for index selection and gain projection. Cited in: Cotterill, P.P. and Dean, C.A. 1990. *Successful tree breeding with index selection*. CSIRO, Melbourne, Australia: 80pp.

Tallis, G.M., 1962. A selection index for optimum genotype. *Biometrics* **18**: 120-124.

Turner, H.N. and Young, S.S.Y., 1969. Quantitative genetics in sheep breeding, In: Cotterill, P.P. and Dean, C.A. 1990. *Successful tree breeding with index selection*. CSIRO: 80pp.

van Buijtenen J.P., 1976. Mating designs. In: *Proceedings of the IUFRO meeting on advanced generation breeding*, Bordeaux, INRA, Cestas, France: 11-27.

van Buijtenen, J.P. and Burdon, R.D., 1990. Expected efficiencies of mating designs for advanced-generation selection. *Canadian Journal of Forest Research* **20**: 1648-1663.

van Wyk, G., 1986. Hybrid programme: *P. elliottii* x *P. caribaea* var *hondurensis*. In: *Research Review 1985/86*. South African Department of Environmental Affairs: 8-9.

Volker, P.W., Cameron, J.N., 1988. Non-additive genetic variance in *Pinus radiata* and implications for breeding strategy. In: *Proceedings of the 10th meeting of representatives Research Working Group No. 1 of the Australian Forestry Council*, Gympie, Queensland, Australia: 94-97.

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

Wilcox, M.D., 1983. Inbreeding depression and genetic variances estimated from self- and cross-pollinated families of *Pinus radiata*. *Silvae Genetica* **32**: 89-96.

White, T.L., 1987. A conceptual framework for the tree improvement programs. *New Forests* **4**: 325-342.

White, T.L., (in press). Advanced generation breeding populations: size and structure. In: *Proceedings of the IUFRO Conference*, Cali, Colombia, 1992.

White, T.L., Hodge, G.R., 1989. *Predicting breeding values with applications in forest tree improvement*. Kluwer Academic Publishers: 367pp.

White, T.L., Hodge, G.R. and Powell, G.L., (in press). An advanced generation tree improvement program for slash pine in the Southeastern United States. Silvae genetica, in press.

Woolaston, R.R., Kanowski, P.J. and Nikles, D.G, 1990. Genetic parameter estimates for *Pinus caribaea* var *hondurensis* in coastal Queensland, Australia. *Silvae Genetica* **39**: 21-28.

Woolliams, J.A., 1989. Modifications to MOET nucleus breeding schemes to improve rates of genetic progress and decrease rates of inbreeding in dairy cattle. *Animal Production* **49**: 1-14.

Woolliams, J.A., 1990. Strategies to maximise selection progress in dairy cattle. In: *Proceedings of the 4th world congress of genetics applied to livestock production*, Edinburgh, Scotland **14**: 15-34.

Wright, J.W., 1976. *Introduction to forest genetics.* Academic Press. New York: 463pp.

Yamada, Y., 1962. Genotype by environment interaction and genetic correlation of the same trait under different environments. *Journal of Genetics* **37**: 498-509.

Zhiang, P., 1989. *Provenance test of slash and loblolly pine in China: 8 year results.* Research Institute of Forestry and the Chinese Academy of Forestry. Research Report: 37pp.

Zobel, B.J. and van Buijtenen, J.P., 1989. *Wood variation. Its causes and control.* Springer-Verlag, Berlin, Heidelberg: 363pp.

Zobel, B.J. and Talbert, J., 1984. *Applied forest tree improvement.* John Wiley and Sons, New York: 505pp.

Appendix I -

Ranks of Least Square means for growth traits, stem straightness and wood density (section 2.6.3) in the the three progeny tests 23a, 23b and 23c, at five, eight and 15 years are listed in Tables 2.1 to 2.13.

Table 2.1 Least Square means in m of height and rankings of 39 families common to the three trials at five years.

Family	23a	Rank	23b	Rank	23c	Rank
88 x 49	6.445	1	6.681	1	4.700	2
224 x 49	6.148	2	6.426	6	4.000	13
88 x 9	6.129	3	6.677	2	4.772	1
128 x 9	6.100	4	6.514	4	4.525	3
128 x 49	6.092	5	6.448	5	4.407	6
58 x 49	6.045	6	6.031	13	3.543	25
200 x 49	5.944	7	6.529	3	4.457	5
173 x 49	5.928	8	6.122	10	4.460	4
172 x 23	5.924	9	5.917	17	4.075	12
76 x 49	5.911	10	6.149	9	3.328	33
58 x 9	5.854	11	5.951	16	3.857	17
88 x 23	5.849	12	6.010	14	4.308	9
86 x 9	5.847	13	5.784	18	4.001	13
174 x 23	5.794	14	5.200	25	3.995	15
175 x 49	5.782	15	5.983	15	4.121	10
203 x 9	5.761	16	6.092	11	4.372	7
128 x 177	5.753	17	6.039	12	4.339	9
58 x 177	5.741	18	5.574	21	3.712	20
132 x 49	5.737	19	6.204	7	3.969	16
57 x 9	5.714	20	5.735	19	3.695	22
203 x 177	5.595	21	5.362	23	4.097	11
176 x 177	5.567	22	4.894	32	3.484	26
176 x 23	5.528	23	4.703	35	3.450	28
200 x 9	5.514	24	6.167	8	3.815	18
76 x 177	5.507	25	5.084	30	3.320	34
125 x 177	5.420	26	5.344	24	3.623	23
126 x 177	5.381	27	5.171	27	3.704	21
173 x 23	5.361	28	5.505	22	3.407	30
173 x 177	5.337	29	5.170	28	3.734	19
125 x 9	5.309	30	5.666	20	3.604	24
89 x 177	5.272	31	4.549	38	3.377	32
57 x 23	5.204	32	5.164	29	3.389	31
89 x 23	5.152	33	4.752	34	3.212	36
132 x 23	5.092	34	5.187	26	2.977	39
200 x 23	5.091	35	5.066	31	3.460	27
125 x 23	5.041	36	4.802	33	3.125	38
175 x 23	5.010	37	4.613	37	3.220	35
175 x 177	4.971	38	4.617	36	3.431	29
43 x 23	4.737	39	4.416	39	3.174	37

Table 2.2 Least square means for height in m and associated ranking for 39 families common to the three trials at eight years.

