GENETIC VARIATION IN A PROGENY TEST OF *EUCALYPTUS CAMALDULENSIS* IN ETHIOPIA

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DEDICATION

I would like to dedicate this thesis to Ato Lemma Gebreselasie who is the Founder of the Ethiopian Forestry Research Centre and to Ato Weldemichael Kelecha who has devoted most of his time in identification of the Ethiopian indigenous species, and to my friend Youseph Alemayehu who died in Australia, while he was reading for his MPhil degree.

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LIST OF ABBREVIATIONS

CADU	**Chillalo Agricultural Development Unit.**
CSIRO	**Commonwealth Scientific and Industrial Research Organisation.**
CSO	**Clonal Seed Orchard**
EFRC	**Ethiopian Forestry Research Centre.**
ELPA	**Ethiopian Electric and Light Power Authority.**
EWUARC	**Ethiopian Wood and Utilization Research Centre.**
FAO	**Food and Agricultural organisation of the United Nations.**
GBP	**Generation breeding population**
GGT	**Genetic gain trial**
IAR	**Institute of Agricultural Science.**
IUFRO	**International Union of Forestry Research Organisations.**
mean	**Overall family mean**
MS	**Mean square**
OECD	**Organisation for Economic Co-operation and Development**
SIDA	**The Swedish International Development Agency.**
SSO	**Seedling Seed Orchard**
UNDP	**United Nations Development program.**
UNSO	**United Nations Sudano- Sahelian Organisation.**

LIST OF SYMBOLS

Symbol	Explanation
km^2	kilometre square
m	metre
mm	millimetre
m^3	cubic metre
°C	degree centigrade
ha	hectare
V_P	Total phenotypic variance
V_E	Environmental variance
V_G	Total genetic variance
V_A	Additive genetic variance
V_{NA}	Non- additive genetic variance
σ_p	standard deviation
T	Number of trees per plot
R	number of replication
F	Number of families
σ_P^2	Total variance
σ_F^2	Family variance
σ_{FR}^2	Family x replication variance
σ_W^2	Within-plot variance
h^2	Narrow-sense single- tree heritability
h_F^2	Narrow-sense family heritability
σ_{h^2}	Standard error of single-tree heritability
$\sigma_{h_F^2}$	Standard error of family heritability
$\Gamma_{p_1 p_2}$	Phenotypic correlation of trait 1 and 2
$V_{p_1} V_{p_2}$	Phenotypic variance of trait 1 and 2
$COV_{p_1 p_2}$	Phenotypic covariance of trait 1 and 2
$\Gamma_{a_1 a_2}$	Genetic correlation of trait 1 and 2
$V_{a_1} V_{a_2}$	Genetic variance of trait 1 and 2
$COV_{a_1 a_2}$	Genetic covariance of trait 1 and 2
s	Selection differential
I	Index value
P_1	Family mean values for height growth
P_2	Family mean values for diameter growth
P_3	Family mean values for stem straightness

b_1	**Index coefficient for height**
b_2	**Index coefficient for diameter**
b_3	**Index coefficient for stem straightness**
W	**Economic weight**

CONTENTS

ABSTRACT

Eucalyptus camaldulensis Dehnh. has a wide latitudinal distribution and occurs in all Australian states except Tasmania. Studies in the past indicated that there is a great genetic diversity among provenances, suggesting that this variability could be exploited through selection for an improvement program. *E. camaldulensis* was introduced into Ethiopia in 1895. The origin of these introductions is not clear, but it appears that the first introduction consisted of a few grams of seed and it is suspected that the genetic base was narrow.

Widespread plantings, using seed collected from the first plantations (local seedlots) continued until now and it is regarded as one of the best-adapted species in the lower altitudes (500 to 1500 m) in Ethiopia. However, its low volume production and poor stem form restricts its use as a commercial plantation species although it is one of the most reliable for production of fuel wood and short posts in the drier part of Ethiopia.

In 1991 genetic improvement of *E. camaldulensis* has been started by importing open-pollinated seed of 405 families included in six provenances from Queensland, Australia for the purpose of progeny testing. The decision to use provenances from Queensland was based on their early success in most tropical and sub-tropical countries. The major objectives of the progeny test are to identify superior provenances, and families within-provenances, with vigorous growth and straight stems for use in breeding and seed production.

Genetic variations were detected by analysis of variance and the results showed that there were significant differences between the family means for total tree height, diameter at breast height and stem straightness at the age of 34 months. The greatest proportion of the observed variation is accounted for by differences between trees within plots, by family x replication interaction and between families for the traits studied. Narrow-sense family heritablity values indicated that stem straightness was under the most genetic control (0.56) followed by tree height (0.46) and then by diameter (0.32). There was a strong genetic correlation between tree height and diameter at breast height (0. 791) whereas the genetic correlations for tree height and diameter with stem straightness (0.390 and 0.410) were low. Due to the weak genetic correlation for growth traits (height & diameter) with stem straightness, selecting for growth does not provide maximum gain for straightness or *vice versa.*

A multiple-trait selection index which was constructed using equal economic weights provides optimum simultaneous gain for the three traits and is used for selection of families for the next stage of the breeding program. Based on the ranking of the multiple-trait index, the progeny trial could be converted to a seedling seed orchard by roguing the inferior families to provide first generation improved seed for commercial purposes and to establish the next generation breeding population. The open-pollinated breeding method is the one chosen for production of genetically improved seed at the early stage of the breeding programme. Vegetative propagation through cloning is considered as a second alternative and will be implemented at a later stage of the improvement program for production of high quality seed.

Key words: *Eucalyptus camaldulensis*, progeny test, genetic parameters, genetic gain, selection methods and breeding strategy.

CHAPTER 1

General Introduction

Historical evidence reveals that in the beginning of the 19th century 40 percent (53 million hectares) of the total land mass of Ethiopia was covered by dense forest (Breietenbach, 1963; FAO/World Bank, 1983). There has been accelerated decline in forest land area with an annual loss estimated at 600,000 hectares since the mid-19th century (FAO/World Bank, 1983; Pohjonen, 1989). The main cause of forest depletion in Ethiopia is rapid population growth which has resulted in unabated deforestation. Trees were indiscriminately felled for the purpose of expansion of agricultural land, settlement areas and over exploitation for timber and fuel wood. The overall process of deforestation accompanied by severe erosion and irregular rainfall distribution has resulted in environmental imbalance and intermittent droughts which have repeatedly visited the country over the last few decades.

Studies carried out on total energy consumption shows that 93 percent of the total energy comes from biomass, out of which wood requirement for fuel and charcoal were estimated to represent one-third (19 million cubic meter per year), while animal dung and crop residue represent the other two - thirds (UNDP/World Bank, 1984; Pohjonen and Pukkala, 1987). A survey carried out by Bowen (1985) indicated that one million hectares of fast growing plantation are needed to satisfy the annual fuel wood demand in Ethiopia. The existing plantation area is estimated to be only 250,000 hectares (World Bank, 1986), and to consist predominantly of various *Eucalyptus* species. Bowen (op. cit) indicates that the supply of fuel wood from plantations is still far less than the demand leading to further exploitation of the remaining natural forests. With a population growth rate of 2.9% per year, it is estimated that the total wood demand will rise to 67 million cubic meter per annum by the year 2000. The plantation area needed to fulfil this demand is estimated at three to four million hectares.

The latest survey by Chaffy (1979), estimated that about 3% of forest cover remains from the 40% of a century ago. The remaining forests are located at valley bottoms and slopes of mountains which are inaccessible for timber extraction.

To prevent further depletion of the forest resource great emphasis is currently given to (i) conservation and management of the remaining forest; (ii) development of agroforestry systems; (iii) rehabilitation of denuded areas by planting of trees; (iv) increasing the productivity of existing plantations; and (v) establishment of fast growing plantations for domestic and industrial use on a sustainable basis (FAO, 1988a). Over the last two decades more emphasis has been given to *Eucalyptus* species rather than indigenous species for plantation establishment. The main reason given for this trend is that little is known of the silvicultural characteristics of species indigenous to Ethiopia.

Out of the 62 introduced *Eucalyptus* species, greatest emphasis has been given to *E. globulus, E. camaldulensis, E. grandis and E. saligna* (Davidson, 1989; Getahun *et al.*, 1990). These four species comprise around 90% of the annual planting programme.

There are however no data to suggest whether the existing land races are from the most suitable origins or not because of the absence of seed collection records. The only evidence available is that a few grams of seed for *E. globulus* and *E. camaldulensis* were brought probably from France in 1895. There is no record of when *E. grandis* and *E. saligna* were brought to Ethiopia; they were included in a species elimination trial in 1956 and it is believed their seed source might be from South Africa (Poulsen, 1973). From the available information it is clear that in the past many experiments, mostly species elimination trials involving *Eucalyptus* were carried out in different parts of Ethiopia using seed collected from the first plantations.

Davidson (1989) concluded that neither the existing plantations nor the old experimental plots have much value from the point of further genetic improvement. This is because: (i) the seed source and the genetic base of the base population (first plantation) is not known; (ii) the first plantation was established using a few grams of seed, probably collected from very few trees (narrow genetic base); (iii) the seed source used to establish the experimental plots was from the first plantation in which the probability of inbreeding and selfing is very high; and, (iv) most of these

experimental plots lack standard experimental designs to generate sound scientific information.

Davidson (op. cit) suggested that a breeding programme for *Eucalyptus* in Ethiopia should start with a known base population. It was then decided to start such a programme by using seed sources from CSIRO, Australia. In 1990 seeds of *E. globulus, E. camaldulensis, E. grandis* and *E. saligna* were imported from Australia to conduct provenance and progeny experiments. In this dissertation it is intended to evaluate the genetic variation between open pollinated families of *E. camaldulensis.* Efforts are made to select a breeding population and a future breeding strategy is proposed based on the results of these experiments.

1.1 Description of the Study Country

1.1.1 Location and physiography

Ethiopia is located in the horn of Africa between 3° -18° North and 33°- 48° East having an area of 1.25 million km^2 (National Atlas of Ethiopia, 1988). It is a country of great geographical diversity consisting of high mountains, flat topped plateaux, deep gorges and rolling plains. The unevenness of its land surface is associated with the volcanic features which resulted in the formation of lava plateaux and rift systems.

Based on differences in the landscape pattern, Ethiopia is divided in to five major regions: (i) The western highlands; (ii) the south eastern highlands; (iii) the central lowlands; (iv) the lower rift valley, and (v) the Red Sea coastal plain. The Ethiopian relief includes altitudes stretching from 110 m below sea level (Depression of Kobar Sink), to the highest peak (Ras Dejen), 4,620 m above sea level. Within these extremes around 50% of the country is greater than 1500 m above sea level (Fig 1).

1.1.2 Climate

Ethiopia lies entirely within a tropical zone. Despite this it offers a range of climatic types from tropical to warm temperate, and a range of annual rainfall from almost nil to about 2500 mm. The mean annual rainfall ranges from 350-700 mm in the north, 1050-1200 mm in the central highlands, and 1400-2500 mm in the south-west of the country. The north-east and central parts of the country are marked by a single rainy season between June and September, whereas most of the south and west which is influenced by monsoon climate receives rainfall throughout the year (Vernede, 1955).

Altitude plays the major role for the variation in climate and vegetation types. The high plateaux generally have a temperate type of climate throughout the year with a minimum temperature of 16 °C and a maximum of 20 °C. The lowlands exhibit a hot climate with arid tropical conditions; a minimum temperature of 20 °C and a maximum of 29 °C. Most of this area receives as little as 200 mm rainfall with the dry season lasting eight months. Humidity ranges from 20% in the north to 80% in the south-west (Bowen, 1985).

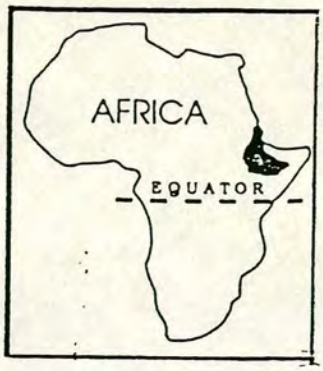
1.2 General Information On *Eucalyptus*

1.2.1 The genus Eucalyptus

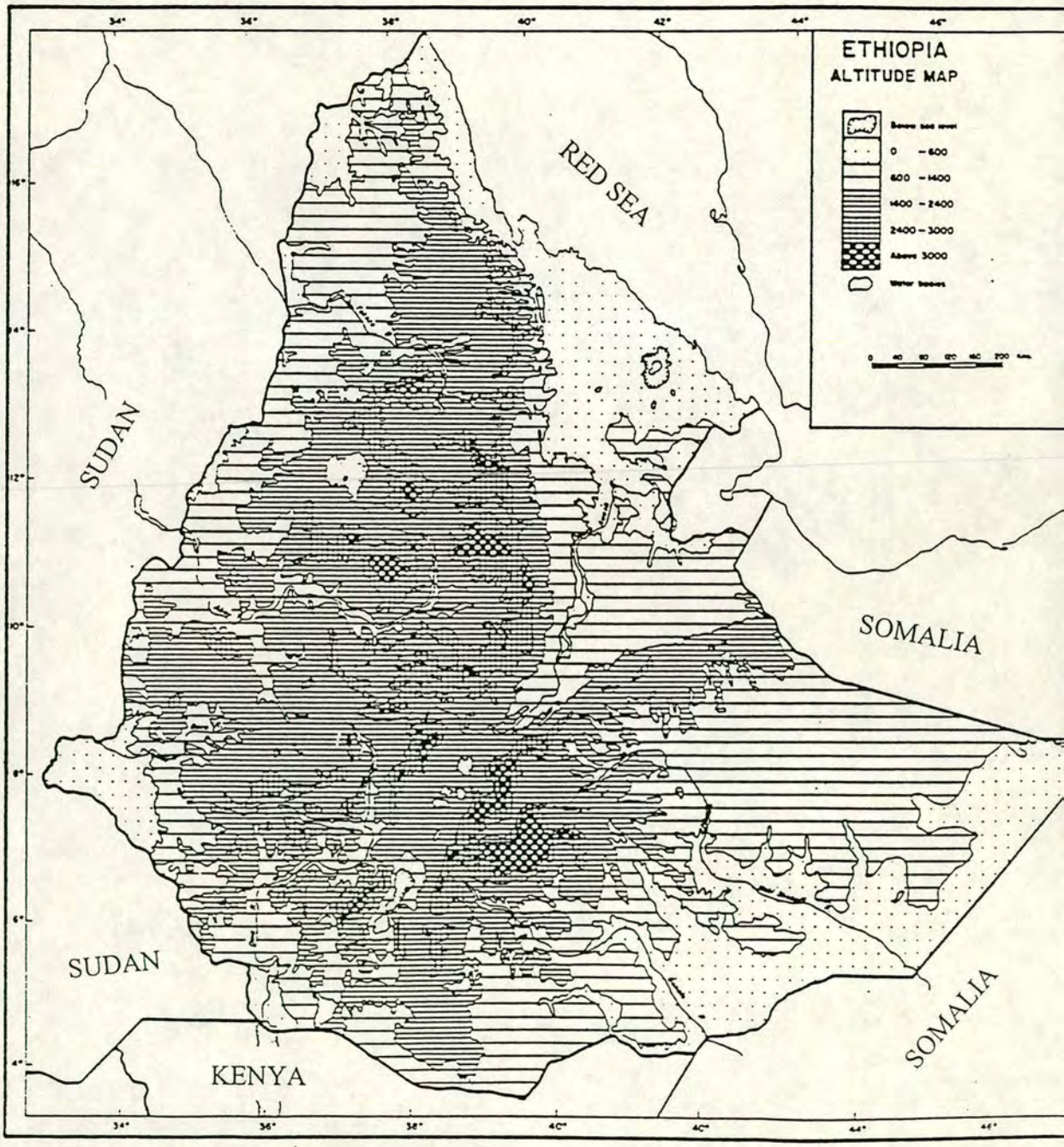
Eucalyptus found naturally in Australia and parts of South east Asia between latitude 7° N and 44° S. More than 600 species of *Eucalyptus* are known, and new ones are still being identified (Blake, 1953). The genus grows under a wide range of rainfall and temperature in its native range: in high rainfall areas some of the giant trees have a top height of 90 m, whereas, dwarf forms of *Eucalyptus* are quite common in open scrub and low rainfall areas (FAO, 1979). Most of the species are found growing naturally in Australia, but *E. urophylla* and *E. deglupta* are only found in South east Asia, in the Islands of Indonesia, Papua New Guinea, and southern Philippines.

Based on taxonomic classification of Johnson (1971) and Briggs (1983), (see Eldridge *et al.*, 1993) the genus *Eucalyptus* contain 8 sub-genera out of which the

Figure 1 Top: Position of Ethiopia in Africa. **Bottom:** Land classification of Ethiopia based on elevation.



ETHIOPIA



sub-genus *Monocalyptus* (with one operculum) and *Symphyomyrtus* (with two opercula) represent the largest.

The sub-genus *Symphyomyrtus* consists of nine sections out of which section Transversaria (*E. grandis*, *E. saligna*, and *E. urophylla*), section Exsertaria (*E. camaldulensis*, *E. exserta*, and *E. tereticornis*) and section Maidenaria (*E. dalrympleana*, *E. globulus*, *E. gunnii*, *E. maidenii*, *E. nitens*, and *E. viminalis*) are the most commonly planted *Eucalyptus* species throughout the world.

When planted outside their natural habitat many species of *Eucalypts* have shown promising results and a high degree of tolerance to extremes of latitude and altitude; having been planted in tropical and temperate regions between latitudes of 40° N to 45° S (Eldridge *et al.*, 1993).

Where it is grown as an exotic, its wide range of adaptation to different planting sites, simplicity of management system, ability to grow even on waste lands and high yield compared to other species make *Eucalyptus* one of the most widely propagated genera throughout the world (Eldridge *et al.*, 1993). The success of *Eucalyptus* in new environments is due to more favourable environmental factors such as soil, rainfall and temperature relative to their native environment, and plantation management techniques such as initial spacing, weeding, and thinning which favour tree growth in a plantation environment (Eldridge *et al.*, 1993).

On moderate planting sites, in temperate and tropical countries eucalypts have a mean annual increment ranging from 10 to 15 m^3 ha^{-1} y^{-1}, while on the best sites mean annual increments of 70 to 90 m^3 ha^{-1} y^{-1} were obtained at the age of 6-8 years in Africa, Brazil and Papua New Guinea (Eldridge *et al.*, 1993).

It is believed that *Eucalyptus* was probably first grown as an exotic in Portugal about 400 years ago and thereafter planting activities were expanded to many tropical and Mediterranean countries. Large scale plantations of *Eucalyptus* have been established in Brazil, India, South Africa, Portugal, Spain, Angola, China, Ethiopia, Argentina, Morocco, Uruguay, Peru and Chile, totalling 6 million hectares in 1985 (Eldridge *et al.*, 1993). Out of these the greatest hectarage occurs in Brazil (2,500,000 ha) followed by India (550,000 ha) and South Africa (470,000 ha). Ethiopia now has an area of 250,000 ha of *Eucalyptus* plantations.

Though it is still widely planted throughout the world, there has been some recent adverse public reaction against the planting of *Eucalyptus* in many countries. The main arguments against *Eucalyptus* are: (i) it removes too much water from streams or under ground water supplies; (ii) it conflicts with the idea of conserving native species; (iii) it has low recreational and aesthetic values (FAO, 1985). Most of these criticisms would equally apply to all fast growing exotic species (Davidson, 1989; Eldridge *et al.*, 1993) and the merits and demerits of *Eucalyptus* should be judged fairly from the social, economic and ecological points of view. Thus, the advantage of planting *Eucalyptus* outweighs the disadvantage in countries like Ethiopia and it is one of the best species to fulfil the urgent demand of wood material for fuelwood and construction material.

1.2.2 Reproductive biology of Eucalyptus

For most *Eucalyptus* species the time required between planting and seed production is 4 to 7 years (FAO, 1979). Regeneration of the subsequent breeding population by open-pollinated seed is the least expensive method compared to controlled pollinated seed and provides substantial genetic gain when broad base breeding population is used (Shelbourne, 1991). Therefore knowledge about the sexual reproduction of *Eucalyptus* is necessary for the breeder to plan any breeding strategy and seed production efficiently. Eldridge *et al.* (1993) listed the distinctive characteristics of the sexual reproduction of *Eucalyptus* as follows:

(i) flowers are hermaphrodite (male and female organs in the one flower);

(ii) pollination is by animals (mainly by insects and birds) not by wind;

(iii) out crossing is favoured by various mechanisms including protandry, which means that the stigma is not receptive until some days after the pollen has started shedding from anthers;

(iv) the breeding system is predominantly out crossing but there is also a considerable degree of self fertility as for many tree-crop species;

(v) fruits are dry woody capsules and seeds are very small in the species used to establish fast-growing plantations (100,000 to 600,000 kg^{-1});

(vi) seed production varies enormously under the influence of such non-genetic factors such as spacing, site and seasonal condition, effectiveness of pollen vectors and predation of the developing seed crop by insects;

(vii) species differ greatly in many aspects of flowering and seed production so that detailed information for one species does not necessary apply to others, even those which are closely related.

1.2.3 Sexual reproduction and hybridisation

The regeneration of *Eucalyptus* in nature is generally by seed through sexual reproduction. According to Griffin (1989) the reproductive attributes which may affect improvement strategy and seed production are:

(i) sexual system - the spatial and temporal distribution of male and female function within and between individual trees;

(ii) phenology - the time and duration of flowering;

(iii) precocity and fecundity - the age at which flowering commences and the adequacy and reliability of seed crops;

(iv) pollinators and pollen dispersion - the presence of adequate pollinators and the distance of the seed orchard from neighbouring plantations to avoid pollen contamination.

Griffin (op. cit) reported that the phenology of *Eucalyptus* varies between species, within-species and between provenance of the same species, thus knowledge regarding the phenology of particular species is essential to determine whether the future breeding strategy is based on open-pollinated seed or clonal orchards.

Inbreeding is common in *Eucalyptus* and results in low germination capacity of seed and stunted growth of the seedlings (FAO, 1979). In natural stands of *Eucalyptus*, inbreeding is caused by: (i) selfing, and (ii) neighbourhood inbreeding effects (mating between close relatives) (Griffin, 1989). The problem of inbreeding depression is great in natural stands compared to plantations, this happens because regeneration has been by seed dispersal from old trees with big-crown diameter. In such a situation it is likely that a group of trees surrounding the seed trees have the same mother and also have a high chance of having the same father (Eldridge *et al.*,

1993). On the other hand when seed is collected from a tree in a plantation the neighbourhood inbreeding is broken because it is unlikely the neighbouring trees in a plantations are from close relatives due to mixing up of the seed during plantation establishment.

Even though inbreeding is common in *Eucalyptus*, studies using isoenzymes reveal that the greater proportion of the seeds produced from open pollinated parents are out crossed seeds. This happens because in *Eucalyptus* most of the pollen is shed within hours of the opening of the operculum, whereas the stigma is generally not fully receptive until four to seven days later (FAO, 1979).

Even when the stigma is receptive and control-pollinated by pollen from two different sources, i.e., (i) pollen from the same flower cluster to that of the sigma, and (ii) pollen from a different flower - the ovules which develop into mature seed are predominantly out crossed ones. This happens because pollen tubes of foreign pollen grow relatively fast on the stigma (Griffin, 1989). For example, according to Griffin *et al.* (1987) after pollinating *E. regnans* with a 1:1 ratio of self and out cross pollen, 81% of viable seed produced was from out crosses (see Griffin 1989).

Eucalyptus species will hybridise rather freely within the same sub-genus (Griffin *et al.*, 1989) and it is possible to manipulate hybrids between any species to produce hybrid vigour. The work done by Aracruz Florestal in Brazil crossing *E. urophylla* and *E. grandis* provides hybrid vigour. The problem with inter-specific hybridisation arises when seed is collected from F1 hybrid parents to establish the second generation. Due to segregation of genes, the F1 hybrid breaks down in F2 and results in inferior individuals. Vegetative propagation of the F1 hybrid parents by cloning is the only way to capture the hybrid vigour and this method has been used in a large scale operational planting programme in Brazil (FAO, 1979).

1.2.4 Historical background to Eucalyptus in Ethiopia

Eucalyptus was first introduced to Ethiopia in 1895 during the reign of Emperor Menelik II to solve the problem of fuelwood in the capital city, Addis Ababa. The initial introduction of *Eucalyptus* species was suggested to the Emperor by a French railway engineer Mondon Vidallet (Breitenbach, 1961; Harvath, 1968).

A total of 15 *Eucalyptus* and some *Acacia* species were imported during the initial introduction. *E. globulus* and *E. camaldulensis* were among the first introduced species.

Historical evidence reveals that in the 18th century the French obtained seed for many *Eucalyptus* species from Australia for planting in France. Seed collected from stands in France was then distributed to Africa and to other Mediterranean lands (Davidson, Personal communication). There is still doubt as to the precise origin of the first *Eucalyptus* seed imported into Ethiopia.

The first planting was done around Addis Ababa and it is said that even the Emperor participated during the planting activities. Since all the first introductions were planted together they were used for demonstration and species elimination purposes. Among the tested species *E. globulus* showed superior growth performance and became the main species planted around the city. The performance of *E. globulus* attracted the attention of village people and further planting spread fast throughout the country. Further expansion proved *E. camaldulensis* to be the best species at lower altitudes for production of construction material and fuel wood (Breietenbach, 1961; Mirhetu *et al.*, 1983; Bowen, 1985; Jackson, 1975).

To support the planting activities and identify further potential planting sites, the first formal experimental plot was established in 1956 by the Institute of Agricultural Research (IAR). In this experiment 15 tree species (most of them eucalypts) were included and the seeds used were collected from the first plantation (Breietenbach, 1961; Getahun *et al.*, 1990).

Between 1956 and 1975, Institutions such as Chilalo Agricultural Development Unit (CADU), Alemaya College and Jimma College of Agricultural Science have undertaken trial plots involving *Eucalyptus,* other exotic species and some selected indigenous species (Getahun *et al.*, 1990). Most of the experimental plots established during this period were discontinued and abandoned without generating scientific information. This happened due to a lack of co-ordination between institutions involved in research activities and the absence of a formal authorised body and trained research staff to co-ordinate activities.

In 1975, the UNDP/FAO project "Assistance to Forestry Research Centre" was started with the objective of manpower development. At this time the present Ethiopian Forestry Research Centre was founded. The main responsibilities of the centre were: (i) To co-ordinate and expand the scope of research activities throughout the country; (ii) to follow up the already established experiments, and (iii) to collect and distribute tree seed on a national level.

The support from the project was continued until 1985. During this period several experiments mostly comprising species elimination trials were established in northern, north-eastern, central, south-western and eastern parts of the country. About 62 different species of *Eucalyptus* were tested for their growth potential in various agro-ecological zones (Getahun *et al.*, 1990). From these trials *E. globulus* was found to be most suitable for high altitudes, *E. camaldulensis* for low altitudes, and *E. grandis* and *E. saligna* for mid-altitudes (Mirhetu *et al.*, 1983; Davidson, 1989; Pohjonen, 1989).

1.3 Tree Improvement

The aim of tree improvement is to select a superior phenotype and evaluate its breeding potential through progeny testing on representative sites, and to re-select superior genotypes for mass propagation (Wright, 1976; Zobel & Talbert, 1984). If the species under investigation is an exotic it should be tested for adaptability before using the species for plantation. This is done because trees have their own climatic and soil requirements for growth. To match species with site types, information such as latitude, longitude, altitude, and climatic factors (mean annual rainfall and temperatures) in the country of origin are compared with the new environments where the introduced species are going to be planted (Burley, 1969).

If species are moved beyond their natural range they may sometimes hardly survive, putting most of their energy into withstanding the unfavourable local climate and edaphic conditions rather than into producing the highest expected yield (Nickles, 1970). Matching the new planting site with the natural conditions under which the particular species is growing is the practice that has been used as a guide for species introduction. However, for *Eucalyptus* spectacular results have been

achieved in many parts of the world when planted beyond their natural range. For example, *E. camaldulensis* which occurs between 30 and 600 m altitude in its home land, Australia, shows promising results at an altitude of 2,000 m in Ethiopia, suggesting that species testing in the exotic environment is an important stage in tree improvement programme.

Burley and Wood (1976) stated that: (i) proper species introduction; (ii) provenance testing of the best and most productive species; (iii) selection of superior individuals from the best provenance for progeny testing; and (iv) re-selection of superior individuals for further progeny testing is the different stages to be followed in a tree improvement programme. However, it is possible to combine the different stages in one programme provided that, the level of technical skill and funding is available.

Selection of superior individuals and testing alone do not provide maximum gain in breeding programme. It should be combined by appropriate silvicultural operations and forest management practices (Zobel *et al.*, 1987). Therefore, efforts should be made to consider all the factors which affect tree growth in addition to the breeding work.

1.3.1 Principles of provenance and progeny testing

There is confusion and misunderstanding in using the terms provenance, seed origin and seed sources in the literature. The terms provenance, geographic source or geographic race are the same and they are used interchangeably to mean the same thing, whereas 'seed source' is different and should not be used synonymously with the other three (Zobel & Talbert, 1984). For better understanding the definitions used by Zobel and Talbert (1984) and OECD (1974) are repeated below.

According to Zobel and Talbert (1984):

1. "Provenance, geographic source or geographic race. These denote the original geographic area from which seed or other propagules were obtained (Callaham, 1964; Jones and Burley, 1973). If, for example, seed of *E. grandis* were obtained from Coff's Harbour, New South Wales, Australia, and grown in

Zimbabwe, they would be classified as the Coff's Harbour provenance (or geographic source or geographic race)."

2. "Seed source - If seed from the trees grown in Zimbabwe were harvested and planted in Brazil, they would be referred to as the Zimbabwe *seed source* and the Coff's Harbour provenance. The term *origin* is used by Barner (1966) in the same way as *seed source*."

According to OECD (1974):

1. "Provenance (location of seed source): The place in which any stand of trees is growing. The stand may be indigenous or non-indigenous."
2. "Origin: For an indigenous stand of trees the origin is the place in which the trees are growing; for a non-indigenous stand the origin is the place from which the seed or plants were originally introduced."

In this dissertation the definition used by OECD (1974) is used to describe seed origin and provenance.

The main objective of provenance trials is to locate well-adapted and productive provenances as quickly as possible for use as a seed source, or to use their seeds to establish improved seed stands for the purpose of large scale planting (Lines, 1967; Nikles, 1970; Burley & Wood, 1976).

The importance of using the correct provenance in exotic forestry is highlighted by many people. For example, Squillace (1966) and Steenberg (1983) indicated that the success from exotic forestry and the genetic gain from tree improvement is mainly determined by the quality of the seed origin, and thus, much effort should be made to locate the correct provenance before extensive planting and intensive breeding work is started (see Zobel *et al.* 1987).

Adaptation of the population to the environment, particularly latitude, altitude, climate and soil are responsible for provenance variation (Lines, 1967). For naturally grown species variation exists: (i) at the provenance level; (ii) between sites within a provenance; (iii) between stands within sites, and (iv) between trees within sites (Zobel & Talbert, 1984). Provenance and within provenance variation is genetically fixed and typically accounts for about 90% of the total variation, whereas the

variation between sites and stand within sites is mainly caused by environmental differences.

Once the right species is chosen the yields of forest trees can be considerably improved by selecting the best provenances and individuals within provenances (Burley, 1969; Zobel & Talbert, 1984). The most suitable provenance should be located for the planting site by growing different seed origins under common environmental and management techniques.

If little is known about a species, the location of the seed collection sites should cover the entire geographical range of the species including isolated and extreme populations (Burley & Wood, 1976). For a discontinuous population which is separated by lakes, valleys, mountains and etc., the exact boundary between provenances can utilise these natural boundaries, whereas for a continuous population it may be difficult to draw a clear line between them. Widespread species tend to be genetically more variable than restricted ones because of the diverse environments to which they have adapted, and it is therefore suggested that intensive sampling should be done to capture their wide range of genetic diversity (Lines, 1967; Callaham, 1964; Burley, 1969).

Once the provenance boundary and representative samples within the boundary are located it is not difficult to choose outstanding stands for seed collection. However, without making a genetic test there is no way to confirm whether the superiority of a given stand is due to its inherent quality or to the particular environment in which it has been grown.

Lines (1967) fully explained the mistakes that have been made in the past by intentionally choosing only superior stands as a source of seed for provenance trials. The best example is cited for *P. contorta* where seed was collected from two contrasting populations - one in the coastal area of British Columbia where the trees are very short and poorly performing and the other in Alberta with tall and straight trees - whose progeny have been planted on infertile exposed sites in Scotland. The coastal provenances show better survival and resistance to blasting winds and have growth rates as high as from Alberta due to their inherent qualities.

Due to the difficulties of estimating genetic values of forest stands and individuals within stands based on their phenotypic appearance, Callaham (1964) and Burley & Wood (1976) suggest that seed collection for provenance tests must consider the following guidelines:

(i) the stands to be selected for provenance seed collection must represent part of the species range;

(ii) the population should be large enough and well stocked to provide a wide genetic base and enough seed trees;

(iii) the seed trees should be selected randomly;

(iv) immediate neighbours and isolated individuals should be avoided to reduce the risk of inbreeding and selfing; a 100 m distance is commonly used between seed trees;

(v) the number of seed trees representing a provenance can be from 5 to 10 for homogeneous populations and 25 to 50 for heterogeneous population; and,

(vi) the same quantity of mature fruits should be collected from healthy individuals as far as possible to have equal representation.

1.3.2 Stages of provenance testing

Provenance can be evaluated in the following three stages or phases: (i) range-wide provenance phase; (ii) restricted-provenance phase, and (iii) provenance-proving or crop performance phase.

According to Lines (1967) and Burley & Wood (1976) the purpose of the range- wide provenance phase is to include as many provenances as possible (e.g. 25-40) and identify the best from the worst. That of the restricted provenance phase is to test the growth performance of these best provenances (5-10) and that of the crop performance phase is to test a few superior provenances (2-3) for their productivity under normal plantation conditions.

For range-wide sampling a small size of replicated plots consisting of 16 to 25 trees can be used, with tree height and survival being the important traits to be measured for one-quarter to one-half rotation. For restricted sampling larger plots consisting of 49 to169 trees are commonly used with height and diameter growth as

the principal production variables to be assessed over a full rotation. For the proving or crop performance phase 2 to 5 hectares of plantation is needed and the plots should be maintained for a full rotation to assess the major economic traits and to predict yield.

The importance and existing knowledge of the species determine whether to carry out all three stages of provenance test separately or in combination. If the species is an exotic and little is known about it, information on the extent of the natural range and growth potential should be collected both from literature and from correspondence with the country of origin and other countries where the species is growing. Such information assessment can reduce the cost of the experiments and give a clear indication where to concentrate. For economic reason and due to the urgent need for improved material it is often necessary to combine species and provenance tests, provenance and progeny tests, and seed production areas with progeny tests.

1.3.3 Field testing

The purpose of field testing is to locate the best provenance for a given planting site. In a situation where experimental results from multi-site tests are available it can provide additional information to investigate provenance-environment interaction. Provenance-environment interaction appears when there is change in relative ranking of the provenances between the test sites (Callaham, 1964; Zobel & Talbert, 1984).