Family	23a	Rank	23b	Rank	23c	Rank
88 x 9	11.119	1	10.636	2	7.799	1
88 x 49	10.106	2	10.869	1	7.691	2
128 x 9	11.059	3	10.463	3	7.540	3
224 x 49	10.982	4	10.214	5	6.716	12
58 x 49	10.952	5	9.818	10	6.303	19
200 x 49	10.873	6	10.203	6	7.330	5
76 x 49	10.804	7	9.895	8	5.669	33
128 x 49	10.800	8	10.223	4	7.240	7
58 x 9	10.745	9	9.484	15	6.224	20
172 x 23	10.738	10	8.833	20	6.717	11
57 x 9	10.638	11	9.743	13	6.310	18
128 x 177	10.591	12	9.239	18	7.358	5
88 x 23	10.582	13	9.518	14	7.091	8
173 x 49	10.562	14	9.828	9	7.324	6
203 x 9	10.534	15	9.768	12	6.911	9
86 x 9	10.471	16	9.242	17	6.209	21
58 x 177	10.453	17	8.711	22	6.189	23
200 x 9	10.413	18	9.794	11	6.544	16
125 x 177	10.258	19	8.418	24	6.208	22
132 x 49	10.243	20	10.006	7	6.677	13
175 x 49	10.199	21	9.292	16	6.903	10
203 x 177	10.172	22	8.528	23	6.560	15
125 x 9	10.158	23	9.080	19	5.825	29
176 x 23	10.134	24	7.920	31	5.951	27
176 x 177	10.134	25.5	8.053	29	5.811	30
174 x 23	10.008	25.5	8.287	26	4.610	14
76 x 177	9.932	27	9.984	30	5.075	39
57 x 23	9.885	28	8.796	21	5.830	28
126 x 177	9.855	29	8.066	28	6.467	17
89 x 23	9.777	30	7.570	34	5.500	36
173 x 23	9.768	31	8.403	25	6.065	25
125 x 23	9.526	32	7.565	35	5.318	37
173 x 177	9.507	33	7.859	33	6.067	24
89 x 177	9.473	34	7.138	38	5.503	35
200 x 23	9.324	35	7.908	32	5.797	31
175 x 23	9.317	36	7.513	36	5.620	34
175 x 177	9.258	37	7.194	37	5.977	26
132 x 23	9.209	38	8.233	27	5.109	38
43 x 23	8.825	39	7.047	39	5.742	32

Table 2.3 Least square means for height at 15 years and associated rankings for 39 families common to the three progeny trials.

Family	23a	Rank	23b	Rank	23c	Rank
43 x 23	17.298	39	12.819	38	10.699	36
57 x 23	18.749	27	16.118	20	11.496	21
57 x 9	19.372	14	17.209	11	11.570	20
58 x 49	19.423	11	17.800	6	11.899	16
58 x 177	18.957	20	15.327	23	11.938	15
58 x 9	19.384	12	17.155	12	12.485	7
76 x 49	19.383	13	17.758	8	11.178	30
76 x 177	18.306	35	14.829	25	10.846	34
86 x 9	19.146	17	16.364	18	11.853	17
88 x 23	18.931	22	15.511	21	12.318	12
88 x 49	19.945	2	18.512	1	12.747	6
88 x 9	20.027	1	18.195	4	13.363	1
89 x 23	18.794	25	13.872	35	11.293	27
89 x 177	18.178	36	12.948	37	10.654	37
125 x 23	18.553	28	13.668	36	11.236	28
125 x 177	18.413	30	14.800	28	11.396	24
125 x 9	19.098	18	16.375	17	11.711	18
126 x 177	18.313	34	15.343	22	11.361	25.5
128 x 49	19.335	15	17.887	5	12.928	3
128 x 177	19.483	8	16.284	19	12.794	4
128 x 9	19.554	4	17.639	9	13.155	2
132 x 49	18.374	33	17.521	10	11.116	32
132 x 23	17.949	37	14.827	26	10.278	39
172 x 23	19.529	6	16.575	16	12.464	8.5
173 x 23	18.858	23	14.526	31	11.448	23
173 x 49	19.467	9	17.767	7	12.464	8.5
173 x 177	18.469	29	14.533	30	10.988	33
174 x 23	19.545	5	15.216	24	12.457	10
175 x 23	18.375	32	14.390	33	10.832	35
175 x 49	18.783	26	17.085	13	11.475	22
175 x 177	17.813	38	12.533	39	10.514	38
176 x 23	19.304	16	14.705	29	11.361	25.5
176 x 177	18.948	21	14.801	27	11.125	31
200 x 23	18.397	31	14.096	34	11.182	29
200 x 49	19.426	10	18.322	3	12.373	11
200 x 9	19.857	3	16.893	15	11.999	14
203 x 177	18.810	24	14.464	32	11.742	19
203 x 9	19.054	19	16.987	14	12.764	5
224 x 49	19.499	7	18.399	2	12.287	13

Table 2.4 Least squares means in cm of diameter and rankings of 39 families common to the three progeny trials at five years.

Family	23a	Rank	23b	Rank	23c	Rank
88 x 9	12.314	1	13.157	1	8.455	1
88 x 49	12.287	2	12.499	2	8.305	2
128 x 9	11.885	3	12.411	3	7.870	3
58 x 9	11.543	4	12.241	4	6.901	11
128 x 49	11.460	5	11.677	9	7.298	8
172 x 23	11.406	6	11.146	12	7.334	7
88 x 23	11.344	7	11.142	13	7.479	5
58 x 49	11.224	8	11.108	14	5.957	27
200 x 9	11.174	9	12.211	5	6.595	17
125 x 9	11.172	10	11.985	7	6.454	20
200 x 49	11.109	11	12.122	6	7.492	4
224 x 49	11.102	12	11.059	15	6.364	21
86 x 9	11.096	13	11.045	16	6.645	15
203 x 9	11.942	14	11.706	8	7.337	6
57 x 9	10.919	15	10.959	17	6.009	25
126 x 177	10.905	16	9.890	23	6.900	12
173 x 49	10.793	17	11.165	12	7.280	9
174 x 23	10.778	18	9.815	24	6.725	15
125 x 177	10.695	19	10.424	22	6.544	19
175 x 49	10.685	20	10.921	18	6.824	13
128 x 177	10.416	21	10.594	20	7.280	10
58 x 177	10.403	22	10.554	21	6.067	23
132 x 49	10.291	23	11.424	10	6.544	18
76 x 49	10.274	24	10.652	19	5.148	38
125 x 23	10.097	25	9.054	31	5.591	34
89 x 23	10.071	26	8.904	32	5.720	30
203 x 177	10.048	27	9.414	28	6.634	16
89 x 177	9.945	28	8.280	37	5.987	26
132 x 23	9.884	29	9.681	26	5.143	39
173 x 23	9.879	30	9.712	25	5.808	28
176 x 23	9.866	31	8.535	35	5.739	29
57 x 23	9.771	32	9.483	27	5.710	31
76 x 177	9.713	33	8.494	36	5.200	37
176 x 177	9.653	34	8.627	34	5.579	35
175 x 23	9.606	35	8.748	33	5.662	32
173 x 177	9.561	36	9.374	29	6.294	22
43 x 23	9.158	37	8.186	39	5.636	33
200 x 23	9.142	38	9.368	31	6.015	24
175 x 177	9.070	39	8.195	38	5.490	36

Table 2.5 Least square means for diameter in cm and associated rankings for 39 common families in the three progeny trials at eight years.

Family	23a	Rank	23b	Rank	23c	Rank
88 x 9	18.852	1	19.426	1	13.827	1
128 x 9	18.572	2	18.272	3	13.229	3
88 x 49	17.985	3	18.341	2	13.452	2
58 x 9	17.626	4	17.947	4	11.113	19
57 x 9	17.616	5	17.651	6	11.420	15
200 x 9	17.563	6	17.899	5	12.076	10
58 x 49	17.440	7	16.582	11	10.885	20
125 x 9	17.435	8	17.470	8	11.339	16
172 x 23	17.400	9	15.527	19	12.340	6
203 x 9	17.390	10	17.620	7	12.130	8
88 x 23	17.191	11	16.508	13	12.672	4
128 x 49	16.986	12	16.577	12	12.353	5
200 x 49	16.966	13	16.739	10	12.260	7
86 x 9	16.647	14	16.078	17	10.821	22
175 x 49	16.543	15	16.193	15	11.947	12
224 x 49	16.481	16	15.996	18	10.836	21
125 x 177	16.305	17	14.420	23	11.300	17
173 x 49	16.191	18	16.225	14	12.256	8
132 x 49	16.106	19	16.911	9	11.497	14
76 x 49	15.952	20	16.132	16	9.719	37
58 x 177	15.846	21	14.542	21	10.491	29
128 x 177	15.835	22	14.047	24	11.946	13
126 x 177	15.664	23	13.301	30	11.981	11
174 x 23	15.542	24	13.955	25	11.220	18
125 x 23	15.355	25	13.792	27	10.424	30
89 x 23	15.319	26	13.463	28	10.650	26
57 x 23	15.190	27	14.997	20	10.639	27
176 x 23	14.929	28	12.861	33	10.747	23
173 x 23	14.920	29	13.834	26	10.665	25
132 x 23	14.871	30	14.534	22	9.898	35
175 x 23	14.773	31	12.930	32	10.289	32
203 x 177	14.688	32	13.132	31	10.318	31
89 x 177	14.534	33	11.805	38	10.089	33
76 x 177	14.522	34	12.579	34	8.979	39
176 x 177	14.508	35	12.476	36	9.740	36
200 x 23	14.236	36	13.389	29	10.734	24
43 x 23	14.130	37	12.311	37	10.496	28
173 x 177	13.835	38	12.504	35	10.042	34
175 x 177	13.427	39	11.497	39	9.617	38

Table 2.6 Least square means for diameter at 15 years and associated rankings for 39 families common to the three progeny trials.

Family	23a	Rank	23b	Rank	23c	Rank
43 x 23	20.810	39	17.160	37	17.134	33
57 x 23	23.551	23	22.559	19	18.439	22
57 x 9	26.121	8	27.802	5	19.783	13
58 x 49	24.732	14	26.933	8	19.316	17
58 x 177	23.582	22	21.788	22	17.941	27
58 x 9	27.027	4	29.491	2	21.032	5
76 x 49	23.241	25	25.186	13	18.145	26
76 x 177	21.706	35	18.859	28	16.653	36
86 x 9	25.523	12	24.936	15	19.246	19
88 x 23	25.774	9	22.253	20	20.592	7
88 x 49	27.195	3	29.282	3	22.524	2
88 x 9	29.274	1	30.636	1	23.008	1
89 x 23	22.465	32	18.261	34	18.173	25
89 x 177	21.433	36	16.917	38	16.937	34
125 x 23	23.279	24	18.739	31	18.203	24
125 x 177	23.601	21	20.425	25	18.612	20
125 x 9	26.656	6	27.318	7	20.540	8
126 x 177	23.931	19	21.969	21	19.303	18
128 x 177	24.037	18	21.027	23	19.438	16
128 x 49	24.589	15	25.152	14	20.368	10
128 x 9	27.640	2	28.586	4	21.699	3
132 x 23	22.884	28	20.414	26	17.419	31
132 x 49	22.930	27	25.453	12	18.568	21
172 x 23	26.413	7	24.097	18	20.488	9
173 x 23	22.611	29	18.822	30	17.526	30
173 x 49	24.401	17	24.641	16	19.720	14
173 x 177	21.196	37	18.022	35	16.618	37
174 x 23	25.684	11	20.995	24	19.717	15
175 x 23	23.155	26	19.143	27	17.773	28
175 x 49	24.487	16	25.976	11	20.030	12
175 x 177	20.954	38	16.206	39	16.415	38
176 x 23	22.583	30	18.468	33	16.681	35
176 x 177	21.886	34	18.839	29	16.291	39
200 x 23	22.544	31	18.658	32	17.750	29
200 x 49	25.150	13	26.600	10	20.614	6
200 x 9	25.745	10	26.932	9	20.216	11
203 x 177	22.425	33	17.842	36	17.410	32
203 x 9	27.025	5	27.658	6	21.601	4
224 x 9	23.771	20	24.272	17	18.359	23

Table 2.7 Least square means in dm^3 and associated rankings for volume at age at five years in the three trials.

Family	23a	Rank	23b	Rank	23c	Rank
88 x 49	35.486	1	38.309	2	13.659	1
88 x 9	33.398	2	41.918	1	13.374	2
128 x 9	31.247	3	36.579	3	11.689	3
128 x 49	29.758	4	32.147	7	10.181	5
58 x 9	28.567	5	33.572	6	8.644	12
172 x 23	28.480	6	28.564	12	9.632	7
58 x 49	27.931	7	28.276	14	6.161	23
88 x 23	27.672	8	27.792	16	9.840	6
224 x 49	27.571	9	29.413	11	7.312	18
200 x 49	26.534	10	35.443	4	10.479	4
86 x 9	26.276	11	27.988	15	7.148	20
200 x 9	25.397	12	34.304	5	7.560	16
203 x 9	25.253	13	31.117	9	9.381	10
173 x 49	25.209	14	28.289	13	9.410	9
174 x 23	24.789	15	19.599	25	7.938	14
57 x 9	24.583	16	26.294	19	5.467	25
125 x 9	24.589	17	31.244	8	6.689	22
175 x 49	24.267	18	26.787	18	8.130	13
76 x 49	23.561	19	26.845	17	4.856	28
126 x 177	23.288	20	21.200	23	8.848	11
128 x 177	23.139	21	25.867	20	9.614	8
58 x 177	23.120	22	24.314	21	6.748	21
125 x 177	22.529	23	22.638	22	7.292	19
132 x 49	22.413	24	29.508	10	7.927	15
203 x 177	20.948	25	18.631	26	7.464	17
176 x 177	19.685	26	15.108	32	4.679	30
176 x 23	19.616	27	14.002	36	4.683	29
89 x 177	19.579	28	12.841	37	4.859	27
173 x 23	19.400	29	19.868	24	5.017	26
76 x 177	19.127	30	14.442	35	2.934	39
125 x 23	19.089	31	15.568	31	4.292	34
89 x 23	19.001	32	14.686	33	4.412	33
132 x 23	18.483	33	18.625	27	3.933	35
57 x 23	18.314	34	17.450	29	4.605	32
173 x 177	18.177	35	17.291	30	6.154	24
175 x 23	16.805	36	14.499	34	3.879	36
200 x 23	16.242	37	17.493	28	4.637	31
175 x 177	15.000	38	12.733	38	3.866	37
43 x 23	14.593	39	12.045	39	3.737	38

Table 2.8 Least squares means for volume in dm^3 and its rankings of the families common to the three progeny trials at eight years.