The number of test sites to be established is mainly determined by the variation between planting sites and the resources available to carry out the experiments (Lines, 1967). When resources are the limiting factor the test site should represent the major planting area. If provenance-environment interaction is detected the most productive provenances should be assigned according to their best performance: in such a case separate breeding zones are recommended and if the best provenances in one zone prove to be superior in all zones future breeding work may be concentrated in one representative breeding zone (Nikles, 1970; Mathson & Raymond, 1984).

When experimental results show minor differences between provenances the separation of the few top ranking provenances using their mean trait values might be difficult. In such a situation seed from either a provenance mix or separate provenances can be used to establish seed stands. When seed from a provenance mix is used knowledge about flowering periodicity is important. If provenances included in the same seed stands or seed orchards flowers at different times management of the seed stand is difficult and the cost of seed production is expensive. For example, in Zimbabwe Mullin and Pswarayi (1990) reported significant differences in flowering periodicity between four provenances of *E. camaldulensis*, indicating that the inclusion of these provenances in a single seed stand is not advisable.

Libby (1973) describes how both methods have their advantages and disadvantages (see Eldridge *et al.*, 1993). When seed from a provenance mix is used to establish seed stands:

(i) the identity of individual provenance is lost through gene recombination;
(ii) in the long-term, one land race is developed which has wide genetic base; and
(iii) the provenance mix has an advantage of producing inter- provenance hybrids which might be better than the two parents and do not exist in natural stands.

When seed from separate provenance is used to establish seed stands:

(i) the genetic identity of individual provenance is maintained;
(ii) different land races are developed, and
(iii) it has an advantage of gene conservation in a situation when the base population is threatened or endangered.

1.3.4 Selection of plus trees and the need for progeny testing

The general objective of progeny testing is to produce a breeding population with genetically improved material for traits that have major economic importance. Selection of suitable provenances and superior individuals within provenance can obtain the largest, quickest and cheapest gains if properly implemented (Callaham, 1964; Burley; 1969; Zobel & Talbert, 1984).

Individual selection followed by progeny testing provides information about the genetic superiority or breeding values of the selected parents, provided their

progeny have been grown on homogenous sites and under similar management conditions. No matter how complex the breeding programme, if an efficient selection method and wide genetic base population are not used the return from tree improvement is disappointing; efforts should therefore be made to increase the selection differential without narrowing the genetic base (Cotterill & Dean, 1990; Lindgren, 1991).

In theory it is a straightforward task to select dominant and co-dominant trees and use them as a mother trees for seed collection. However, the difficulty is to determine whether the phenotypic appearance of individuals is due to an inherent quality or whether micro-environment has played the major role. Cotterill and Dean (1990) explained that without progeny testing it is not possible to measure the genetic superiority of individuals and thus using only phenotypic superiority as a selection criteria is not an appropriate method especially for traits with low heritability. Thus, for traits which are under strong genetic control, such as stem straightness and branching habit, mass or individual selection without progeny testing is effective, whereas, for traits which are under less genetic control such as growth rate, individual selection without progeny testing is not an effective method (Zobel & Talbert, 1984).

Tree improvement is a continuous process and requires resources and time. Therefore, maximum gain from individual selection cannot be achieved in one generation. Gain is maximised and accumulated through a continuous process of selecting the best individuals, testing, crossing the best and re-selecting through successive generations (Bridgwater & Ledig, 1986).

1.3.5 Base population for plus tree selection

Once the well-adapted and productive provenances have been identified for planting sites, gain can be capitalised by individual selection within the provenance. The decision on where to select the individuals is mainly based on the availability of the base population.

If the species is an exotic, selection can be made from: (i) a land race (seed stand, plantation or provenance trial) provided that seed source and genetic base are

well known, and (ii) natural stands in the country of origin. In a situation where seed stands or plantations are not available provenance trials can be used for base material, provided they have a broad genetic base and the population is large enough to allow intensive selection of best individuals (Eldridge *et al.*, 1993).

Unless conditions prevent it, individual selection from the land race has a great advantage because individuals are well adapted to the local environment in which they have been grown; in addition, it is likely that individuals in a plantation or seed stands have gone through different stages of selection (Zobel & Talbert, 1984). For example, individuals selected from plantation in Congo and from natural stand in Timor, Indonesia were compared for their growth characteristics for *E. urophylla*. The better growth of the Congo land race suggests, in plantation the neighbourhood inbreeding effects have been broken down and there has been more recombination of genetic material by out crossing than in the natural stand (see Eldridge *et al.*, 1993).

CHAPTER 2

Description of *E. Camaldulensis*

2.1 Taxonomic Classification

E. camaldulensis is classified under sub-genus *Symphyomyrtus* (With two opercula), and section Exsertaria *(E. camaldulensis*, *E. exserta*, and *E. tereticornis). E. camaldulensis,* Dehnh., River red gum, is a large evergreen tree which can grow between 25 and 50 m high under natural conditions. It has a stout trunk that is often short and crooked and reaches a basal diameter of 0.6 to 1.0 m.

Blake (1953) describes *E. camaldulensis* as follows:

> "tree of varied habitat with smooth, deciduous, white or pale grey bark over the greater part, often with patches of darker grey, and sometimes with a variable amount of grey, flaky bark persisting on the lower part; branchlets often long and pendulous. Juvenile leaves opposite for a few pairs, petiolate, ovate to broadly lanceolate, glaucous. Intermediate leaves broadly lanceolate to lanceolate, up to about 16 x 7.5 cm, glaucous. Adult leaves dull and often pale-coloured, more or less dropping, alternate, prominently petiolate or narrowly lanceolate, acute or acuminate, 6-30 cm long, 0.8-2 cm wide, about 8-20 times as long as wide, with between 20 and 40 pairs of lateral veins at an angle of 40°-50° with the midrib, the intramarginal vein about 0.9-1.5 mm from the margin. Inflorescence of axillary, 5-10-flowered umbels; peduncles slender, 6-15 mm long; pedicels slender, 3-8 mm long. Buds broadly or occasionally narrowly ovid, rostrate, acuminate, or acute, rarely obtuse, 6-10 mm long, 4-5 mm wide, with a short and broad calyx-tube and a longer (up to 3 times as long), rostrate-acuminate or apiculate (rarely bluntly rounded) operculum. Anthers versatile, obovoid-oblong with parallel cells opening in longitudinal slits. Ovary prominently domed. Fruits subglobose to ovoid in outline, 5-8 mm long, slightly narrower to slightly wider than long, with a short calyx-tube, a high domed disc, and stout, deltoid valves strongly incurved from a slightly spreading base".

2.2 Natural Distribution and Habitat

The species *E. camaldulensis* is the most widely distributed *Eucalyptus* on mainland Australia and occurs between 12° 48' and 38° 15' south in all states except Tasmania (Fig 2).

In the hot dry inland of Australia, it is confined to water courses and flood plains where it relies on stored ground water for growth (CSIRO, 1978; Midgley *et al.*, 1989). In less arid areas it spreads up to plains and hill slopes from its typical riverine habitat (Eldridge *et al.*, 1993). Soil requirements are typically sandy alluvium, although sometimes it can be found on the margins of salt lakes and on shallow soils over limestone. It is known to grow over an altitudinal range of 20 to 700 m; with mean annual rainfall varying from 200 to 1200 mm, and it can tolerate drought of 4 to 8 months or more.

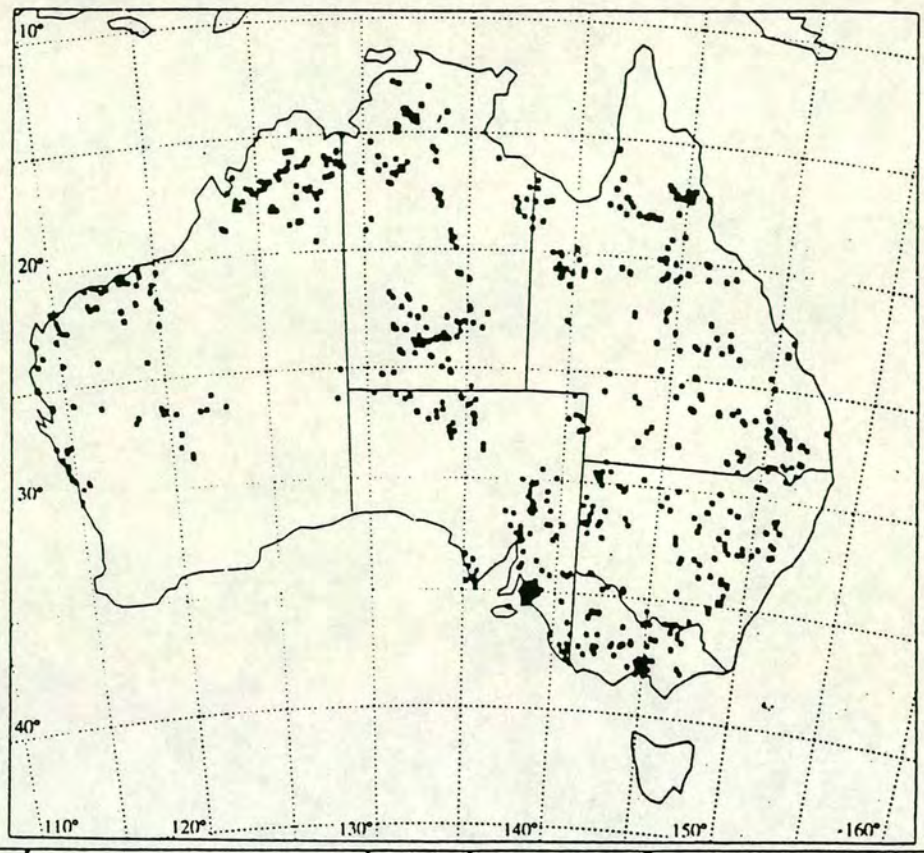
2.3 Reproductive Biology and Phenology

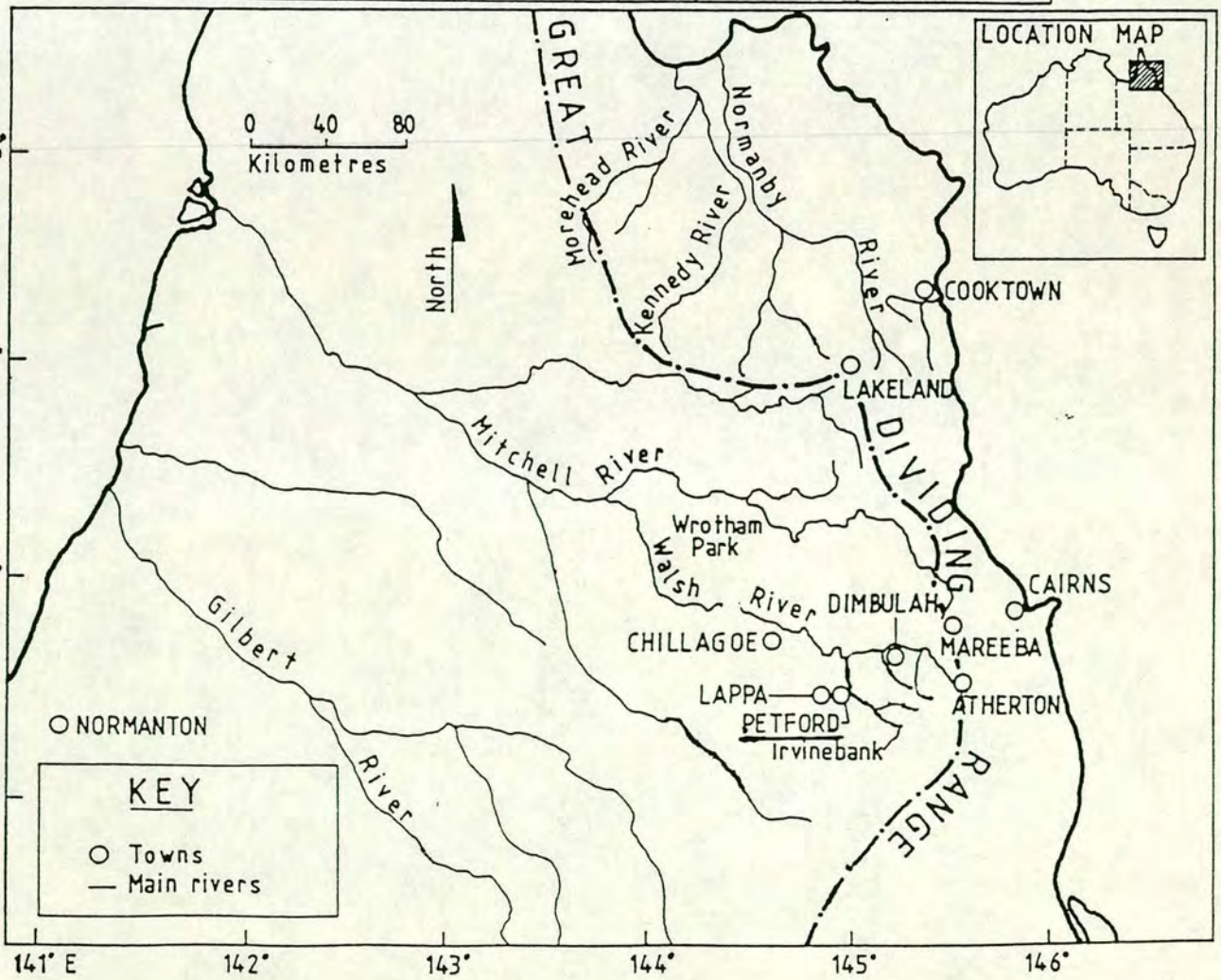
The reproductive process of *Eucalyptus* takes place in an inflorescence which is the arrangement of individual flowers on the stem. The male and female organs are in the same flower of the same plant (hermaphrodite) (Blake, 1953).

The flowers of *E. camaldulensis* are pollinated mainly by insects, particularly bees and sometimes by birds and a certain amount of self pollination can also occur (FAO, 1979). Burgess and Griffin (1990) pointed out that the flowering season for Eucalypts in natural stands varies widely within site, within provenance, from tree to tree within species and from year to year (see Eldridge *et al.*, 1993).

For *E. camaldulensis* significant variation has been detected between provenances in flowering season and duration when planted together (Mullin & Pswarayi, 1990; Emery & Ledig, 1987). In Ethiopia detailed study has not been carried out on the phenology of *E. camaldulensis*; however, the main seed collection season is between January and February.

Figure 2 Top: Natural distribution of *E. camaldulensis* in Australia. **Bottom** : Detail of the Petford region of North Queensland (maps from CSIRO).





2.4 Seedling Production

The usual method of raising *E. camaldulensis* seedlings is by broadcasting on a seed bed, or by sowing a pinch of seed directly into planting tubes. Direct broadcasting of the seeds on planting sites is also practised by individual tree planters. This method is successful in high rainfall areas when the planting site is totally cultivated.

The quantity of seed per kilogram ranges from 700,000 to 800,000, of which about 500,000 viable seeds are found (Pohjionen, 1989). The sowing rate recommended is 1 gm per 85 containers or 12 gram per square meter on seed beds (FAO, 1979). In Ethiopia germination takes place uniformly within 7 to 12 days and seedlings are usually kept in the nursery for five months and attain a height between 25 to 40 cm before the planting season commences.

2.5 Growth and Yield

E. camaldulensis is one of the most extensively planted species of *Eucalyptus* in the world (FAO, 1979). The greatest areas planted are in Italy, Uruguay, Chile, South Africa, India, United States, Peru, Kenya and Ethiopia. In Ethiopia it is well known to grow in the lowlands and mid altitudes between 700 and 2000 m above sea level, sometimes extending to 2500 m, where the rainfall ranges from 550 to 2200 mm (Mirhetu *et al.*, 1983; Bowen, 1985).

In countries where the correct provenance is planted, it is an efficient source of timber yielding maximum biomass production under short rotations. In drier countries typical plantation yields are 5-10 m^3 ha^{-1} y^{-1} on a 10 -20 year rotation, whereas in an area of sufficient moisture for its growth, up to 30 m^3 ha^{-1} y^{-1} has been recorded (FAO, 1958; Evans, 1989). Studies carried out following different types of ground preparation before planting show that total cultivation can increase the yield of *E. camaldulensis* by three-fold (unpublished data; Ethiopian Forestry Research Centre).

Spacing normally varies with the objectives of the plantation. In Ethiopia close spacing of 1 m × 1 m is used in community woodlots and gives high volume production up to age three. Thinning at age four is done to reduce the number of

stems by 50 percent, and thereafter successive thinning is done every year until the final harvest at around ten to twelve years (Pohjionen, 1989). The wood product from the early thinning is used for roof construction and from later thinning is used for fencing posts and house construction. Alternatively, coppice production is commonly practised and it is one of the species with appreciable coppicing ability. According to FAO (1979), a rotation age of four to seven years is commonly used for optimal biomass production from coppice.

2.6 Wood Properties and Utilisation

The wood of *E. camaldulensis* is strong, hard and heavy, durable and resistant to termites. As noted in the review of Midgley *et al.* (1989) the following basic density were recorded: (i) 444 to 593 kg/m^3 at age 10 in Italy; (ii) 487 to 576 kg/m^3 at age 8 in Zimbabwe; and (iii) 610 to 640 kg/m^3 in Sri Lanka for trees grown in plantation. Sap wood is thick and pale red and the heart wood is from reddish to dark red in colour. It is not difficult to saw, but it tends to warp in drying and care has to be taken during seasoning. The wood has an average energy content of 19.8 MJ/kg; it burns quickly and makes good charcoal (FAO, 1958). The only limitation on its use in open fire places is that the wood produces dense smoke.