Family	23a	Rank	23b	Rank	23c	Rank
88 x 9	142.610	1	144.750	1	60.554	1
88 x 49	130.980	2	130.910	2	56.261	2
58 x 9	123.820	3	115.570	4	33.160	19
58 x 49	121.940	4	101.890	11	32.872	20
203 x 9	120.300	5	113.480	5	42.289	7
57 x 9	119.320	6	110.260	6	33.369	18
172 x 23	118.900	7	85.369	19	43.837	4
200 x 9	117.910	8	117.150	3	39.714	10
128 x 49	114.880	9	101.550	12	42.909	6
200 x 49	113.940	10	107.260	8	43.733	5
125 x 9	113.490	11	106.920	9	32.785	21
88 x 23	112.360	12	96.858	15	46.172	3
224 x 49	108.900	13	97.431	13	33.500	17
86 x 9	108.380	14	95.256	16	27.273	24
76 x 49	103.300	15	97.235	14	26.504	27
175 x 49	102.940	16	90.990	18	37.160	11
173 x 49	102.400	17	94.837	17	41.186	9
128 x 9	102.030	18	107.400	7	35.053	15
132 x 49	98.866	19	103.610	10	37.118	12
58 x 177	98.702	20	75.731	20	30.887	22
125 x 177	98.231	21	68.874	23	35.166	14
128 x 177	96.563	22	71.188	22	41.956	8
174 x 23	89.905	23	63.200	25	33.647	16
126 x 177	88.760	24	60.934	27	36.467	13
203 x 177	84.665	25	59.962	28	28.719	23
125 x 23	83.900	26	56.808	29	23.238	32
89 x 23	83.287	27	52.333	31	25.516	29
57 x 23	83.156	28	72.502	21	26.407	28
176 x 23	82.471	29	51.997	32	26.552	26
176 x 177	80.859	30	51.690	33	22.789	35
173 x 23	80.804	31	61.625	26	26.899	25
76 x 177	77.832	32	50.197	34	19.536	38
89 x 177	77.157	33	40.356	38	22.849	34
132 x 23	76.769	34	67.434	24	23.382	31
175 x 23	74.523	35	49.161	35	20.947	36
200 x 23	69.972	36	54.675	30	22.991	33
173 x 177	69.907	37	48.614	36	23.684	30
43 x 23	65.549	38	42.084	37	20.690	37
175 x 177	63.911	39	39.223	39	18.920	39

Table 2.9 Least square means for volume at 15 years and associated rankings for 39 families common to the three progeny trials.

Family	23a	Rank	23b	Rank	23c	Rank
43 x 23	280.89	39	160.89	37	98.4	38
57 x 23	382.82	23	313.41	20	151.17	20
57 x 9	480.97	8	495.56	6	164.80	18
58 x 49	431.36	15	472.86	9	166.68	17
58 x 177	391.08	20	306.94	21	152.17	19
58 x 9	515.12	4	553.97	3	203.82	6
76 x 49	383.39	22	412.21	14	135.11	25
76 x 177	318.02	35	210.86	28	105.97	36
86 x 9	459.66	11	418.11	12	151.13	21
88 x 23	451.94	12	300.54	22	191.48	8
88 x 49	529.03	3	571.01	2	252.59	2
88 x 9	613.32	1	624.25	1	270.81	1
89 x 23	347.83	32	185.61	36	127.91	28
89 x 177	305.38	37	157.66	38	102.24	37
125 x 23	377.08	24	201.30	33	133.55	26
125 x 177	371.24	25	248.49	25	148.19	22
125 x 9	495.64	7	467.17	10	177.93	12
126 x 177	385.31	21	318.39	19	170.01	15
128 x 177	432.26	14	414.63	13	190.02	9
128 x 49	409.98	17	291.97	23	184.31	11
128 x 9	542.30	2	537.38	4	227.34	3
132 x 23	351.15	30	242.09	26	119.64	32
132 x 49	356.26	29	410.92	15	139.73	24
172 x 23	504.99	6	395.10	18	217.34	4
173 x 23	356.85	28	205.14	31	125.61	29
173 x 49	415.65	16	399.88	16	172.07	14
173 x 177	305.75	36	186.94	35	106.47	35
174 x 23	472.97	9	277.90	24	187.90	10
175 x 23	361.43	27	205.57	30	121.52	31
175 x 49	402.35	18	242.92	11	167.22	16
175 x 177	290.12	38	141.07	39	90.81	39
176 x 23	365.65	26	210.46	29	116.19	33
176 x 177	339.97	34	228.61	27	113.45	34
200 x 23	345.05	33	204.71	32	122.39	30
200 x 49	437.92	13	473.17	8	195.69	7
200 x 9	472.28	10	482.26	7	174.57	13
203 x 177	350.38	31	193.59	34	129.54	27
203 x 9	506.96	5	498.20	5	215.37	5
224 x 49	398.60	19	395.59	17	143.72	23

Table 2.10 Least square means and associated rankings for stem straightness at five years in the three trials.

Family	23a	Rank	23b	Rank	23c	Rank
200 x 49	4.762	1	4.471	1	4.323	1
224 x 49	4.625	2	4.024	5	3.638	21
172 x 23	4.606	3	3.659	22	3.906	10
58 x 49	4.537	4	3.883	11	3.577	29
173 x 49	4.451	5	3.864	12	4.039	2
76 x 49	4.444	6	3.841	14	3.483	34
132 x 49	4.425	7	4.179	3	3.762	16
200 x 23	4.398	8	4.057	4	3.967	5
200 x 9	4.391	9	4.221	2	3.955	6
88 x 49	4.350	10	4.007	6	4.033	3
175 x 49	4.341	11	3.846	13	3.902	11
176 x 23	4.337	12	3.802	15	3.705	18
57 x 9	4.320	13	3.963	9	3.715	17
128 x 49	4.291	14	3.665	21	3.867	12
88 x 23	4.213	15	4.000	7	3.929	8
128 x 9	4.190	16	3.773	17	3.970	4
58 x 9	4.188	17	3.719	18	3.621	24
173 x 23	4.161	18	3.714	19	3.599	28
57 x 23	4.143	19	3.983	8	3.770	15
125 x 23	4.117	20	3.467	28	3.411	37
174 x 23	4.093	21	3.481	27	3.859	13
86 x 9	4.064	22	3.601	23	3.943	7
58 x 177	4.038	23	3.191	35	3.433	35
88 x 9	4.023	24	3.793	16	3.928	9
89 x 23	4.004	25	3.693	20	3.606	26
176 x 177	3.987	26	3.558	25	3.637	22
125 x 177	3.972	27	3.083	37	3.493	33
132 x 23	3.967	28	3.918	10	3.312	39
128 x 177	3.950	29	3.231	34	3.682	19
175 x 23	3.924	30	3.439	30	3.632	23
125 x 9	3.897	31	3.530	26	3.615	25
203 x 9	3.863	32	3.591	24	3.771	14
76 x 177	3.849	33	3.254	33	3.320	38
126 x 177	3.839	34	3.160	36	3.532	31
43 x 23	3.835	35	3.835	35	3.603	27
89 x 177	3.825	36	3.361	31	3.655	20
173 x 177	3.814	37	3.338	32	3.432	36
175 x 177	3.564	38	3.033	39	3.503	32
203 x 177	3.565	39	3.065	38	3.065	39

Table 2.11 Least squares means for stem straightness and associated rankings of 39 families to the three progeny trials at eight years.