E. camaldulensis is valuable for many purposes including shelter and honey production. The wood is used for construction materials, railway sleepers and charcoal in many parts of the world. In Australia it is extensively used for railway sleepers, heavy construction timbers, fences, flooring and the foundation of wooden houses (FAO, 1955). In Ethiopia it is mainly used for construction poles, fuel, fence posts and traditional house furniture. Currently the Ethiopian Electric Power Authority (ELPA) has a high demand for *E. camaldulensis* transmission poles, because it is more resistant to termite and fungal attack than *E. grandis* and *E. saligna.*

2.7 Provenance Variation

2.7.1 Genecology

Despite its wide range of distribution throughout Australia the genecology of *E. camaldulensis* can be divided into just two major divisions - the Northern forms (tropical zone) and the Southern forms (temperate zone) (Banks and Hillis, 1969). The ideas of Banks and Hillis (op. cit) were supported by Pryor and Byrne (1969), after recognising the differences in lignotuber frequency, leaf characteristics, oil gland density, bud shape, juvenile leaf morphology, bark colour and branching habit between the Northern and Southern populations.

Eldridge (1975) conducted several studies and made extensive sampling of *E. camaldulensis* populations throughout its natural range (see Midgley *et al.*, 1989). They came up with the consensus that there is wide genetic variation between and within populations due to the enormous range of climate and soil conditions occurring through its natural habitat. However, there is no definite boundary between the northern and southern population, and this has been confirmed by the latest study of Eldridge *et al.* (1993).

In tropical climate where seed sources from both north and south were planted together in one trial there was a 60 percent overlap for growth rate and survival between the seed sources. The Katherine provenance from Northern Territory, the Petford from Queensland and the Lake Albacutya from Victoria cannot be separated statistically, but they show superior performance over the other provenances (Davidson, 1989). For example, studies in Bangladesh showed that the seed from Petford provenance, Queensland produced 17 m^3 ha^{-1} y^{-1}, whereas the seed from Fitzroy Crossing provenance, Western Australia produced 2.2 m^3 ha^{-1} y^{-1} at the age of five years (see Midgley *et al.*, 1989).

2.7.2 Results from provenance trial outside Ethiopia

A summary of provenance results in different parts of the world is presented in Table 1. The earliest provenance studies for *E. camaldulensis* were carried out by Franclet (1956), Karschon (1960), and Giordano (1961), and these pioneer studies

show that there is significant genetic variation for growth rate, lime tolerance and stem straightness between the provenances (see Midgley *et al.*, 1989).

Wide-range provenance seed collection for *E. camaldulensis* was initiated in 1964 by FAO, Mediterranean Forestry Research Committee in collaboration with the Australian Tree Seed Centre. The seeds of 40 provenances were collected throughout the geographical range of the species in Australia. Thirty-two comparative trials were established between 1966 to 1972 in 14 Tropical and Mediterranean countries (Lacaze, 1977).

When most of the trials were 8 to 10 years old, the results from 24 of them were reported by Lacaze (1977). Results show that Katherine, Northern Territory and Petford, Queensland provenances have superior performance in the tropical zones for both growth and stem straightness while the Lake Albacutya provenance from Victoria was an outstanding performer in the Mediterranean zone. This study also indicated that the Katherine provenance shows superiority over Petford in an areas with severe dry seasons. Eldridge *et al.* (1993) confirmed that the Katherine, Petford and the Lake Albacutya provenances performed well even when planted outside their geographical range and show a wide range of adaptability. Provenance results reported from different countries were summarised and listed in Table 2.1.

From the evidence available in the different parts of the world it can be concluded that the Northern provenances are best suited for tropical climates, while the Southern Provenances are most suited to temperate climates. The Petford provenance from Queensland, Katherine from the Northern Territory and Lake Albacutya from Victoria regions are exceptional and show a wide range of adaptability and less provenance/ environment interaction.

Table 2.1 Summary of provenance results for *E. camaldulensis* in different parts of the world.

Author(s)	Country	Study Age (years)	General Results
Karschon (1967)	Israel		21 Australian provenances covering a wide range of geographical origin were included. The frequency of lignotubers, oil gland density, length/width ratio of leaves and colour of the foliage were investigated. Based on the study the whole population were divided into two distinct groups of ecotypes, the Northern and Southern group.
Banks & Hillis (1969)	Australia		Samples of mature leaves and seed from 62 localities were examined for polyphenolic component. Results from the chemical analysis showed the whole population can be divided in to the Northern and Southern division and 6 geographical regions.
Pryor & Byrne (1969)	Australia		9 provenances and 22 families within provenances were tested to investigate the Northern and Southern division of the species. Tree characteristics such as height growth, frost damage, lignotuber frequency and flower buds were studied. Significant variation between provenances and families within provenances were observed for all traits. Height growth and lignotuber frequency increases with decrease in latitude, while forest tolerance increases with increase in latitude. The operculum of flower buds is typically rounded for Northern and rostrate for Southern populations.
Ghosh *et al.* (1977)	India	8	Significant differences were observed for 12 provenances for growth potential. Provenances from Petford, Queensland and Katherine, Northern Territory exhibited superiority over the others, Katherine being the best.
Siddiqui *et al.* (1979)	Pakistan	10	12 Australian provenances were planted and assessed for tree height, diameter and volume growth. Considerable variation were observed for all the three traits between the provenances. The best provenances yielded 15.4 m3/ha, while 5.5 m3/ha was recorded for the worst provenance.
Darrow, W. K. (1983)	South Africa		Provenance trial consisting 26 seed origins for *E. camaldulensis* and 23 seed origins for *E. tereticornis* were planted at nine sites. Significant provenance x environment interaction in growth rate and survival were detected for both species.

Table 2.1 Continued

Quaile & Mullin (1984)	Zimbabwe	3.5	Using the seed sources from the provenance trial 26 half-sib families were planted and assessed for height, diameter and stem straightness. Significant genetic differences were observed between the families for all traits. Family heritability values of 0.77, 0.70 and 0.61 were recorded for height, stem straightness and diameter respectively.
Otegbeye (1985)	Nigeria	13	Significant variation for height and diameter growth were observed between 16 provenances. The best provenances were those from the Northern part of Australia and the poorest from the South. Among the Northern provenances Petford out-ranked all, followed by Katherine. Height at 5-year was found to be highly correlated with 13-year height.
Emery & Ledig (1987)	California	5.5	23 provenances were assessed for height, diameter, stem straightness and flowering. Significant variation were observed for all the traits between the provenances. The South Australian and Victoria provenances were found superior over the others in growth performance while the western and Northern Australian provenances were the best in stem straightness. The Southern provenances produces abundant flower compared to the Northern ones.
Mullin & Psawaryi (1990)	Zimbabwe	10	4 provenances were tested for flowering periodicity. Significant differences were observed between the provenances. Some provenances showed year round flowering while others showed distinct flowering period.
Otegbeye & Samarawira (1991)	Nigeria	18	10 provenances were included in provenance experiment. Significant variation were observed between the provenances for height, diameter, first forking height, stem form, branch diameter and taper. The Petford provenance from Queensland showed fastest growth rate, straightest stem and highest fork height. The Silverton provenance from the New South Wales exhibited the slowest growth rate, lowest forking height, smallest branch diameter and taper. Generally those provenances from the Northern part of Australia showed faster growth than those from the Southern part of the country.
Eldridge *et al.* (1993)	Australia		Most of the variation exists between the Northern and Southern parts of the species is clinal variation. There is no distinct boundary between the North and South population.

2.7.3 Summary of results from species/provenance trials in Ethiopia

Preliminary results from species elimination trials show that *E. camaldulensis* is the only species which performed well in low rainfall and less fertile areas (Breietenbach, 1961; Mirhetu *et al.*, 1983; Bowen, 1985; Orlander, 1986).

At Assassa, Ethiopia (2300 m altitude) where provenances from the Lake Albacutya (Victoria), Mount Newman (Western Australia) and Alice Spring (Northern Territory) were planted together, over 6 m in height growth was recorded 32 months after planting for the Lake Albacutya provenance. This was 50 percent better than that of the Mount Newman and Alice Spring provenances (Poulsen, 1973).

According to Mirhetu *et al.*, (1983) for the species elimination trial which is situated in the rift valley at Dera (altitude: 1700 m; rainfall: 700 mm) provenances from Mount Newman and Alice Springs survived the extreme drought better than the provenances from the Lake Albacutya, while the Lake Albacutya provenance showed a height growth of almost double that of Mount Newman and Alice Spring provenances after five years. Both Poulsen (1973) and Mirhetu *et al.* (1983) reported that the Lake Albacutya provenance were superior in height growth in both high and low altitude zones although they did suffer from drought.

Subsequently, provenance trials containing 10 different seed sources, (three from Queensland, two from Western Australia, two from New South Wales, one from Northern territory, and one from Victoria) were planted over two experimental sites at Negus Galle (altitude: 1656 m; rainfall: 600 mm) and Dera (altitude: 1700 m; rainfall: 700 mm). Mean height growth after six years showed that the Petford (Queensland), Katherine (Northern territory) and the Lake Albacutya (Victoria) provenances ranked among the top five in both experimental sites (Davidson, 1989).

From this evidence it can be observed that the performance of the Petford, Katherine and the Lake Albacutya provenance in Ethiopia is in line with the results that had been achieved in many tropical countries. However, most of the preliminary results were based on data collected from the trials which were partially damaged by animals or people. From the limited evidence available it is still not possible to draw

a definite conclusion related to the performance of *E. camaldulensis* provenances in Ethiopia. To locate the most suitable provenance for growth and stem straightness, further studies across a range of sites are required using seed from the Petford, Katherine, and the Lake Albacutya provenances.

CHAPTER 3

Combined Provenance/Progeny Trial of *E. Camaldulensis*

3.1 Objectives of the Trial

The main objective of the *Eucalyptus* breeding programme in Ethiopia is to develop a breeding population with genetically improved growth characteristics and stem form which will be used as a source of seed to establish seed orchards.

Against this background, the specific objectives of the combined provenance/progeny trial to be extensively reported in this thesis are:

(i) to study the variation between provenances and families within provenances;

(ii) to estimate genetic parameters for height, diameter and stem straightness traits;

(iii) to create a breeding population based on individuals from superior families with multiple traits;

(iv) to establish a seedling seed orchard and produce genetically improved seeds for commercial purposes; and

(v) to use the progeny trial as a source of clonal material and as a gene conservation stand for future selection.

3.2 Materials and Methods

3.2.1 Seed origin

The seed used to establish the combined provenance-progeny trials came from Queensland, Australia between 16° 41' and 17° 29' South and 143° 13' and 145° 09' East having an altitudinal range from 140 to 860 m. The seed was collected from Northern Queensland from an area of the Walsh river drainage, centred on Petford region. The individual trees or families were selected from the natural stands with a minimum distance between collections of 100 m to avoid relatedness (Doran, 1984).

Six provenances, namely Stannary Hills, Dimbulah, Irvine Bank, Wrotham Park, Emu Creek and Petford were included in the experiment. The total number of families was 407 and the distribution of families within provenances ranges from 5 to 256.

Table 3.1 Details of seed sources for the progeny trial of *E. camaldulensis*

CSIRO seedlot no.	Family code	No. of Families	Locality	Provenance	Latitude (S)		Longitude (E)		Altitude
					DEG	MIN	DEG	MIN	M
12187	1-16	16	W Irvine Bank	Irvine Bank	17	24	145	09	680
16533	86-90	5	SE Irvine Bank		17	29	145	13	860
16534	91-95	5	NW Irvine Bank		17	24	145	09	710
TOTAL		26							
16286	17-26	10	Emu Creek	Emu Creek	17	28	145	08	750
16372	27-85	59	Emu Creek and Tributaries		17	25	145	01	600
TOTAL		69							
16535	96-100	5	Stannary Hills	Stannary Hills	17	19	143	13	460
TOTAL		5							
16537	106-110	5	SW Dimbulah	Dimbulah	17	11	145	03	460
16539	111-115	5	W Dimbulah		17	10	144	53	420
16540	116-120	5	W Dimbulah		17	10	144	56	
TOTAL		15							
16533	121-125	5	W Wrotham	Wrotham	16	41	144	54	140
16561	126-130	5	W Wrotham		16	41	143	54	140
14777-14801	383-407	25	SE Wrotham		16	44	144	01	190
TOTAL		35							
14237-14265	232-260	29	NE Petford	Petford	17	14	145	04	490
14268-14272	263-267	5							
14277-14308	272-303	32							
14266-14267	261-262	2	E Petford		17	18	145	00	490
14273-14276	268-271	4							
14340-14353	333-345	13							
14387-14390	379-382	4							
14309-14337	304-332	29	SE Petford		17	24	145	06	630
14354-14386	346-378	33							
16720	131-231	101	Petford		17	25	145	01	600
16536	101-105	5							
TOTAL		257							
G. TOTAL		407							

Details of the seed lots are listed in Table 3.1. The list includes seed lot numbers and their respected latitude, longitude and altitude allocated by the CSIRO division of Forestry Research in Canberra, Australia and lists family code numbers allocated by the Ethiopian Forestry Research Centre (EFRC), Addis Ababa, Ethiopia.

3.2.2 The experimental site

The trial was established at Mankusa, Gojam province, located at 10° 43' North and 37° 23' East in the Northern highlands of Ethiopia at an altitude of 1885 m. The mean annual rainfall of the area is 1080 mm in 132 days and there are two principal rainy seasons - the short period normally about April and the 'long rains' during the months of July, August and September. Rainfall intensity and the duration of the rainy seasons show considerable variation from year to year: in some years the period from October to March is very dry and in others fairly frequent showers may occur. The dry season is critical to the survival of the seedlings and is obviously a limiting factor for growth. Mean temperature varies from 15 °C for the coldest month to 20 °C for the hottest month. The experimental plots were established on a part of the site which has 5 to 10% slope.

3.2.3 Soil

According to Murphy (1968) the major soils of the area are fine-textured nitosols with

(i) more than 35% clay;

(ii) less than 50% base saturation;

(iii) strong to slight acidity (pH 4.5 to 6.5) and thus capable of supplying sufficient calcium and magnesium for plant needs;

(iv) low organic matter and low nitrogen content; and

(v) high in total phosphorus but low in available phosphorus for plant needs.

3.2.4 Seedling production and site preparation

The seedlings of *E. camaldulensis* were raised at a nursery situated close to the planting site. Seed was directly sown in polythene tube containers (5 cm diameter

and 15 cm length). The mixture used for potting materials consisted of 3 parts local soil, 2 parts forest soil and 1 part sand. The average height and the root collar diameter for the seedlings during planting were 25 cm and 17 mm respectively. Holes of 50 cm in diameter and 30 cm in depth were used for planting the seedlings. Spot hoeing was carried out annually for the first two years after planting.

3.2.5 Field trial design and measurement

In July 1991 the 407 families of *E. camaldulensis* were outplanted in a complete randomised block design with 6 replications of 4 -tree square plot at a spacing of 3 m × 3 m between the plants. All trees were assessed for height, diameter and stem straightness at 34 months after planting. Stem straightness was measured on a subjective score method (6-point scoring system where 6 = excellent straightness for the site, and 1 = twisted). Two families, (number 224 and 391) were excluded from the data analysis because of wrong labelling during planting.

3.2.6 Statistical method

The data were analysed using PROC MEANS and PROC ANOVA procedures of the SAS statistical package. Tree variables such as total tree height, diameter at breast height and stem straightness were subjected to analysis of variance (ANOVA) to see if there were significant differences between provenances and families within provenances. The data were fitted to the statistical models (detailed below).

3.2.6.1 Standard model (Model 1a)

The standard model of combined provenance-progeny trial is a form of mixed model and adapted from Harvey & Townsend (1985) and Kanowski & Nikles (1989). The model assumes a replicated trial including provenances, families within provenances and trees within family and is symbolically represented as follows:

$$Y_{ijkl} = \mu + R_i + P_j + F_j{:}\, K + (PR)_{ij} + (FR)_j{:}\, K_i + \varepsilon_{ijkl} \qquad [1]$$

Where

$Y_{ijkl:}$ is the phenotypic value of the l^{th} individual of the k^{th} family from the j^{th} provenance in the i^{th} replicate;

μ: is the fixed term overall mean;

$R_{i:}$ is the fixed effect of the i^{th} replicate;

$P_{j:}$ is the effect of the j^{th} provenance (assumed random)

F_j: K: is the effect of the k^{th} family in the j^{th} provenance;

$(PR)_{ij:}$ is the effect of the interaction between the i^{th} replication and j^{th} provenance

$(FR)_j$: $K_{i:}$ is the effect of the interaction between the i^{th} replicate and the k^{th} family of the jth provenance;

$\varepsilon_{ijkl:}$ is the effect of the l^{th} tree within the k^{th} family of the j^{th} provenance in the i^{th} replicate.

The expected mean square for standard model (Model 1a) is listed in Table 3.2.

Table 3.2 Source of variance and expected mean squares in an analysis of provenances and family within provenances trial, assuming a fully random model (Model 1a).

Source of variation	Degrees of freedom	Mean square	Expected Mean squares
Replication	R–1	MS_6	$\sigma_w^2 + T\sigma_{RF}^2 + TF\sigma_{RP}^2 + TFP\sigma_R^2$
Provenance	P–1	MS_5	$\sigma_w^2 + T\sigma_{RF}^2 + TR\sigma_F^2 + TF\sigma_{RP}^2 + TRF\sigma_P^2$
Prov. x Rep.	(P–1) (B–1)	MS_4	$\sigma_w^2 + T\sigma_{RF}^2 + TF\sigma_{RP}^2$
Families	P(F–1)	MS_3	$\sigma_w^2 + T\sigma_{RF}^2 + TR\sigma_F^2$
Fam. x Rep.	P(F–1)(R–1)	MS_2	$\sigma_w^2 + T\sigma_{RF}^2$
Trees within plots	PRF (T–1)	MS_1	σ_w^2

F, R, P and T refer to the number of families, replications, provenances and trees per family-replication plot respectively. The mean square values represented by σ_w^2,

σ^2_{RF}, σ^2_F, σ^2_R, σ^2_P, and σ^2_{PR} are within plot, replication x family, family, replication, provenance, and provenance x replication variance components respectively.