Family	23a	Rank	23b	Rank	23c	Rank
200 x 49	4.454	1	4.211	1	3.053	1
58 x 49	4.421	2	3.594	15	2.747	7
57 x 23	4.419	3	4.018	5	2.464	23
172 x 23	4.403	4	3.321	25	2.645	13
173 x 23	4.343	5	3.445	21	2.420	25
224 x 49	4.337	6	3.819	6	2.658	12
173 x 49	4.315	7	3.634	13	2.740	8
200 x 23	4.311	8	3.789	7	2.615	15
176 x 23	4.286	9	3.498	20	2.402	28
125 x 23	4.237	10	3.113	29	2.478	22
57 x 9	4.206	11	4.116	2	2.570	18
200 x 9	4.205	12	4.024	4	2.794	3
174 x 23	4.188	13	3.195	28	2.634	14
89 x 23	4.184	14	3.574	17	2.390	29
175 x 49	4.127	15	3.659	10	2.749	5.5
58 x 9	4.122	16	3.420	22	2.501	20
76 x 49	4.114	17	3.632	14	2.363	32
128 x 49	4.113	18	3.505	19	2.717	10
132 x 49	4.109	19	4.085	3	2.731	9
175 x 23	4.089	20	3.368	23	2.407	27
128 x 9	4.073	21	3.650	12	2.695	11
88 x 23	4.029	22	3.657	11	2.764	4
43 x 23	4.028	23	3.210	27	2.435	24
58 x 177	4.021	24	3.886	37	2.320	33
125 x 9	4.017	25	3.265	26	2.581	17
173 x 177	4.008	26	3.047	34	2.380	31
132 x 23	3.973	27	3.752	8	2.291	36
128 x 177	3.963	28	3.047	33	2.481	21
176 x 177	3.937	29	3.082	31	2.315	34
86 x 9	3.920	30	3.363	24	2.527	19
125 x 177	3.913	31	2.714	39	2.411	26
203 x 9	3.892	32	2.512	18	2.594	16
126 x 177	3.872	33	3.035	35	2.389	30
88 x 49	3.839	34	3.675	9	2.889	2
76 x 177	3.823	35	3.060	32	2.057	39
89 x 177	3.766	36	3.083	30	2.239	38
175 x 177	3.667	37	2.900	36	2.291	35
88 x 9	3.648	38	3.593	16	2.749	5.5
203 x 177	3.630	39	2.808	38	2.282	37

Table 2.12 Least square means for stem straightness at 15 years and associated rankings for 39 common families in the three progeny trials.

Family	23a	Rank	23b	Rank	23c	Rank
43 x 23	4.110	6	3.667	33	3.809	19
57 x 23	4.089	8	4.402	12	3.816	18
57 x 9	4.086	9	4.618	4	3.655	32
58 x 177	3.963	22	3.784	30	3.941	11
58 x 49	4.197	4	4.444	8	4.235	3
58 x 9	3.967	21	4.511	5	3.935	12
76 x 49	3.921	25	4.389	13	3.748	24
76 x 177	3.841	34	3.636	34	3.407	39
86 x 9	3.911	29	4.108	19	3.729	27
88 x 23	3.858	32	3.937	24	3.858	15
88 x 49	3.912	28	4.401	11	4.034	6
88 x 9	3.836	35	4.277	15	3.754	22
89 x 23	4.046	14	3.829	27	3.981	8
89 x 177	3.916	27	3.489	37	3.808	20
125 x 23	4.059	13	3.613	35	3.720	28
125 x 177	4.016	15	3.495	36	3.730	26
125 x 9	3.999	18	4.199	17	3.669	31
126 x 177	3.851	33	3.873	26	3.769	21
128 x 149	3.997	19	4.219	16	4.056	4
128 x 177	4.067	12	3.804	29	3.951	10
128 x 9	3.946	24	4.492	6	3.835	17
132 x 23	3.660	38	4.046	21	3.515	38
132 x 9	3.642	39	4.657	3	3.630	33
172 x 23	4.302	2	4.120	18	3.880	14
173 x 23	4.228	3	3.942	23	3.897	13
173 x 49	4.073	11	4.382	14	4.260	2
173 x 177	4.002	17	3.762	31	3.617	34
174 x 23	3.979	20	3.921	25	3.750	23
175 x 23	4.008	16	3.946	22	3.601	36
175 x 49	4.075	10	4.431	10	4.000	7
175 x 177	3.781	36	3.425	39	3.679	35
176 x 23	3.949	23	3.805	28	3.744	25
176 x 177	3.694	37	3.721	32	3.671	30
200 x 23	4.184	5	4.057	20	4.044	5
200 x 49	4.355	1	4.842	1	4.370	1
200 x 9	4.095	7	4.697	2	3.857	16
203 x 177	3.877	31	3.447	39	3.584	37
203 x 9	3.879	30	4.432	9	3.674	29
224 x 49	3.918	26	4.473	7	3.962	9

Table 2.13 **Least square means for wood density at 15 years and associated rankings for 39 common families in the three progeny trials.**

Family	23a	Rank	23b	Rank	23c	Rank
43 x 23	415.66	24	363.45	22	421.59	26
57 x 9	380.88	38	335.91	38	395.15	38
57 x 23	397.54	31	345.68	32	409.59	31
58 x 9	372.20	39	326.43	39	387.67	39
58 x 49	424.21	18	375.32	16	435.23	18
58 x 177	428.45	16	374.46	18	438.51	17
76 x 177	463.81	1	407.28	2	467.51	2
76 x 49	450.22	4	405.90	3	463.36	3
86 x 9	409.74	27	361.60	25	424.54	22
88 x 9	396.62	32	345.95	31	407.15	32
88 x 23	423.99	19	365.28	19	427.12	20
88 x 49	445.54	6	388.68	6	451.57	6
89 x 23	388.01	36	337.27	37	399.39	37
89 x 177	419.79	22	362.16	24	429.57	19
125 x 9	389.28	35	340.50	35	403.86	34
125 x 23	409.85	26	356.06	29	418.86	30
125 x 177	449.22	5	381.45	13	453.16	5
126 x 177	426.95	17	374.83	17	439.38	15
128 x 9	391.23	34	344.08	33	406.41	33
128 x 49	432.63	15	387.87	7	449.43	9
128 x 177	432.73	13.5	379.19	15	444.41	14
132 x 23	410.94	25	364.30	20	424.31	23
132 x 49	438.43	9	392.53	5	448.80	10
172 x 23	407.78	29	356.09	28	421.15	28
173 x 9	382.12	37	340.27	36	401.00	36
173 x 23	417.07	23	362.72	23	425.46	21
173 x 49	434.47	11	387.27	8	449.71	8
173 x 177	438.79	8	386.83	9	450.62	7
174 x 23	419.85	21	360.13	26	420.57	29
175 x 23	407.59	30	356.05	30	422.46	25
175 x 49	432.73	13.5	386.60	10	445.15	13
175 x 177	439.80	7	382.70	12	447.96	11
176 x 23	434.23	12	379.81	14	438.77	16
176 x 177	459.93	3	402.29	4	462.52	4
200 x 9	392.76	33	343.45	34	403.71	35
200 x 23	422.00	20	363.78	21	423.19	24
200 x 49	436.56	10	385.60	11	446.56	12
203 x 9	408.77	28	358.39	27	421.28	27
224 x 49	461.85	2	412.55	1	471.17	1

Appendix II -

The advantages of combined index selection: an example from Zimbabwe's *Pinus elliottii* breeding programme

I.Z. Pswarayi, R.D. Barnes and P.J. Kanowski

Presented at the IUFRO Conference in Cali, Colombia, October 1992.