3.2.6.2 Adjusted model (Model 1b)

The expectation of mean squares presented under Table 3.2 assumes a fully random model. However, Kanowski and Nikles (1989) pointed out in family-within-provenance trials, provenance cannot be considered as a random effect. They suggested an exact test for provenance is only possible if provenance x replication effects are ignored and provenance is tested against families within provenance.

Following the suggestion of Kanowski and Nikles (1989) the model under equation 1 was adjusted by excluding the provenance x replication interaction and symbolically represented as follows:

$$Y_{ijkl} = \mu + R_i + P_j + F_j{:}\ K + (FR)_j + (FR)_j{:}\ K_i + \varepsilon_{ijkl} \qquad [2]$$

The expected mean squares using equation 2 assuming a mixed model are presented in Table 3.3 and it is observed that the mean squares for replication term (R) does not include the variance of provenance x replication (σ^2_{RP}). The mean squares were used to calculate variance components in order to estimate heritability.

Table 3.3 Source of variance and expected mean squares in analysis of provenances and family within provenances trial, assuming a mixed model (Model 1b).

Source of variation	Degrees of freedom	Mean square	Expected Mean squares
Replication	R–1	MS_6	$\sigma^2_w + T\sigma^2_{RF} + TFP\sigma^2_R$
Provenance	P–1	MS_4	$\sigma^2_w + T\sigma^2_{RF} + TR\sigma^2_F + TF\sigma^2_{RP} + TRF\sigma^2_P$
Families	P(F–1)	MS_3	$\sigma^2_w + T\sigma^2_{RF} + TR\sigma^2_F$
Fam. x Rep.	P(F–1)(R–1)	MS_2	$\sigma^2_w + T\sigma^2_{RF}$
Trees within plots	PRF (T–1)	MS_1	σ^2_w

CHAPTER 4

Results and Discussion

4.1 ANOVA Results for Provenance and Family within-Provenance

Results from the analysis of variance (Table 4.1) shows that the differences between replicates for height, diameter and stem straightness are highly significant at 1% significance level, indicating there is considerable variation between replicates across the trial. The results reveal that blocking and randomisation is effective in levelling out the variation between blocks.

There was significant variation between the provenance mean for tree height and stem straightness at 1% and for diameter at 5% significance level. There was also significant variation between families within provenance and family x replication interaction at 1% significance level for all three traits.

4.1.1 Provenance ranking based on mean values

Ranking of provenances based on mean values for height diameter and stem straightness was done to identify the best provenance for each trait (Table 4.2).

The Dimbulah provenance had the highest 34 month mean height (323.9 cm) and the Wrotham Park had the highest mean diameter (2.7 cm) and stem straightness (3.5 point). The slowest growing provenance was the Stannary Hills, which exhibited mean values of 295.8 cm, 2.4 cm and 2.8 point for tree height, diameter and stem straightness respectively.

The range for provenance mean height (28.2 cm), diameter growth (0.3 cm) and stem straightness (0.80 point) show minor differences, suggesting that provenance selection can be ignored and selection should be concentrated on families and individuals within families. Family mean height ranged from 228.2 to 437.3 cm, mean diameter from 1.6 cm to 4.2 cm and mean stem straightness from 1.9 to 4.7 point (Appendix 12). The best families yielding twice as much as the worst family for height and two-half times for diameter and stem straightness. The best and the worst families for height and diameter growth were recorded from Petford

provenance and for stem straightness the best family is from Wrotham Park, while the worst is from Stannary Hills.

Table 4.1 Results from analysis of variance based on provenance and family within provenance, for height, diameter and stem straightness.

Height at 34 months				
Source of variation	**DF**	**MS**	**F-RATIO**	**Remark**
Replication	5	970085.008	168.92	**
Provenance	5	27019.360	4.70	**
Family	399	30680.124	5.34	**
Fam. x Rep.	2020	16612.418	2.89	**
Error	6926	5743.133		
Total	9355			
Diameter at 34 months				
Source of variation	**DF**	**MS**	**F-RATIO**	**Remark**
Replication	5	59.735	51.44	**
Provenance	5	3.414	2.94	*
Family	399	4.788	4.12	**
Fam. x Rep.	1980	3.219	2.77	**
Error	5904	1.161		
Total	8293			
Stem straightness at 34 months				
Source of variation	**DF**	**MS**	**F-RATIO**	**Remark**
Replication	5	95.259	85.51	**
Provenance	5	12.035	10.80	**
Family	399	4.477	4.02	**
Fam. x Rep.	2019	2.033	1.82	**
Error	6917	1.114		
Total	9345			

**= Significant at 1%

*= Significant at 5%

Table 4.2 Provenance mean values of for height, diameter and stem straightness and the total number of families included in each provenance.

Provenance	State	Number of Families	Provenance mean values		
			Height (cm)	Diameter (cm)	Straightness (point)
Dimbulah	Queensland	15	323.98	2.60	3.24
Petford	Queensland	256	318.19	2.66	3.11
Wrotham Park	Queensland	34	314.75	2.68	3.53
Emu Creek	Queensland	69	313.30	2.58	3.16
Irivine Bank	Queensland	26	308.99	2.63	3.13
Stannary Hills	Queensland	5	295.81	2.36	2.77

4.2 Distribution of the Top 40 Families Across Provenances for Each Trait

The distribution of the top 40 selected families for height, diameter, and stem straightness within each provenance are listed in Table 4.3. It is observed, for all three traits, that the number of families qualified to be in the top 40 was proportional to the total number of families included in each provenance. For example, for Petford provenance the total number of families included were 256 out of which 31, 26, and 18 families were included in the top 40 for height, diameter, and stem straightness respectively, whereas for Dimbulah with 15 families only 1, 1, and 3 families were similarly included.

The result reveals that those families which are superior for height, diameter, and straightness are proportionally distributed in all provenances, thus provenance selection does not contributed to maximum genetic gain for all the three traits. Thus provenance identity will be ignored and selection of the top families will be based on their mean values. In fact, the majority of the families in the top 40 for all the three traits were included from the Petford provenance which comprises 256 families out of the 405 families included in the progeny test.

Table 4.3 Distribution of the top 40 families across provenances for each trait.

Provenance	Number of families	Number of families in each provenance		
		height	diameter	straightness
Stannary Hills	5	1	1	0
Dimbulah	15	1	1	3
Irivine Bank	26	2	3	3
Wrotham Park	34	2	4	8
Emu Creek	69	3	5	8
Petford	256	31	26	18
Total	405	40	40	40

4.3 Estimation of Genetic Parameters

4.3.1 Variance components

Variance measures the degree of variability between individuals in a given population. It is an important concept in tree improvement programmes because it provides information to estimate genetic parameters such as heritability and correlation between the traits. Individual variation within a population is caused by:

(i) variation in environment in which the trees are growing;

(ii) genetic differences among trees, and

(iii) the interaction between tree genotypes and the environment (Falconer, 1981; Zobel & Talbert, 1984 ; and Van Buijtenen, 1992).

Following the method of Falconer (1981) the phenotypic variance is symbolically represented as follows:

$$_P = V_G + V_E = V_A + V_{NA} + V_E \qquad [3]$$

Where: V_P = Total phenotypic variance; V_G = Total genetic variance; V_A = Additive genetic variance; V_{NA} = Non-additive genetic variance, and V_E = Environmental variance.

From equation 3 it is observed that if environmental variance is totally eliminated by experimental control the total phenotypic variance equals the genetic variance. Falconer (1981) and Zobel and Talbert (1984) stated that environmental variance can not be totally removed by experimental control, it can only be reduced by using good experimental design and homogenous sites.

The genetic variance which is caused due to genetic effects is further divided into Additive (V_A) and Non-Additive genetic variance (V_{NA}). For open-pollinated families the additive genetic variance is the chief cause of resemblance between the relatives and is an important component in estimating heritability (Falconer, 1981). For the open- pollinated progeny trial of *E. camaldulensis* the additive genetic variances for family, family x replication, and total variance were estimated following the method of Zobel and Talbert (1984).

$$\sigma_F^2 = \frac{MS_3 - MS_2}{TR} = \frac{(\sigma_W^2 + T\sigma_{RF}^2 + TR\,\sigma_F^2) - (\sigma_W^2 + T\sigma_F^{2)}}{TR} \qquad [4]$$

$$\sigma_{RF}^2 = \frac{MS_2 - MS_1}{T} = \frac{(\sigma_W^2 + T\sigma_{RF}^2) - \sigma_W^2}{T} \qquad [5]$$

$$\sigma_P^2 = \sigma_F^2 + \sigma_{RF}^2 + \sigma_W^2 \qquad [6]$$

Where F, R and T refers to the number of families, replications, and trees per family-replication plot, σ_w^2, σ_{RF}^2, σ_F^2, and σ_P^2 are within plot, replication x family, family and total variance components respectively, and MS_1, MS_2 and MS_3 are mean squares as defined in Table 3.2.

The genetic variance components, that is variance due to trees within plot, family, and replication by family were estimated using mean squares from the analysis of variance table (Table 4.1) and are presented in Table 4.4. It is observed (Table 4.4) that the greatest proportion of the observed variation is accounted for by

differences between trees within plots (σ^2_w) followed by family x replication interaction (σ^2_{RF}) and between families (σ^2_F) for the traits studied.

Table 4.4 Values of variance components and their percentages

Variance component	Height (cm)	Diameter (cm)	Straightness (point)
Total Variance (σ^2_P)	9044.72	1.73	1.46
	100%	100%	100%
Family Variance (σ^2_F)	584.27	0.06	0.11
	6.5 %	3.5%	7.5%
Fam. x Rep. (σ^2_{RF})	2717.32	0.51	0.23
	30.0 %	29.5%	15.8%
Error Variance (σ^2_w)	5743.13	1.16	1.12
	63.5 %	67.0 %	76.7%

4.3.2 Heritability

Heritability is the genetic parameter which measures the strength of the resemblance between the relatives; it can be expressed as narrow-sense and broad-sense heritability. *Broad-sense heritability* is particularly used for vegetatively propagated materials and estimated as a ratio of total genetic variance to phenotypic variance, whereas the *narrow-sense heritability* is most commonly used to estimate heritability for open-pollinated families where additive effects are most important and estimated as the ratio of additive genetic variance to phenotypic variance (Zobel & Talbert, 1984; Van Buijtenen, 1992). Narrow-sense heritability is represented as follows:

(i) Individual tree heritability (h^2):

$$h^2 = \frac{V_A}{V_P} = \frac{4\sigma^2_F}{\sigma^2_W + \sigma^2_{RF} + \sigma^2_F} \qquad [7]$$

Where V_A, and V_P refer to additive genetic variance and total phenotypic variance respectively.

The assumption underlying that the calculated variance component for open-pollinated families estimates one-fourth of the additive genetic variance (equation 7) is only true if:

(i) there is no inbreeding in the population;

(ii) dominance does not interfere, and

(iii) random mating has occured and many male parents have contributed equal pollen: if these assumption are not met there is a possibility of over-estimation of heritability values (Falconer, 1981).

(ii) Family heritability (h_F^2):

$$h_F^2 = \frac{\sigma_F^2}{\frac{\sigma_W^2}{TR} + \frac{\sigma_{RF}^2}{R} + \sigma_F^2} \qquad [8]$$

From Equations 7 and 8 it is observed the value of heritability depends on the magnitude of all components of variance, thus the precision of the heritability values is based on the accuracy of the variance components. To know how much errors were associated with the heritability values standard errors of heritability (σ_{h^2}) were calculated following the method of Wright (1976) and represented as follows:

(i) Standard errors of individual tree heritability (σ_{h^2}):

$$\sigma_{h^2} \cong \frac{(1-h^2/4)[1+(NBS)h^2/4]}{NBS[(F-1)/2]^{1/2}} \qquad [9]$$

(ii) Standard error of half-sib family heritability ($\sigma_{h_F^2}$)

$$\sigma_{h_F^2} \cong \frac{(1-t)(1+NBSt)}{[(NBS)(F-1)/2]^{1/2}} \qquad [10]$$

Where t, N, B, S, F refer to intra-class correlation, numbers of trees per plot, number of blocks, number of sites and number of families respectively. The intra-class correlation (t) is equal to one-fourth of the individual tree heritability (Wright, 1976; Falconer, 1981).

Table 4.5 Family mean performance, individual tree (h^2) and family heritability (h^2f) and their standard errors (S.E.)

Traits	**Mean**	**Tree Narrow-sense heritability**	
		$h^2 \pm$ S.E	$h^2f \pm$ S.E
Height (cm)	316.95	0.29 ± 0.01	0.46 ± 0.04
Diameter (cm)	2.69	0.15 ± 0.01	0.32 ± 0.03
Straightness (score)	3.14	0.29 ± 0.01	0.56 ± 0.04

It is observed that from heritability equation (Equations 7 and 8), the heritability values were dependent on the variance components used. Heritability values can be increased by increasing the additive genetic variance for families and this could be done by decreasing the value of family x replication variance, i.e. by using homogenous experimental site (Wright, 1976). In the case of *E. camaldulensis* progeny trial, the existence of high family x replication interaction variance results in low heritability values.

Narrow-sense single-tree heritability and family heritability values indicated that stem straightness was under the most genetic control followed by tree height and then diameter (Table 4.5), suggesting that selection for stem straightness provides maximum genetic gain when compared with height and diameter.

The single-tree heritability values obtained for height and diameter (Table 4.5) from the *E. camaldulensis* progeny trial in Ethiopia is similar to the results reported by Franklin and Meskimen (1973) for *E. robusta* (0.28 for height and 0.13 for diameter) in Florida and Kedharnath and Vakshasya (1978) for *E. tereticornis* (0.26 for height and 0.23 for diameter) at age four years (see FAO, 1979).

On the other hand, in Zimbabwe for 26 open-pollinated families of *E. camaldulensis,* family heritability values of 0.77, 0.61 and 0.70 and overall family mean values of 6.81 m, 5.83 cm and 2.72 point were reported for tree height, diameter and stem straightness respectively at age 3.5 years (Qualie & Mullin, 1984). This result indicated that the Zimbabwean families yielded about twice that of the Ethiopian families for height and diameter growth. There were also high family heritability values for all traits for the Zimbabwean families when compared to the Ethiopian ones. As Van Buijtenan (1992) described, the heritability estimate from the experiment is specific to: (i) the population from which individuals families were chosen; (ii) the environment under which the progenies are growing; and (iii) the traits under consideration.

Other sources of information also indicated that 351 open-pollinated families which were included in the Ethiopian progeny test were planted in Thailand in the same year and at age 36 months, the height growth for the Thailand progeny test was five times that of their Ethiopian relatives (Davidson, pers. comm.).

It is not yet clear why the growth rate of the Australian families is poor in Ethiopia. On a neighbouring plantation site, about 2 miles away, the height growth for the Ethiopian land race was twice that of the Australian families. It is likely there might be differences in soil fertility between the two planting sites which contributed to the differences in growth rate. Thus, it is difficult to conclude whether the growth performance of the Australian families were poor before planting the Ethiopian land race and Australian families together on one planting site.

The differences in elevation between the experimental site (high elevation) and the seed origin in Australia (low elevation) might create problems in adaptability, i.e. the chosen experimental site might not be the most suitable site for the Australian families. Therefore it is recommended that further investigation should be done until the rotation age to reach the final conclusion.

4.3.3 Covariance

Variation among multiple traits in a population is estimated by covariance, that is an average cross product of the variances for the two traits under consideration

(Van Buijtenen, 1992). Covariance can be divided into its components; phenotypic and genetic covariance. The phenotypic covariance includes all covariances attributable to genetic variation as well as environmental variation, where as the genetic covariance includes only covariances attributable to the genetic differences among families (Falconer, 1981; Zobel & Talbert, 1984). In the case of *E. camaldulensis* progeny trial the phenotypic and genetic covariances were calculated using a SAS programme.

Table 4.6 Phenotypic and genetic covariances and variances

Trait	Height	Diameter	Straightness
Height		1.33	0.81
Diameter	86.37		0.01
Stem straightness	34.47	0.43	
	Height	Diameter	Straightness
Phenotypic variance	7760.34	1.27	1.16
Genetic variance	148.86	0.02	0.03

Note: In the upper part of the table, values below the diagonal are phenotypic covariances and those above are genetic covariances

4.3.4 Phenotypic and genetic correlation

The correlation between two traits is estimated as the ratio of their covariance to their standard deviation and it is the measure of the strength of the association between the two traits (Falconer, 1981). Following the method of Van Buijtenen (1992) the phenotypic and genetic correlations were estimated using the following formulae.

$$\Gamma_{p_1p_2} = \frac{COV_{p_1p_2}}{\sqrt{V_{p_1} V_{p_2}}} \qquad [11]$$

where $\Gamma_{p_1p_2}$, $COV_{p_1p_2}$ and $V_{p_1p_2}$ refer to phenotypic correlation, covariance, and variances of traits 1 and 2 respectively.

$$\Gamma_{a_1a_2} = \frac{COV_{a_1a_2}}{\sqrt{V_{a_1}V_{a_2}}} \quad [12]$$

Where: $\Gamma_{a_1a_2}$, $COV_{a_1a_2}$ and $V_{a_1}V_{a_2}$ refer to genetic correlation, covariance, and variances of trait 1 and 2 respectively.

Table 4.7 Phenotypic and genetic correlation for *E. camaldulensis* progeny trial.

	Height	**Diameter**	**Straightness**
Height		0.790	0.390
Diameter	0.870		0.410
Straightness	0.360	0.350	

Note: Values below the diagonal are phenotypic correlation and values above the diagonal are genetic correlation.

There was strong positive genetic correlation between tree height and breast height diameter (0.79), whereas the genetic correlations for tree height and breast height diameter with stem straightness (0.39 and 0.41) were weak. This result reveals that direct selection for height can provide simultaneous gain for diameter on positive direction, whereas direct selection either for height or diameter does not maximise the gain for straightness or *vice versa*.

Further comparisons were done by using family mean values for the top 40 families. The top 40 families were ranked by using mean height, diameter, and straightness independently (Table 4.8).

Table 4.8 : Rank of the top 40 Families using mean height, diameter and straightness and change in ranking postion across traits.

Height	Diameter	Straightness	Rank
Family number	Family number	Family number	
232	303	127	1
103	3	114	2
28	232	101	3
3	344	126	4
314	279	329	5
101	101	43	6
114	243	128	7
168	103	256	8
279	161	27	9
344	368	210	10
244	77	12	11
153	276	48	12
134	185	76	13
161	386	314	14
343	28	42	15
317	343	333	16
240	168	386	17
404	240	397	18
30	329	240	19
99	392	130	20
303	308	201	21
276	80	255	22
247	140	269	23
13	99	400	24
136	294	392	25
258	188	396	26
329	6	149	27
57	314	120	28
160	135	140	29
299	244	188	30
370	404	30	31
113	388	115	32
348	134	147	33
170	13	59	34
246	114	245	35
386	153	81	36
360	364	2	37
150	42	10	38
364	274	212	39
115	53	146	40

Note: Familes joined with arrow lines are common in the three traits

The number of families which are common in the top 40 for height and diameter, for height and stem straightness, and for diameter and straightness are 23, 8, and 9 respectively. Whereas, only 8 families (family 30, 101, 114, 115, 240, 314, 329, and 386) were found in common for the three traits. It is clear that the change in ranking position is significant when the families are compared across the traits.

For example, family 303, which is the very top for diameter is ranked 21 for height and not even included in straightness (Table 4.8). Family 127, which is the very top for straightness is not included both in height and diameter, and family 114, which is the second best for straightness is ranked 35 and 7 for diameter and height respectively. It can be concluded using growth trait as a selection criteria will not at the same time capture those families which are good for straightness or vice versa.

4.4 Estimation of Genetic Gain

4.4.1 Selection for height, diameter, and straightness independently

All the 405 families were ranked by height, diameter and stem straightness independently. Thereafter, genetic gain percentage for selecting the top family, top 20, top 40, top 80, top 120, top 160 and top 200 families were calculated using the overall family mean as 100%, and the results are presented in Table 4.9.

The genetic gain percentage were calculated as the ratio of the selection differential (S) to the overall family mean multiplied by family heritability (equation 13). The selection differential (S) is the mean difference between the selected group and the overall family means. The calculation was done following the methods of Wright (1976) and symbolically represented as follows:

$$Gain\% = \frac{S \times h^2{}_f}{Mean} \times 100 \qquad [13]$$

Where

S = mean of selected family(ies) - overall family mean

h_f^2 = Family heritability

Mean = overall family mean

Table 4.9 Performance of best and top 200 families by trait, showing percentage genetic gain relative to the overall family mean.

	No of family	Height (%)	Diameter (%)	Straightness (%)
Over all family mean	405	100 %	100 %	100 %
Top Family	1	117.4	118.3	127.8
Top 5%	20	111.5	112.9	118.1
Top 10 %	40	109.9	110.7	115.4
Top 20 %	80	107.8	108.5	111.3
Top 30 %	120	106.4	106.8	109.4
Top 40 %	160	105.3	105.4	107.8
Top 50 %	200	104.3	104.3	106.4

The results from the genetic gain Table 4.9 shows that for the same number of families selected for each trait independently, the genetic gain percentage for stem straightness is greater than for height and diameter. This was because stem straightness is under stronger genetic control than height and diameter growth. There are minor differences between height and diameter in genetic gain.

It is observed as the number of families selected increases the genetic gain substantially decreases. For example, selecting the top 20 families results in genetic gain of 11.5%, 12.9% and 18.1% for height, diameter and stem straightness, respectively when the traits are independently selected. Whereas selecting the top 200 families results in genetic gain of 4.3%, 4.3% and 6.4% for the three traits. It can be recommended that selecting few top ranking families provides maximum genetic gain for each trait. However, selecting few families for a breeding population will result in narrowing the genetic base which is a disadvantage in long-term breeding (Falconer, 1981; Zobel & Talbert, 1984).

The conflict between wide genetic base and high selection differential is the main problem in tree breeding. Compromise should be made by choosing an optimum family number that is, not excessively lowering the genetic base by aiming for too high a selection differential. To determine this number, there are divided opinions among tree breeders. For example, Lindgren (1991) recommend from 25 to

50 families is an appropriate number for seed production population. Following this recommendation the top 40 families were chosen as an optimum number to be included in a production population for *E. camaldulensis*; hereafter, in this paper the top 40 families and the overall family mean will be used to calculate genetic gains, and for other comparisons.

4.4.2 Direct selection for first trait and its correlated response in second trait

The top 40 families were ranked by mean height, diameter and stem straightness independently and the list of the families with their corresponding mean values were listed in Appendix 1, 2, and 3 respectively. Thereafter, genetic gain calculations were done for each trait. The genetic gain results for the top 40 families were listed in Table 4.10.

Table 4.10 Performance of best and top 40 families by trait, showing percentage of genetic gain relative to the over all family mean.

Ranking	Height (%)	Diameter (%)	Straightness (%)
Ranking by height	9.9	8.6	4.6
Ranking by diameter	8.5	10.7	4.4
Ranking by form	3.5	3.2	15.4

The results from the genetic gain calculation reveals that using either height or diameter for selection provides almost similar genetic gain for the two traits, this happened because of the strong genetic correlation between the two traits (0.79), suggesting either height or diameter can be used as a selection criteria when the objective of selection is to maximise growth traits. Conversely, ranking either by height or diameter results in genetic gain deterioration for stem straightness or *vice* versa. This happened because of the weak genetic correlation between height and straightness (0.39) and diameter and straightness (0.41).

It can be concluded that when the objective of the selection programme is to optimise genetic gain for the three traits simultaneously single trait selection is not the best method and does not maximise the gain in economic terms. Therefore, since the objectives of *E. camaldulensis* progeny trial is selection of families having vigorous growth and better stem straightness simultaneously, single-trait selection is not the best method to develop the next breeding population.

CHAPTER 5

Multiple-Trait Selection

The objective of tree improvement is to obtain as much gain as quickly as possible through selection. Genetic gain is a function of selection differential (difference between the selected individual and population mean) and heritability (Wright, 1976; Falconer, 1981; Zobel & Talbert, 1984).

Genetic gain can be increased by increasing selection differential, that is by choosing a smaller number of superior individuals from the population. However, with fewer individuals selected relatedness develops more rapidly and the risk of inbreeding is increased (Zobel & Talbert, 1984). Thus, the selection method to be used should provide optimum genetic gain, while maintaining genetic diversity for long-term breeding.

Selection can be done in two ways: (i) Single-trait selection - in which the objective is to obtain the greatest genetic gain in a single trait, regardless of gain deterioration in other traits; and, (ii) multiple-trait selection - in which the objective is to increase economic value as a result of the best possible combination of selection for a number of major economic traits.

Single trait selection can maximise the genetic gain considerably for the trait under investigation, but not the total economic gain. The total gain in economic terms from all traits can be maximised by optimising the gain for all traits, and this can be done by using multiple trait index selection (Hazel, 1943; Cunningham, 1975).

The existence of negative correlation between growth (diameter) and wood quality traits (wood density) has been reported for many tree species, and selection for diameter results in deterioration of gain for wood density or, *vice versa*, suggesting that selection for either trait independently results in a decrease of total economic gain. For example, the adverse correlation between branch diameter and stem diameter for *P. caribaea* (Dean, 1986) (see Cotterill & Dean, 1990) and between wood density and stem diameter for *P. radiata* (Cotterill and Jackson, 1981)

has been reported. In both cases selecting for stem diameter results in gain deterioration, of branch diameter and wood density respectively.

The decision as to whether single-trait or multiple-trait selection is to be employed depends on the objectives of the breeding programme. For example, if fuel wood is the first priority single-trait selection for growth rate would be used. If construction and transmission poles are equally important, simultaneous improvement of growth and stem straightness are needed. In this case multiple-trait selection is the one to use.

Dorman (1976) pointed out that the greatest economic gain from the forest product is the cumulative effect of several traits. However, traits such as pest resistance, wood volume growth, and stem straightness are given higher priorities in most tree breeding programs provided adaptability is well tested in advance.

Disease resistance is an important trait to be consider prior to any breeding work. If there is no knowledge regarding the risk of a particular disease in the given environment, then it could be that putting too much emphasis on that disease in the breeding work might not be justified. According to Zobel and Talbert (1984), disease resistance is found to be independent to major economic traits, such as growth traits (height & diameter) and quality traits (stem straightness, wood density and branching habit). Therefore it is possible to select concurrently for the major economic traits and disease resistance.

In the case of *E. camaldulensis* in Ethiopia the objective of selection is to improve growth rate and stem straightness simultaneously, because these two traits are equally important in economic terms at present. There are currently no major problems regarding adaptability and pest resistance, nevertheless, only healthy and vigorous trees are included in the selection programme.

Once the decision has been made to use selection as a tool for tree improvement the selection method used should be efficient in providing maximum gain. For selection to be effective there should be: (i) variation within the population; (ii) genetic control of the traits to be selected; and (iii) there should be strong positive genetic correlation between the traits— so that direct selection for the

first trait can provide directional gain in the second trait (Dorman, 1976; Falconer, 1981).

For *E. camaldulensis* in Ethiopia genetic correlation of 0.79, 0.35, and 0.41 were recorded between height and diameter, height and stem straightness, and diameter and stem straightness respectively. This shows that selecting for height results in directional gain for diameter. However, the existence of weak genetic correlation between growth rate (height and diameter) and stem straightness suggests that selecting for growth rate does not at the same time maximise gain for stem straightness, and *vice versa*. There is therefore a case to employ multiple-trait selection index to obtain greater simultaneous gain in all the three traits, than could be obtained by single-trait selection.

5.1 Multiple-Trait Selection Methods

The objective of multiple-trait selection is to capture those individuals having more than average genes for all traits under consideration in one selection programme. Three methods of selection are described by Hazel and Lush (1942) which can be used for simultaneous improvement of two or more traits in a tree breeding programme, these are: (i) tandem selection; (ii) independent culling; and, (iii) index selection (see Baker, 1986).

5.1.1 Tandem selection

The technique of tandem selection involves selecting for several traits, one at a time over several generations. One trait is selected until it is improved to a satisfactory level. Then, selection for second trait will be continued within the selected population in the next generation. This process continues until all traits are improved. The disadvantages of tandem selection are: (i) it will require a long time if many traits are included in the breeding programme; and (ii) long-term selection on one trait may lead to unacceptable deterioration in other adversely correlated traits. For example, selecting for one or two generations to improve growth rate in *P. caribaea* and *P. radiata* in Australia would lead to deterioration in branch form and wood density (see Cotterill & Dean, 1990).

5.1.2 Independent culling

Under this method of selection individuals falling below the predetermined culling level for a given trait will be rejected regardless of their superiority in other traits. The advantage of this method is that culling can be carried out for different traits either simultaneously or at different times in the one generation. The disadvantage of independent culling is: (i) the method is inflexible; (ii) it is difficult to decide the appropriate culling levels for each trait when three or more traits are subjected to independent culling; and (iii) it does not provide gain simultaneously for adversely correlated traits.

5.1.3 Index selection

The technique of index selection involves combining information from multiple sources into one index value. The objective of index selection is to maximise gain for all the traits included simultaneously. Multiple-trait selection indices such as: (i) Base index— described by William (1962); (ii) Elston index— described by Elston (1963); and (iii) Smith-Hazel index— described by Smith (1936) and later by Hazel (1943) are all used to maximise gain for two or more traits in one selection programme (see Cotterill & Dean, 1990). The first two are considered as a simple indices and used when there is no reliable information about genetic parameters. They will not be further discussed in this dissertation. The index which was described by Smith and Hazel is found to be most successful for optimising genetic gain when the number of traits included in the index increases and information regarding genetic parameters are available (Baker, 1986). The Smith-Hazel index has been employed here for multiple-trait selection of *E. camaldulensis*. The process involved will be expanded upon in detail in the forthcoming sections.

5.2 Relative Efficiency of Tandem Selection, Independent Culling, and Index Selection

The relative efficiency of tandem selection, independent culling, and index selection were compared by Hazel and Lush (1942) and Young (1961) for

independent, correlated and uncorrelated traits. Their findings were included in the literature review by Baker (1986) and Cotterill and Dean (1990). The following points were extracted from each of these reviews:

For uncorrelated traits (Hazel & Lush, 1942): (i) independent culling is intermediate to index and tandem selection; (ii) the efficiency of independent culling approaches that of index selection as the number of traits decreases, and as the intensity of selection increases; and (iii) the advantage of independent culling over tandem selection will decrease as the number of traits increases and when selection intensity decreases.

The following three comparisons were based on Young (1961):

(i) Independent traits - index selection is more efficient than tandem selection as the number of traits increases;

(ii) Uncorrelated traits - the superiority of index selection over independent culling was greatest when the traits were of equal economic importance and when selection intensity was low to intermediate; and,

(iii) Correlated traits - index selection is as efficient as independent culling which, in turn is as efficient as tandem selection.

5.3 The Smith-Hazel Index

Two types of indices are used under the Smith-Hazel index, these are: (i) The unrestricted index - which is commonly used for positively correlated traits aimed at optimum gain for all the traits simultaneously; and (ii) the restricted index - which is used for adversely correlated traits where restriction will be made on the first trait, while maximum gain will be achieved from the second.

For example, in Australia, for *P. radiata*, the correlation between wood density and stem diameter is negative. Thus, selecting for stem diameter resulted in deterioration of wood density when equal economic weightings were assigned to both traits (Dean *et al.*, 1983). The restricted index was employed to prevent deterioration in wood density, while maximum gain can be achieved for diameter growth. Such type of restriction is called a Kempthorne restriction (see Cotterill and

Dean, 1990). When a Kempthorne restriction is applied to wood density it assumes the gain expected in wood density will be positive, otherwise, it should be maintained at its present level.

Because of its flexibility in handling adversely correlated traits and its efficiency in optimising gain, the Smith-Hazel index is found to be the most successful and widely used one compared to the other multiple-trait selection methods. However, in the past its wide usage and applicability has been limited by three main problems: (i) uncertainty regarding how economic weights should be determined; (ii) lack of reliable estimates of heritability and genetic correlation; and, (iii) lack of expertise and computing facilities needed to solve the sets of equation required to construct the indices (Hazel, 1943).

The major advantage of index selection over independent culling and tandem selection is: (i) it can combine information from relatives (individual values and family mean) into one index; (ii) when two adversely correlated traits are included in one index, restriction can be used to maintain the second trait at its present level while maximum gain is achieved from the first trait; and (iii) strong weighting can be assigned to traits of high economic importance.

Both Hazel (1943) and Lin (1978) strongly emphasised that the gain in individual traits from multiple-trait index selection is mainly determined by: (i)the reliability of genetic parameter estimation; (ii)the intensity of selection; and (iii) the economic weight assigned to each trait included in the index.

Hazel (1943) pointed out that the selection index constructed using genetic information from one site can not be used for a range of sites. This is because the genetic parameters are specific to a given population, the management techniques applied, and the environment from where the population belongs. If there is a need to extend the use of index for a range of sites within a region, the genetic parameters for each planting sites should be calculated and mean values of the sites used to construct an index which can be applied to the whole region.

Generally there is no limit to the number and type of traits which can be included in the Smith-Hazel index. However, its efficiency decreases as the number of traits included increases and as also the gain for an individual trait rapidly

diminishes, especially when the traits are adversely correlated (Cotterill & Dean, 1990).

To achieve optimum gain from a multiple trait selection index, Cotterill and Jackson (1985), pointed out: (i) the number of traits included in the selection index should be kept as low as possible, (ii) traits of low economic importance should not be included unless they were used to achieve indirect gain for other traits of economic importance; and (iii) the use of two highly correlated traits (e.g. height & diameter) in the same index does not provide extra advantage in terms of genetic gain, because selection on one trait will produce a strong indirect gain in the second trait; rather they can be used as a component in the form of volume. However, for *E. camaldulensis* the two traits are used independently because volume estimation is found to be inaccurate at this early stage.

5.3.1 Construction of Smith-Hazel index for E. camaldulensis

Under section 4.4.2 Table 4.10, it was stated that direct selection for growth traits (height or diameter) does not maximise the genetic gain for stem straightness simultaneously, or *vice versa* for *E. camaldulensis*. Because of this the Smith-Hazel index was employed in order to simultaneously increase economic gain for all the three traits combined. The family mean values for height, diameter and stem straightness were multiplied by their corresponding index coefficients and summed together to produce the index value. Following the method of Cotterill & Jackson (1981) and Baker (1986) the multiple trait selection index for *E. camaldulensis* can be represented symbolically as follows:

$$I = P_1b_1 + P_2b_2 + P_3b_3 \qquad [14]$$

Where; P_1, P_2, and P_3 are family mean values and b_1, b_2, and b_3 are index coefficients for height, diameter and stem straightness respectively and I is the index value.

The computer programme used to compute the index coefficients, or 'b' values were called RESI (Restricted Selection Index). Compiled by Cotterill and Jackson (1981) it can accommodate up to 50 traits into one index and can evaluate both restricted and unrestricted indices in one extended computation scheme.