Oxford Forestry Institute
Department of Plant Sciences
University of Oxford
South Parks Road
Oxford OX1 3RB
England

Abstract

As in most tree improvement programmes, selection of plus trees in the Zimbabwean breeding population of *Pinus elliottii* has traditionally been made phenotypically. The recent advent of user-friendly software packages for combined index selection now allows selection on the basis of genetic information. This paper compares the results of combined index selection at ages five, eight and 15 for a typical *P. elliottii* breeding population. In all cases, selection for increased mature stem volume was based on a combination of stem diameter, height and straightness. The greatest annual gains in the breeding objective resulted from selection at eight years, on an index combining diameter and stem straightness; gains from selection at five years were marginally less. Selection at age five was most efficient, and the most efficient indices at all ages were those which included all three selection traits. Those indices were also the most accurate at ages eight and 15 years; at age five, an index based on height alone was marginally more accurate. In terms of practical breeding, selection based on both height and diameter at age five would probably be preferable and would produce 65% more gain per year than selection at age 15. As the genetic parameters that characterise this population of *P. elliottii* are typical of many populations of industrial trees, similar advantages can be expected in comparable breeding programs.

Introduction

The tree breeding cycle consists of two major activities, *viz* selection and mating (White 1987), and the rate of genetic progress depends on both being conducted efficiently and effectively. Cotterill (1986a) and Dean (1990) have made the point that, historically, tree breeders have emphasised mating designs to the relative neglect of efficient selection. Selection can be phenotypic, where genetic information is not available or not used, on a family/within family basis (Cotterill and Dean 1990) where family mean information is used to determine those families in which individuals will be selected phenotypically; or entirely on the basis of genetic information, through index selection. The use of family/within family selection and index selection is effectively restricted to individuals of known pedigree planted in replicated tests; it is not, for example, applicable to selection in wild or plantation populations. Where it is feasible, index selection is always superior, in terms of genetic gain, to alternatives (Falconer 1981). For this reason, index selection methodologies have been well-developed by animal breeders (*eg* Turner and Young 1969, in Cotterill and Dean 1990) and long recommended by tree breeders (*eg* Baradat 1976, Burdon 1979, Dean *et al* 1983). In the case of typical genetic parameters and generation intervals for populations of industrial trees, Cotterill (1986a and b) demonstrated that the use of index selection in conjunction with simple mating designs returned genetic gains per unit time comparable to those associated with more elaborate mating schemes.

Combined index selection, which takes account of both individual and family performance, is the most efficient form of index selection (Cotterill and Dean 1990). Use of a combined index allows individual superiority to compensate, to some extent, for poor family performance, and vice versa. As heritability decreases, individual phenotype becomes a less accurate guide to an individual's genetic worth; consequently, relatively more weight is placed on family mean performance. As the heritabilities of most traits of interest in tree breeding programmes are no more than moderately strong, combined index selection is particularly appropriate.

The *Pinus elliottii* var. *elliottii* Engelm. breeding programme in Zimbabwe began in 1963 (Barrett and Mullin 1968), and is now into its second generation (Barnes 1991). First-generation plus trees were selected phenotypically in plantation stands; their open and control-pollinated progeny were established in an extensive series of progeny tests, from which second-generation trees were selected.

This study compares the expected gains, selection efficiencies and accuracies of selection resulting from combined index selection at ages five, eight and 15 years in the Zimbabwean *P. elliottii* breeding programme. The breeding objective was to maximise sawn timber production at maturity; in Zimbabwe at present, this effectively corresponds to maximising volume production. Volume at age 15 was used as the best proxy to this objective. Assessment data for stem diameter, height and straightness were available for use as selection traits.

Materials and Methods

Progeny test location and management

The progeny test from which data used in this study originate was established by the Zimbabwe Forestry Commission and is identified locally as 23b. It was planted on quartzite/dolerite derived soils at Stapleford, in the Eastern Highlands of Zimbabwe (latitude 18^0 44'S, longitude 32^0 49'E, altitude 1760 m, mean annual rainfall 1836 mm). The site is typical of those in the Zimbabwean Eastern Highlands on which commercial plantations of *P. elliottii* are established. After disc-harrowing of the sites, the progeny test was planted between January and February 1976, at a spacing of 1.5 m x 1.5 m. The test was established as a randomised complete block with six replications; each family was represented in every replicate by a 10 tree line plot. No fertilization was carried out in the field; weeding was manual when necessary during the test's early life. The test was pruned at five years and thinned at eight years by systematically removing every other tree, to leave 50% of the original trees standing.

Genetic material

The progeny test included a total of 142 of the possible 207 controlled crosses in a factorial mating design between 23 female and 9 male parents. The 32 parents used in the factorial were selected as superior phenotypes from unimproved plantations in both Zimbabwe and South Africa. Little is known of their origin or degree of relatedness, but it is assumed that they are unrelated. The South African plantations in which parents were selected originated from seedlots in Georgia, S. Carolina and Central Louisiana, USA; the Zimbabwean plantations were derived from seed collected in South African plantations. The crosses represented in the test are depicted in Table 1.

Table 1. Parents and families included in the progeny test.

Parental codes	Males								
Females	22	23	45	49	129	137	177	9	130
58	X	X	X	X	X	X	X	X	
76	X	X	X	X	X	X	X	X	
87		X	X	X	X	X	X	X	
126	X	X	X	X	X	X	X	X	
128	X	X	X	X	X	X	X	X	
174	X	X	X	X	X	X	X	X	
175	X	X	X	X	X	X	X	X	X
200	X	X	X	X	X	X	X	X	X
28	X			X			X	X	
43	X	X		X	X			X	
57	X	X	X		X	X	X	X	
125	X	X			X		X	X	
132	X	X	X	X	X	X	X	X	
138	X	X	X	X			X	X	X
172	X	X		X				X	
173		X	X	X		X	X	X	X
176	X	X			X	X	X		
86			X	X			X	X	
88	X	X	X	X		X		X	
89		X		X	X	X	X		
203		X					X	X	
224		X		X	X		X	X	
234	X							X	

The test was assessed for a variety of traits at five, eight and 15 years after planting. Traits relevant to this study are stem diameter over bark (DBH), measured by girth tape; stem height (HT), measured by metre rods; and stem straightness (STR), subjectively assessed on a predetermined scale of 1 (worst) to 7 (best).

Data from the five, eight and 15 year assessments of diameter, height and stem straightness were used as the basis for combined index selection. The general Equation on which selection was based is given by Cotterill and Dean (1990, Chapter 9):-

$$I = b_1P_1 + b_2F_1 + b_3P_2 + b_4F_2 + \ldots + b_nP_j + b_{n+1}F_j \quad (1)$$

where P_j and F_j represent phenotypic and family mean values, respectively, for the j^{th} trait. A coefficient of relationship amongst full-sibs of 0.5 was assumed. The index coefficients b_1 to b_n were calculated assuming a constant 60 progeny per family at age five and 30 progeny per family at ages eight and 15 due to the 50% thinning effected at age eight, following Cotterill and Dean (1990), according to Equation (2):-

$$b = P^{-1}Aw \quad (2)$$

where b = vector of index coefficients;

P^{-1} = phenotypic variance-covariance matrix;

A = matrix of additive genetic variances and covariances;

w = vector of economic weights.

The objective of the combined index is to maximise gain in a breeding objective H (Cotterill and Dean 1990, Chapter 8); in order to calculate b, it is therefore necessary to define the breeding objective. Here, the most appropriate breeding objective was simply:-

$$H_1 = W_1 A_{vol} \quad (3)$$

where H_1 = genetic worth;

W_1 = the weighting factor;

A_{vol} = the individual tree's breeding value for volume.

In this case, W_1 was set to unity, so that the breeding objective corresponded to volume production.

Six combined selection indices were constructed in order to estimate genetic gains. Individual and family mean data were available for all traits at all ages with the exception of height at age eight, for which only family mean data from felled trees were available. The indices were:-

$I_1 = b_1 P_{HT} + b_2 F_{HT}$

$I_2 = b_1 P_{DBH} + b_2 F_{DBH}$

$I_3 = b_1 P_{HT} + b_2 F_{HT} + b_3 P_{DBH} + b_4 F_{DBH}$

$I_4 = b_1 P_{HT} + b_2 F_{HT} + b_3 P_{DBH} + b_4 F_{DBH} + b_5 P_{STR} + b_6 F_{STR}$

$I_5 = b_1 P_{DBH} + b_2 F_{DBH} + b_3 P_{STR} + b_4 F_{STR}$

$I_6 = b_1 P_{HT} + b_2 F_{HT} + b_3 P_{STR} + b_4 F_{STR}$

where b_n, P_i and F_j are as described for Equation (1).

In this study, ages five and eight were considered juvenile; age 15 was considered to approximate maturity.

Gains per year in H_1 from indirect (juvenile) selection and direct (mature) selection were estimated by the programme RESI (Cotterill and Dean 1990):-

(4)

$$G_1 = i_j \frac{\frac{w'Gw}{b'Pb}}{T_j}$$

where G1 = annual gains from indirect selection;

i_j = selection intensity at age j, here five and eight years, estimated as 2.665 (1:100) at five years and 2.421 (1:50) at eight years and 15 years;

w' = transpose of the vector of economic weights;

G = genotypic variance-covariance matrix of traits in the breeding objective;

w = vector of economic weights;

b' = transope of the vector of the index coefficients;

P = phenotypic variance-covariance matrix of traits in the index;

b = a vector of the index coefficients;

T_j = the generation interval for juvenile selection;

where j = the time to selection, here five or eight years;

y = as defined above, here estimated as eight years.

Similarly, gains in volume from direct selection based on mature traits were estimated as in Equation (5):-

(5)

$$G_2 = i_m \frac{\frac{w'Gw}{b'Pb}}{T_m}$$

where G_2 = annual gain from direct selection;

i_m = selection intensity at m (15 years), here estimated as 2.421 (1:50), due to the 50% thinning at eight years;

T_m = m+y; the generation interval for mature selection;

where m = the time to selection, here 15 years;

y = the breeding interval, that is, the estimated time between selection of parents and establishment of the next generation, here estimated as eight years;

and w', G, w, b', P and b are as defined above.

Efficiency of selection

The efficiency of selection of an index was estimated following Lambeth (1980), according to Equation (6):-

$$E = \frac{G_1}{G_2} \qquad (6)$$

where G_1 = annual gains from indirect selection;

G_2 = annual gains from direct selection.

Accuracies of selection

Accuracies of selection are defined as the correlation between the selection criteria and the breeding objective (Nicholas 1987). Accuracies of selection for combined index selection were estimated by the programme RESI (Cotterill and Dean 1990):-

$$\rho A = \sqrt{\frac{C' V^{-1} C}{\sigma_a^2}} \qquad (7)$$

where ρA = accuracy of selection;

C' = transpose of the covariance matrix;

V^{-1} = inverse of the variance-covariance matrix;

C = covariance matrix;

σ^2_a = additive genetic variance for volume.

Genetic parameter estimates

Genetic parameters were estimated from maternal components of variance by the program REML, which is fully described elsewhere (Patterson and Thompson 1971, 1974, Robinson 1987, Searle 1987). The derivation of those used in this study is detailed elsewhere (Pswarayi *et al* in preparation); estimates are presented in Table 2. Genetic correlations between HT8 and traits at 15 years were based on family means rather than individual tree data.

Table 2. Heritabilities and associated standard errors (bold on diagonal), relevant genetic correlations genetic correlations and associated standard errors (above diagonal), and phenotypic correlations (below diagonal) for selection traits at five, eight and 15 years. Genetic parameters were estimated from maternal component variance in the factorial mating design.

Trait	HT5	DBH5	STR5	HT8	DBH8	STR8	HT15	DBH15	VOL15	STR15
HT5	**0.27±0.09**	0.65±0.12	0.50±0.17							0.64±0.13
DBH5	0.72	**0.24±0.08**								0.81±0.08
STR5	0.31	0.21	**0.12±0.06**							0.26±0.22
HT8				**0.39±0.13**	0.80±0.08	0.26±0.21				0.88
DBH8				0.82	**0.26±0.09**	0.17±0.22				0.91±0.04
STR8				0.45	0.38	**0.29±0.10**				-0.07±0.23
HT15							**0.26±0.09**	0.74± 0.10	0.43±0.20	0.79±0.09
DBH15							0.80	**0.26±0.10**	0.37±0.21	0.98±0.01
STR15							0.59	0.60	**0.31±0.05**	0.37±0.21
VOL15	0.59	0.70	0.25	0.88	0.84	0.35	0.59	0.94	0.55	**0.10±0.11**

Results

Genetic gains and efficiencies and accuracies of selection are presented in Table 3. Gains are expressed in absolute units on an annual basis, assuming generation intervals of 13, 16 and 23 years when selection was effected at five, eight and 15 years, respectively, and in terms of percentage gain per generation.

Table 3. Estimated annual gains (dm^3), percentage gains per generation (bracketed), efficiencies and accuracies of selection to improve breeding objective H_1 from selection at three ages.

	Gains in breeding objective H_1 from selection at three ages			Efficiencies of selection at three ages to improve H_1			Accuracies of selection to improve H_1 from selection at three ages		
Index No and composition	5	8	15	Age 5	8	15	5	8	15
I_1 - HT	14.9 (54.2)	12.6 (56.4)	7.30 (47.1)	1.76	1.41	0.77	0.63	0.67	0.56
I_2 - DBH	15.3 (56.0)	13.1 (58.8)	9.10 (58.7)	1.71	1.36	0.95	0.57	0.65	0.70
I_3 - HT,DBH	15.6 (56.9)	14.2 (63.8)	9.46 (61.1)	1.82	1.47	0.95	0.61	0.70	0.70
I_4 - HT,DBH,STR	14.4 (52.5)	12.1 (54.3)	9.07 (58.5)	1.85	1.59	0.99	0.62	0.76	0.73
I_5 - DBH,STR	14.5 (52.9)	15.8 (70.9)	9.30 (60.0)	1.72	1.44	0.97	0.57	0.69	0.72
I_6 - HT,STR	15.2 (55.5)	13.8 (61.8)	7.77 (50.1)	1.80	1.54	0.82	0.60	0.74	0.60

The greatest gain per unit time and per generation in the breeding objective resulted from selection at eight years on an index based on diameter and stem straightness. Efficiencies of selection were greatest for selection at age five, and greatest at all ages for the index that

included all three traits. Indices which included all three traits were most accurate at ages eight and 15 but, at age five, the index based on height alone was marginally more accurate.