5.3.2 Parameters required for RESI

Under section 5.3.1, equation 14, it is observed the family mean values for each trait was multiplied by their respective index coefficient, or 'b' values and summed across to produce an index value (I). To calculate the index coefficients, or 'b' values Cotterill and Dean (1990) used the following sets of simultaneous equation and matrix calculation for index combining three traits.

$$\begin{aligned} b_1\sigma^2_{P_{11}} + b_2\sigma^2_{P_{12}} + b_3\sigma^2_{P_{13}} &= w_1\sigma^2_{A_{11}} + w_2\sigma^2_{A_{12}} + w_3\sigma^2_{A_{13}} \\ b_1\sigma^2_{P_{21}} + b_2\sigma^2_{P_{22}} + b_3\sigma^2_{P_{23}} &= w_1\sigma^2_{A_{21}} + w_2\sigma^2_{A_{22}} + w_3\sigma^2_{A_{23}} \\ b_1\sigma^2_{P_{31}} + b_2\sigma^2_{P_{32}} + b_3\sigma^2_{P_{33}} &= w_1\sigma^2_{A_{31}} + w_2\sigma^2_{A_{32}} + w_3\sigma^2_{A_{33}} \end{aligned} \qquad [15]$$

Where, $\sigma^2_{P_{11}}, \sigma^2_{P_{22}}$ *and* $\sigma^2_{P_{33}}$ *and* $\sigma^2_{A_{11}}, \sigma^2_{A_{22}}$ *and* $\sigma^2_{A_{33}}$ are phenotypic and genetic variances; $\sigma^2_{P_{12}}, \sigma^2_{P_{13}}$ *and* $\sigma^2_{P_{23}}$ *and* $\sigma^2_{A_{12}}, \sigma^2_{A_{13}}$ *and* $\sigma^2_{A_{23}}$ are phenotypic and genetic covariances; b_1, b_2 *and* b_3 *and* w_1, w_2 *and* w_3 are the respective index coefficient and economic weight for each trait.

Equation 15 are usually expressed in Matrix Notation as follows:

$$\begin{pmatrix} P_{11}P_{12}P_{13} \\ P_{21}P_{22}P_{23} \\ P_{31}P_{32}P_{33} \end{pmatrix} \begin{pmatrix} b_1 \\ b_2 \\ b_3 \end{pmatrix} \begin{pmatrix} A_{11}A_{12}A_{13} \\ A_{21}A_{22}A_{23} \\ A_{31}A_{32}A_{33} \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix} \qquad [16]$$

Or using short hand:

[p] [b] =[A] [w]; Or when simplified: [b] = $[p]^{-1}$ [A] [w].

Where [p] and [A] are matrices of the phenotypic and additive genetic variances and covariances respectively, and [b] and [w] are vectors of index coefficients and economic weights.

In the case of *E. camaldulensis* progeny trial the complicated matrix algebra listed under equation 16 were not used to calculate the index coefficients, or 'b' values. The computer programme called RESI were used to calculate the index coefficients using five sets of input parameters: (i) heritabilities; (ii) phenotypic variances; (iii) phenotypic correlations; (iv)genetic correlations; and (v) economic weights. The genetic parameters (heritabilities, variances and correlation between the traits) were estimated from the field data using the SAS statistical package and economic weightings will be estimated in the forthcoming section by the method of Cotterill and Jackson (1985).

5.3.3 Methods of economic weight determination

In a situation where information about the market price is scarce for the different forestry products, it is difficult to determine the economic weights for individual traits. Cotterill and Jackson (1985) pointed out that when the objective of a breeding programme is to increase simultaneous gain in all traits, economic weight can be determined by methods of equal emphasis (placing equal weightings on all the traits included in the index). This method of determining economic weights had been used in Australia for *P. radiata* and *P. caribaea* and is found to be successful for positively correlated traits (see Cotterill and Dean, 1990).

According to Shelbourne and Low (1980) and Cotterill and Dean (1988), (see Cotterill & Dean, 1990) the method of equal emphasis economic weighting assumes that a one unit increase in trait X is as equally important in economic terms as a one unit increase in trait Y, and in such a case the economic weight (W) can be determined as $W = \frac{1}{\sigma_p}$, where, σ_p represents standard deviation of the trait .

Cotterill and Dean (1990) pointed out that the population mean and standard deviation will probably differ from site to site. Thus, determination of economic weights on equal weightings is specific to particular populations and the environment

in which they are growing, suggesting index constructed using this method is also limited to specific planting sites.

Once the weighting coefficients have been determined on an equal emphasis basis as a base line for all traits, different weightings can be assigned to each of the different traits (e.g. by halving or doubling the coefficient for the first trait, while keeping that for the second trait constant, or *vice versa*) to produce a whole range of combinations of 'b' values. Once the family means are multiplied by the respective 'b' values it is possible to rank families by the combined index value and then calculate individual trait genetic gain according to that combination of 'b' values. In this way the genetic gain per trait can be compared across a range of economic values until the desired combination is obtained.

In this study, the method of equal emphasis was adopted for determination of initial economic weights for the following reasons:

(i) the aim of multiple-trait selection is to optimise gain for height, diameter, and stem straightness simultaneously;

(ii) the correlation between the three traits are positive, suggesting that the method of equal weightings is most appropriate; and,

(iii) it is a simple and easy method to determine economic weights.

Overall family mean values of 316.95 cm, 2.69 cm, and 3.14 points (and corresponding standard deviation of 88.09 cm, 1.13 cm, and 1.08 points) were recorded for height, diameter, and straightness respectively, at 34 months. Following the method of equal emphasis, corresponding weighting coefficients of 0.01, 0.88, and 0.93 were determined as a base line for these three parameters. Thereafter, 17 sets of economic weights were determined which were then used, in turn, to calculate the corresponding index coefficients.

5.3.4 Methods of computing the index coefficients using RESI

The input data required for RESI, in order to calculate the index coefficients are listed in Appendix 4. The genetic parameters used to calculate the index coefficient, or 'b' values are constant. The only variable which can be altered is the

economic weightings and altering the economic weightings (Appendix 4) for each trait within the same index and between different indices results in change of the corresponding 'b' values for each trait (Appendix 5). Using the economic weightings and genetic parameters listed in Appendix 4 the RESI programme calculated 18 index coefficients or 'b' values listed in Appendix 5 for each trait. Thereafter, SAS programme listed in Appendix 6 produces 18 different indices by using the calculated index coefficients or 'b' values.

5.3.5 Family ranking using multiple-trait selection index and single-trait selection

The SAS programme listed in Appendix 6 was also used for ranking of families. For each index families were ranked according to their index score and each index was used to calculate genetic gain for each trait.

The main difference between the single-trait selection and multiple-trait index selection is that in the former, families were ranked based on their measured mean values for one trait (Appendix 1, 2, and 3). In the case of multiple-trait selection families were ranked based on their index score for all the three traits (Appendix 7, 8, 9 and 10).

The numbers of families found in common in the top 40 and their position of ranking, were shown in Table 4.8 (section 4.4.4), where the families were ranked by height, diameter, and stem straightness independently. Table 4.8 will be compared with Table 5.1 to see the difference between family ranking using single trait and multiple-trait index. Diameter trait was excluded from Table 5.1 because ranking by height will provide similar result in terms of family number included in the top 40.

Table 5.1: Rank of the top 40 Families in descending order by mean height, stem straightness, and by index 1 (the best index for multiple-trait selection).

Rank by height	Rank by index 1	Rank by Straightness	RANK
232	101	127	1
103	329	114	2
28	114	101	3
3	314	126	4
314	303	329	5
101	103	43	6
114	240	128	7
168	386	256	8
279	28	27	9
344	245	210	10
244	188	12	11
153	3	48	12
134	127	76	13
161	276	314	14
343	126	42	15
317	275	333	16
240	30	386	17
404	392	397	18
30	244	240	19
99	43	130	20
303	185	201	21
276	256	255	22
247	48	269	23
13	146	400	24
136	344	392	25
258	140	396	26
329	348	149	27
57	130	120	28
160	27	140	29
299	115	188	30
370	317	30	31
113	12	115	32
348	113	147	33
170	75	59	34
246	265	245	35
386	161	81	36
360	374	2	37
150	136	10	38
364	168	212	39
115	76	146	40

Note: the numbers listed in the table are representing family identity.

: families joined by the arrow line are common in the three ranking methods.

It is clear (Table 5.1) that index selection has brought a significant change in family ranking position relative to height only or straightness only. For example, family 127, which is ranked top for straightness is not included in the top 40 when ranking is done using height trait. However, using the multiple-trait it was ranked 13. It is observed that index selection reduced the number of families included in the top 40 for the two traits compared with single-trait selection for same parameters. For example, 21 families were included for height and 22 for stem straightness in the top 40 ranked by index. A total of 8 families (30, 101, 114, 115, 240, 314, 329, and 386) are found in common for height, straightness and index rankings. It can be concluded that index 1 which was constructed on the basis of equal economic weightings has the advantage of representing similar numbers of families for height and straightness in the top 40.

5.3.6 Expected genetic gain from multiple trait selection index

All 405 families were ranked in descending order based on the calculated index value using the SAS programme listed in Appendix 6. This was repeated for all 18 indices. The top 40 families were then selected and genetic gains were calculated relative to the population mean for each trait within each index (Table 5.2). Genetic gain calculations were carried out according to the method of Wright (1976):

$$Gain(\%) = \frac{\left(s \times h_f^2\right)}{Mean} \times 100 \qquad [17]$$

Where; h_f^2 = family heritability; Mean = overall family mean; s = selected family mean - Mean (represents selection differential).

It is clear from Table 5.2 that not all the indices provided maximum gain for the three traits simultaneously. This was because of the differences in economic weights, (the only variable which was altered between runs of RESI) (Appendix 4). All 18 indices produce positive genetic gains and may be compared in 4 different

ways which maximise gain: (i) for height growth; (ii) for diameter growth; (iii) for stem straightness; and (iv) a combination of height, diameter, and stem straightness.

Table 5.2 Results of genetic gain(%) for the top 40 families.

	Percentage Genetic Gain			
	Height	**Diameter**	**Straightness**	**Remark**
Index 1	7.3 (1)	7.4 (1)	11.1 (1)	*** Equal weight
Index 2	9.1 (10)	8.2 (1)	5.3 (1)	*H
Index 3	8.6 (1)	10.0 (10)	7.9 (1)	*D
Index 4	3.1 (1)	3.0 (1)	14.7 (10)	*S
Index 5	6.6 (10)	5.7 (1)	12.2 (10)	*S
Index 6	5.8 (1)	6.3 (10)	13.5 (10)	*S
Index 7	5.7 (10)	5.7 (10)	13.3 (20)	*S
Index 8	3.8 (1)	3.9 (10)	14.7 (20)	*S
Index 9	3.9 (10)	3.9 (1)	14.3 (20)	*S
Index 10	9.5 (10)	9.4 (10)	5.7 (1)	*H, *D
Index 11	6.9 (10)	6.9 (20)	12.0 (20)	**
Index 12	3.7 (10)	3.9 (20)	14.5 (50)	*S
Index 13	6.2 (10)	6.8 (50)	13.1 (50)	**
Index 14	4.7 (20)	4.7 (20)	13.8 (50)	*S
Index 15	3.4 (20)	3.1 (1)	14.5 (50)	*S
Index 16	3.1 (1)	3.5 (20)	14.5 (50)	*S
Index 17	6.5 (50)	6.3 (20)	12.2 (50)	**
Index 18	6.9 (20)	6.9 (50)	12.6 (50)	**

H*: Represents maximum gain for height growth.
D*: Represents maximum gain for diameter growth.
S*: Represents maximum gain for straightness.
**: Represents possible optimum economic gain for height, diameter, and straightness combined.
***: Equal weighting coefficient
The numbers in the brackets represent relative economic weightings.

5.3.7 Effect of economic weightings on genetic gain within the same index

The change in economic weighting for traits combined in the same index has resulted in significant differences in genetic gain, suggesting it is an important parameter in constructing an index. The expected genetic gain by trait in each index does vary as a result of the differences in their corresponding economic weights. It is observed the higher the economic weighting assigned to the trait the higher the index coefficient, or 'b' values for that trait (Appendix 4 & 5). To demonstrate the effect of economic weight on genetic gain indices 10, 3, and 4 (Table 5.2) which produces the greatest genetic gain for height, diameter, and straightness were compared with index 1 (equal emphasis economic weighting).

Index 1 can be expected to give a 7.3%, 7.4%, and 11.1% in genetic gain for height, diameter, and straightness respectively. Placing a higher economic weight on height whilst keeping diameter the same will increase the genetic gain for each traits (index 2). This occurs because of the strong positive genetic correlation between height and diameter (0.79). Placing a high economic weighting coefficient on height (index 2) and diameter (index 3), or on both (index 10) will reduce the gain for straightness, and placing high weighting coefficient for straightness (index 4), will similarly reduce the gain for height and diameter.

Index 10, 3, and 4 would appear to be the best indices to maximise gain for height, diameter, and stem straightness respectively, but they are not the best to optimise the gain for the three traits simultaneously. Therefore they will not be used for selection of multiple traits.

5.3.8 Comparison of genetic gain from multiple- trait selection index with single trait selection

The main purpose of multiple-trait selection is to identify the top families which can produce optimum gain in height, diameter, and stem straightness. It is observed from Table 5.2 indices 1, 11, 13, 17, and 18 produces optimum gain for height, diameter, and stem straightness. The genetic gain from these indices is compared with single-trait selection gains in Table 5.3.

Table 5.3 Results of genetic gain from single-trait selection and multiple-trait selection indices for the top 40 families

Type of selection	Rank by	Percentage Genetic Gain			Remarks
		Height	Diameter	Straightness	
Single-trait (Independent-culling)	Height	9.9	8.6	4.6	Selecting for height
	Diameter	8.5	10.7	4.4	Selecting for diameter
	Straightness	3.5	3.2	15.4	Selecting for straightness
Multiple-trait	Index 1	7.3	7.4	11.1	** Equal weight
	Index 11	6.9	6.9	12.0	
	Index 13	6.2	6.8	13.1	
	Index 17	6.5	6.3	12.2	
	Index 18	6.9	6.9	12.6	

The shaded values in Table 5.3 represent the maximum genetic gains for height, diameter, and stem straightness for the top 40 families when the traits are independently selected. For example:

(i) selecting for height provides maximum genetic gain of 9.9% for height and corresponding genetic gain of 8.6% for diameter, and 4.6% for stem straightness;

(ii) selecting for diameter provides maximum genetic gain of 10.7% for diameter and 8.5% for height, and 4.4% for stem straightness; and

(iii) selecting for stem straightness provides maximum genetic gain of 15.4% for stem straightness and 3.5% for height, and 3.2% for diameter. It can be concluded that single-trait selection either for height or diameter results in reduction of genetic gain for stem straightness, or *vice versa.*

On the other hand when multiple-trait selection index (index 1) is used it provides genetic gain of 7.3%, 7.4% and 11.1% for height, diameter and stem straightness respectively. It is observed that the genetic gain from multiple-trait selection index is reduced for all traits when compared to the genetic gain from the single trait selection maximum for individual trait, i.e. tree height reduced from 9.9%

to 7.3%, diameter from 10.7% to 7.4%, and stem straightness from 15.4% to 11.1%. These result reveals that the loss in genetic gain for each trait is low for multiple-trait selection index and this loss can be justified by optimum simultaneous gain for all traits aiming for maximum gain in economic terms.

There is little difference in the gains for height, diameter and stem straightness obtained using indices 1, 11, 13, 17, or 18. Any one of these indices may offer the optimum genetic gain for the three traits compered to single trait selection. Among these indices, index 1 is probably the best because it is constructed on the assumption that a change of one unit in standard deviation in height is equally important as a change of one unit standard deviation in diameter or straightness. The assumption of equal economic weight for height, diameter and straightness is well fitted to the present market condition for *E. camaldulensis* in Ethiopia, and it is more logical and practical to use index 1 as the first priority for ranking and selection of families.

CHAPTER 6

Development of a Breeding Strategy

6.1 The Importance of Defining a Breeding Strategy

A breeding strategy is a method of continuous selection and regeneration of the breeding population to obtain maximum gain over a period of time in a tree improvement programme. According to Namkoong (1974) the amount of genetic gain obtained in each generation depends on the genetic diversity of the material used, the selection intensity and the heritability of the trait under investigation (see Van Buijtenen, 1975). Therefore, it is suggested that a breeding programme should start with a well recorded population of wide genetic base which provides maximum opportunity for intensive selection in successive generations (Cotterill, *et al.*, 1989; Shelbourne, 1991).

Cotterill (1983), Shelbourne *et al.* (1989) and Eldridge *et al.* (1993) strongly emphasised that a breeding strategy should include both short term genetic gain and maintenance of a wide genetic base breeding population for the long term breeding programme.. Thus, they describe three types of population:

(i) **base or gene resource population** - the bottom level of the hierarchy consisting of millions of trees in the natural forest or plantation offering a wide range of genetic variation (e.g. the natural stand of *E. camaldulensis* in Petford, Australia from which the seed collected for progeny test in Ethiopia);

(ii) **breeding population** - consisting of 300-500 plus trees each selected based on phenotypic superiority from the base population for progeny testing and they are the bases for regenerating successive breeding population (e.g. the 405 families of *E. camaldulensis* which was progeny tested in Ethiopia); and,

(iii) **seed production population** - a subset of the breeding population representing the upper level of the hierarchy, consisting of intensively selected trees, commonly fewer than 100 individuals. These trees provide rooted cuttings and grafting material for the establishment of a clonal seed orchard (e.g. the top 40 families from the first generation (F1) breeding population in Ethiopia).

In the case of *E. camaldulensis* in this study the base population, the breeding population, and the seed production population are the same at the beginning of the breeding programme; separate breeding and seed production populations will be established after the first generation of progeny tests.

Van Buijtenen (1975) stated that a breeding method which: (i) provides maximum gain per year rather than per generation; (ii) produces improved seed as quickly as possible; (iii) requires low technical skill; and (iv) secures a wide genetic base for long term breeding programme is relatively attractive compared to more complicated methods. Thus, it can be suggested that production of seed for a large scale planting programme by using advanced breeding methods such as controlled-pollination is very expensive: the extra cost entailed might be avoided for commercial seed production and only accepted on a small scale for experimental purposes.