Discussion

Although the greatest gains per generation resulted, almost universally, from selection at age eight, gain per unit time is likely to be a more appropriate criterion for selection (Cotterill 1986a and b). There is little difference, in terms of gain per unit time in the breeding objective, in selection on Index 3 (DBH+HT) at age five or Index 5 (DBH+STR) at age eight. The former is about 25% more efficient but about 12% less accurate than the latter; in terms of practical tree breeding, it would probably be preferable to select earlier on the relatively cheaply assessed growth traits at age five. Further, given that "maximising response from tree breeding is basically a matter of efficient selection" (Cotterill 1986b), the breeder is more likely to favour the more efficient selection at the earlier age.

These results demonstrate the potentially substantial advantages of index selection. Gains per unit time from selection at age five were some 65% greater than those from selection at age 15, and only around 12% less accurate. The relatively high genetic correlations between selection traits and the breeding objective, which were responsible for this result, are typical of those reported previously for *P. elliottii* (Allen 1985, Cotterill *et al* 1987, Dorman and Squillace 1974) and for other industrial species, including *P. banksiana* (Riemenschneider 1988), *P. caribaea* (Woolaston *et al* 1990), *P. pinaster* (Cotterill *et al* 1987), *P. radiata* (Cotterill and Dean 1988), *P. taeda* (Foster 1986), *Pseudotsuga menziesii* (King *et al* 1988) and *Eucalyptus globulus* (Borralho *et al* 1992). Similar advantages from index selection can therefore be expected in many other breeding programs for industrial species.

The work reported here is a preliminary study preceding more thorough investigations of a broader range of breeding objectives and selection indices for *P. elliottii* in Zimbabwe. The results of these studies will be used to optimise selection procedures and breeding strategy for the diverse objectives of *P. elliottii* breeding program in Zimbabwe.

Acknowledgements

This work is part of the senior author's doctoral research at the Oxford Forestry Institute, supported by the UK Overseas Development Agency, the British Council and the Zimbabwe Forestry Commission. The Zimbabwe Forestry Commission allowed use of data for this

study; we gratefully acknowledge the work of many Commission staff in establishing, maintaining and assessing the progeny test.

References

Allen, P.J. 1985. Estimation of genetic parameters for wood properties in slash pine in south east Queensland. *Department of Forestry Queensland,* Research note 41 Department of Forestry, Queensland, Australia: 15pp.

Baradat, P.H., 1976. Use of juvenile-mature relationship and information from relatives in combined multitrait selection. In: *Proc., IUFRO Meeting on Advanced Generation Breeding,* Bordeaux, France: 121-138.

Barnes, R.D., 1991. *The Forest Genetics Programme in Zimbabwe, Part II. Plan of work for 1991/92.* Overseas Development Adminstration/ Zimbabwe Forestry Commission: 298pp.

Barrett, R.L. and Mullin, L.J. 1968. A Review of Introductions of Forest Trees in Rhodesia. In: *The Rhodesia Bulletin of Forestry Research 1.* Rhodesia Forestry Commission: 227pp.

Borralho, N.M.G., Kanowski, P.j., and Cotterill, P.P. 1992. Genetic control of growth of *Eucalyptus globulus* in Portugal. I. Genetic and phenotypic parameters. *Silvae Genetica* **41**: 39-45.

Burdon, R.D., 1979. Generalisation of multi-trait selection indices using progeny test information from several sites. *New Zealand Journal Forest Science* **9**: 145-152.

Cotterill, P.P., 1986a. Genetic gain expected from alternative breeding strategies including simple low cost options. *Silvae Genetica* **35**: 212-223.

Cotterill, P.P., 1986b. Breeding strategy: don't underestimate simplicity! In: *Proc. Joint IUFRO Meet. Working Parties on Breeding Theory, Progeny Testing and Seed Orchards,* Williamsburg, Virginia: 8-23.

Cotterill, P.P., and Dean, C.A. 1988. Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. *Silvae Genetica* **37**: 138-146.

Cotterill, P.P., and Dean, C.A. 1990. *Successful Tree Breeding with Index Selection.* CSIRO, Melbourne: 80pp.

Cotterill, P.P., Dean, C.A., and van Wyk, G. 1987. Additive and dominance genetic effects in *Pinus pinaster, P. radiata* and *P. elliottii* and some implications for breeding strategy. *Silvae Genetica* **36**: 221-232.

Dean, C.A., 1990. *Genetics of growth and wood density in radiata pine.* Unpublished Ph.D. Thesis. University of Queensland, Brisbane, Australia: 76pp

Dean, C.A., Cotterill, P.P., and Cameron, J.N. 1983. Genetic parameters and gains expected from multiple trait selection of radiata pine in eastern Victoria. *Australian Forest Research* **13**: 271-278.

Dorman, K.W. and Squillace, A.E. 1974. Genetics of slash pine. *USDA Forest Service Research Paper*, Handbook no. 471, Washington: 20pp.

Falconer, D.S. 1981. *Introduction to Quantitative Genetics.* Second Edition. Longman, London: 340pp.

Foster, G.S. 1986. Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *Forest Science* **32**: 944-958.

King, J.N., Yeh, F.C., Heaman, J.C. and Dancick, B.P. 1988. Selection of wood density and diameter in controlled crosses of coastal Douglas-fir. *Silvae Genetica* **37**: 152-157.

Lambeth, C.C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. *Forest Science* **26**: 571-580.

Nicholas, F.W. 1987. *Veterinary Genetics.* Clarendon Press, Oxford: 580pp.

Patterson, H.D. and Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**: 545-554

Patterson, H.D. and Thompson, R. 1974. Maximum likelihood estimation of variance components. *Proceedings of the 8th International Biometric Conference* 197-207.

Pswarayi, I.Z, Kanowski, P.J., Birks, J.S, and Barnes, R.D. In preparation. Genetic parameter estimates for *Pinus elliottii* in Zimbabwe.

Riemenschneider, D.E. 1988. Heritability, age-age correlations, and inferences regarding juvenile-selection in jack pine. *Forest Science* **34**: 1076-1082.

Robinson, D.L., 1987. *REML User Manual.* Estimation of variance components in non-orthogonal data by residual maximum likelihood. Scottish Agricultural Statistics Service: 33pp.

Searle, S.R. 1987. *Linear Models for unbalanced data.* John Wiley and Sons: 536pp.

White, T.L. 1987. A conceptual framework for tree improvement programs. *New Forests* **1**: 342-352.

Woolaston, R.R., Kanowski, P.J. and Nikles, D.G. 1990. Genetic parameter estimates for *Pinus caribaea* var *hondurensis* in coastal Queensland, Australia. *Silvae Genetica* **39**: 21-28.