Cotterill *et al.* (1989) describes, keeping the breeding programme as simple as possible in terms of cost and technical skill is advantageous, unless the gain obtained from the programme justifies high costs. He pointed out, that a seedling seed orchard derived from progeny tested families through recurrent selection provides substantial genetic gain with low cost, provided enrichment of the breeding population is done from other improved source to reduce the risk of inbreeding.

Eldridge *et al.* (1993) listed the following points to be considered and used as a guide for development of the breeding programme.

(i) is there any need for a breeding programme?

(ii) what products are required (fuel wood, poles, pulp wood, saw logs and etc.)?

(iii) do the available species, provenances, varieties, or clones match well with the intended range of site condition and with the country's expectations?

(iv) what traits are to be selected for? how are these traits assessed? are they easy to measure?

(v) what is the economic importance of the traits being considered?

(vi) what evidence is there that these traits have enough genetic variation and high enough heritability for selection to be effective?

(vii) how much money is available to invest in breeding and for how long is the investment likely to be sustained?

(viii) is there a long-term breeding objective over several decades or a short term objective, or both?

(ix) what are the alternative breeding strategies and are they biologically and silviculturally practical?

(x) for each strategy, what is the expected genetic gain per decade in the chosen traits, and what are the financial costs and benefits?

For *E. camaldulensis* in Ethiopia most of the above questions have been discussed in the previous chapters and will not be repeated here. Questions related to breeding methods, breeding objectives and the advantages and disadvantages of alternative breeding methods will be covered in section 6.2.

Campinhos and Ikemori (1989) stated that the main objective of a breeding programme is to establish a seed orchard for the production of high quantities of high quality seed, as quickly as possible, for commercial purposes. However, establishment of seed orchards is expensive, requiring time and high technical skills, and is therefore, not the immediate solution to solve the urgent demand of seed for an afforestation programme. In many parts of the world, experience has shown that good natural or planted stands can be used as a seed source for a plantation programme until genetically improved seed is available from seed orchards in large quantities.

The main objective of seed orchard establishment is the production of genetically improved seed in large quantities. Various breeding methods have been described in the past for the production of genetically improved seed both for coniferous and *Eucalyptus* species. Shelbourne (1991) evaluated alternative breeding methods used based on: (i) expected genetic gain; (ii) cost of the breeding programme; (iii) level of technical skills; and (iv) time required for each method; for *E. regnans* in New Zealand. He concluded that:

(i) a seed production area established using seed from mass selection in a suitable provenance, without keeping family identity, can provide some genetic gain at little cost and low technical skill;

(ii) a progeny trial established from open-pollinated families retaining family identity, and then converted to a seedling seed orchard by roguing, is as valuable as an untested clonal orchard;

(iii) a tested clonal orchard derived either from grafted material or rooted cuttings is as valuable as a seedling seed orchard derived from controlled-pollination.

(iv) a seedling seed orchard derived from controlled-pollination provides maximum genetic gain, however, it is expensive, needs high technical skills, and requires longer time.

Based on Shelbourne (1991) it can be concluded that, the more advanced the breeding methods: (i)the higher the genetic gain; (ii) the more expensive the cost of breeding; (iii) the higher the skilled man power required; and (iv) the longer time needed to produce improved seed.

For *Eucalyptus* species 5 types of breeding methods used in the past have been listed by Eldridge *et al.* (1993) and all the lists will not be repeated here. The one described by Franklin and Meskimen (1984) and Franklin (1986) (see Eldridge *et al.*, 1993) which was used for breeding of *E. grandis* in Florida, United States of America is well fitted to the *E. camaldulensis* progeny trial already established in Ethiopia and will be adapted, with some adjustments.

6.2 Proposed Breeding Methods for *E. camaldulensis* in Ethiopia

The development of a breeding strategy starts by including the objectives listed under section 3.0 of this dissertation. Great emphasis will be placed on available resources (man power, technical skill, money and time) and biological characteristics of the species. The breeding strategy followed combines a provenance/progeny test, genetic base population and seedling seed orchard in a single plantation. After the first generation of progeny tests, separate breeding and seed production populations will be established.

Using the same breeding and seed production population has advantages and disadvantages. Regarding this point, Namkoong (1974) (see Van Buijtenen, 1975) explained that the scheme has short term advantage: (i) it reduces the cost of breeding programme, and (ii) provides improved seed after one generation by converting the progeny trial into a seedling seed orchard through thinning. The disadvantage is that thinning will reduce the original base population and increase the risk of inbreeding .

Eldridge *et al.*(1993) acknowledged using the same breeding and production population for short term genetic gain, especially when money is the limiting factor. However, they strongly emphasise that a breeding strategy should include both short term genetic gain and maintenance of a wide genetic base breeding population for the long term breeding programme and recommended separate breeding and seed production populations if conditions permit.

Inbreeding depression which is the result of selfing, or mating among close relatives is a serious problem in *Eucalyptus* species (Griffin, 1989) when open-pollinated families were used as a source of seed. The condition is even more severe when seed is collected from the natural stand rather than a plantation, because it is likely that individuals in the natural stand are more related than in the plantation (Eldridge *et al.*, 1993). Shelbourne (1991) pointed out that the degree of inbreeding in a breeding population is high once selection is made to eliminate the inferior individuals, because individual selection eliminates all the inferior families and over represent individuals from few top families. On the other hand family selection eliminates those worst families and at the same time eliminate best individuals from the worst family because of their family average. Therefore, combined family and within-family selection should be done to maintain genetic diversity while at the same time obtaining optimum genetic gain. This can be done by using low selection ratio (2 in 3) between families and high selection ratio (retaining best tree per family) within-families in successive generation (Shelbourne *et al.*, 1989).

6.2.1 Breeding objectives

A. Short-term

1. Production of genetically improved seed as quickly as possible for plantation establishment.
2. Establishment of a wide genetic base breeding population.

B. Long-term

1. Conservation of the gene resource population for a long-term breeding programme.
2. Establishment of a clonal seed orchard with genetically improved material.

6.2.2 Base population

Prior to the establishment of a progeny trial for *E. camaldulensis*, all the plantations in Ethiopia was studied by Davidson (1989). He concluded that the existing plantations have no value from the point of further genetic improvement due to their narrow genetic base, suggesting that a breeding programme in Ethiopia should start with a new, well-recorded base population. Following this recommendation seed of 405 open-pollinated families was imported from Australia to provide material for a base population. The 405 families came from six provenances within Queensland region, seed being collected from selected individuals in natural stands.

6.2.3 Breeding and seed production population

At the beginning of breeding programme, the breeding and seed production populations are the same. Thereafter, seed from the progeny trial or base breeding population (F_0) will be used to establish a first generation breeding population (F_1), and so on. This method of recurrent selection will be repeated until genetic gain is maximised. At each stage, selection of the next breeding population will be based on the results of the progeny tests and all the poorer material will be culled out prior to seed collection to establish the next breeding population (Fig.3).

According to Shelbourne *et al.* (1989), selection for the regeneration of a breeding population can be done in two ways, namely: (i) "Forward" selection -

selection of the best individuals among the progeny; and (ii) "Backward" selection - Selection of parents by the performance of their progeny.

Backward selection is preferred for those species which requires many years to produce seed. For example, in the case of Sitka spruce (*Picea sitchensis*) in Britain, growth traits can be estimated accurately as early as 6 years, but it is 20 years before any regular flowering (Lee, 1992). To reduce the generation interval backward selection of superior parents can be based on the results of the progeny test and regeneration of the next breeding population can be done through cloning (either grafts or rooted cuttings). For species such as *Eucalyptus* it is possible to get seed as early as 5 years from the tested individuals, and regeneration of the breeding population by forward selection is advantageous.

6.3 Selection Strategy for Maximising Genetic Gain while Maintaining Genetic Diversity

The objective of selection in any breeding programme is to capture individuals with the best genes for the traits under consideration. Selection based on phenotypic appearance only results in maximum genetic gain when the heritability of the trait is high (Van Buijtenen, 1975; Zobel & Talbert, 1984).

According to Falconer (1981), selection can be done in three ways, namely: (i) individual selection - when the heritability is high; (ii) family selection - when the heritability is low; and, (iii) combined selection (among and within-families) - most commonly used to achieve a compromise between the conflicting requirements of maximum genetic gain and a broad genetic base, and well-suited for an advance breeding programme.

Shelbourne (1991) states that whichever method is used, selection generally results in a loss of part of the breeding population and increases the chance of inbreeding. On the other hand, converting the progeny trial into a seedling seed orchard by roguing inferior individuals is a simple, inexpensive and quick method for the production of genetically improved open-pollinated seed.

In the case of *E. camaldulensis* maintaining the genetic base of all the Australian families for a long-term breeding programme and production of genetically improved seed from the progeny trial are of equal importance for Ethiopian conditions. In this situation between family and within-family selection method will be used concurrently to convert the progeny trial into a seedling seed orchard through roguing.

In practice it seems difficult to achieve the two major objectives of breeding programme in Ethiopia, (that is, short-term genetic gain and maintenance of wide genetic base population) if the progeny trial is converted to a seedling seed orchard.

This situation can be better explained by using examples: Firstly, if the top 40 families were selected out of 405 families, using multiple-trait selection index (Index 1) - genetic gains of 7.3%, 7.4%, and 11.1% were recorded for height, diameter, and straightness respectively. Secondly, if 200 families were selected using the same index - genetic gain of 3.3%, 3.1%, and 4.8% would be recorded for the three traits. The former method produces greater genetic gain, but retains only 10% of the breeding population and the latter method produces lower genetic, but retains 50% of the breeding population. Both methods have their advantages and disadvantages. Compromise should be made to fulfil the two objectives by determining the effective population size.

To achieve the best compromise between maximum genetic gain and maintenance of genetic diversity there is a general consensus among tree breeders to use the effective population size. However, concerning the actual family number which represents the effective population size a wide range of alternatives have been suggested. For example: (i) Fletcher (1992) used 40 clones in the clonal orchard as a seed production population for Sitka spruce in Britain; (ii) Lindgren (1991) suggests 15-50 families with 10-20 individuals per family for parental ranking in the progeny test; (iii) White *et al.* (1993) suggests 20-100 families are an appropriate number to be included in the breeding programme; and (iv) Shelbourne *et al.* (1989) and Eldridge *et al.* (1993) recommend 300-500 families for breeding population. Based on this evidence it has been decided to use the top 120 and 40 families as a first

generation (F_1) breeding and seed production population respectively for *E. camaldulensis*.

6.3.1 Selection of first generation breeding and seed production population

In the case of *E. camaldulensis* development of the breeding programme will mainly depend on recurrent selection methods together with open-pollinated mating system rather than controlled-pollinated mating system, because the former is less costly and can be applied with a low level of technical skill.

The first generation improved seed will be produced as early as 5 years from already established plants by directly converting the progeny trial into a seedling seed orchard. This will be done by roguing the inferior individuals based on the results of the progeny trial. The combined selection (selection among families and within families) method will be adopted to retain families and individuals within families which will be used for production of first generation improved seed and at the same time as a base population for seed collection to establish the first generation breeding population.

Based on the ranking of multiple trait index (index 1) selection of the superior families from the progeny trial or base breeding population (F_0) will be done in the following ways.

Firstly, within-family selection will be applied to retain all families and the best individual tree representing each family. It is assumed all the 405 families will contribute pollen to the first generation breeding population (top 120 families). This method of within-family selection will increase the genetic gain for the next breeding population and at the same time broaden the genetic base of the selected families.

Secondly, open-pollinated seed will be collected from the best individuals (top120 families) by maintaining family identity to establish the first generation breeding population.

Thirdly, second thinning will be done to retain the top 120 families (the very best individual trees for each family), and thereafter, bulk seed will be collected for commercial purposes.

The first generation breeding population (top120 families) will be progeny tested and based on the results of the progeny trial within-family selection will be done following two stage thinning. First thinning will be done to retain the best individual trees per plot for all families. Second stage thinning will be done to retain the very best trees for each family. Thirdly, rooted cutting material will be collected from the top 40 families (individuals) to establish clonal seed orchard. Fourthly, the top 120 families (individuals) can be used as a source of open-pollinated seed to establish the second generation (F_2) breeding population.

This type of recurrent selection can be repeated to regenerate the next breeding population and the cycle can be continued for some generations until genetic gain optimise in relation to resources available to continue breeding. The recurrent selection breeding strategy, will eventually narrow the genetic base of the breeding population. Therefore, it is necessary to enrich the breeding population by superior individuals from other improved sources and this will be considered at the later stage of the breeding programme (Fig 3).

6.4 *Ex-situ* Gene Resource Conservation of the Australian Families

In the case of *E. camaldulensis* progeny trial the genetic base population (F_0) are the original 405 families from the Petford, Australia. All the Australian families will be maintained and preserved to secure the genetic diversity, and this will be done as follows. Firstly, those individuals which were eliminated when converting the progeny trial into a seedling seed orchard will be regenerated by coppice system, only the very best individual in each family will be allowed to coppice (one shoot per stump) and this will be based on the original assessment of the progeny trial.

Preservation of all the Australian families in the first generation progeny trial will provide several advantages:

(i) the material will serve as an ex-situ gene conservation resource or genetic pool, in case the original base population in Australia is lost.

(ii) as a source of rooted cutting material when ever there is a need;

(iii) as a potential seed source for bulk collection until the national demand is fulfilled from seed orchards.

6.5 Establishment of Clonal Seed Orchard

Vegetative propagation of trees is a useful tool in traditional tree improvement for the production of clonal orchards and mass multiplication of the particular genotypes. Clonal propagation by it self does not bring about new genetic recombination, it is the efficient ways of picking the best genotypes available in a particular generation (Zobel, 1993). Clonal propagation can capture both additive and non-additive genes and it is one of the ideal method for production of hybrids, especially if segregation of genes happens meiosis in F_2 generation if propagated through seedling (FAO, 1979).

Cloning of *Eucalyptus* by rooted cuttings has been carried out in tropical, subtropical, and Mediterranean regions for nearly 20 years (Eldridge et al., 1993). In the past open-pollinated, clonal, and controlled-pollinated seed orchards of *Eucalyptus* have been used for production of genetically improved seed in different parts of the world. The first is the most commonly used, especially when budgets are limited, whereas the last one is used on a small scale for experimental purposes and for the production of hybrids (Eldridge, 1975).

Clonal orchards using rooted cuttings is used for production of genetically improved seed and it is found to be successful for some species. However, the success of vegetative propagation using rooted cuttings is limited to those species which sprout vigorously and root easily. Eldridge *et al.* (1993) suggested that establishment of clonal orchards either by grafting or rooted cuttings is possible for most of *Eucalyptus* species; however, the problem associated with graft incompatibility and decline in rooting of the cuttings with age hinders the advancement in clonal propagation. Therefore, basic knowledge is required on the suitability of the particular species to the techniques of vegetative propagation. According to Eldridge *et al.* (op. cit) graft incompatibility can be solved to some degree by using the same parent tree both for seed collection and raising the root

stock and scion collection, and better rooting ability can be obtained by using rooted cuttings from coppice shoots.

In some countries clonal propagation of hybrids using rooted cuttings has become an operational programme for some *Eucalyptus* species (e.g. *E. grandis* x *E. urophylla* in Brazil; and *E. tereticornis* x *E. saligna* and *E. urophylla* x *E. alba* in the Congo). For Example, in the Congo inter-specific hybridisation of the best provenances provides a genetic gain of 50 to 80% from the F_1 hybrid and further cloning of the F_1 hybrid provides additional gain of 100 to 150% in volume production, suggesting that the additional cost for production of rooting cutting can be compensated by the genetic gain from clonal propagation (Chaperon, 1978b) (see FAO, 1979),

Currently, the largest operational programme is done by Aracruz Florestal in Brazil, where mass vegetative propagation using rooted cuttings is becoming the standard method for species such as *E. grandis* and *E. urophyla*, and establishment of clonal orchards by rooted cuttings is found to be the most successful and widely used method for these species (Campinhos and Ikemori, 1989).

The advantages of clonal propagation are numerous. According to Libby (1985) (see Leakey, 1987) some of the points are listed below:

(i) multiply without altering gene combination for superior genotypes;

(ii) uniformity and desirability of wood produced;

(iii) maintain selected clones on a clonal bank or clonal orchards where gene recombination can be done through controlled pollination; and

(iv) obtain improved genotypes from hybridisation that can be mass produced for commercial purposes.

The disadvantages of clonal propagation are as follows:

(i) a narrowing the genetic base of the material under investigation through selection of few out standing clones;

(ii) creates genetically less diverse stands with increased risk of pest and disease attack, especially when single clone is used; and

(iii) it does not involve gene recombination and it is the dead end in the long-term genetic improvement, unless it is supported by controlled crossing. However,

the first two points is under the control of the tree breeder, i.e. optimum number of clones can be used to maintain the genetic diversity although using many clones creates a problem in management of the forest stands.

For *E. camaldulensis* the first rooted cutting was discovered in Morocco in 1950 when shoot pruning of seedlings was done to produce more uniform and hardy planting stock (see Eldridge *et al.*, 1993). Thereafter, in 1954 the first trial was established using cuttings from matured *Eucalyptus* and the investigation was continued for 20 years. According to Franclet (1970) the ability of cuttings to produce roots declines with the age of the ortet or parent tree, better rooting ability was recorded for those cuttings collected from ortets aged up to 5 years, ortets older than five years will be rejuvenated using a coppice and hedging system (see Eldridge et al., 1993).

In the case of *E. camaldulensis* in Ethiopia the establishment of clonal orchards using rooted cuttings is possible and will be considered. Clonal orchard is proposed at the latter stage of the improvement programme (10-years after the establishment of the base breeding population), due to the following reasons.

Firstly, the growth performance of the base breeding (Fo) population or first progeny trial is poor and the obtained result is less than what has been expected at age 3-years. Their might be change in ranking position between families at the latter stage and it seems unwise to use rooted cutting materials from this progeny trial based on the result of the first assessment.

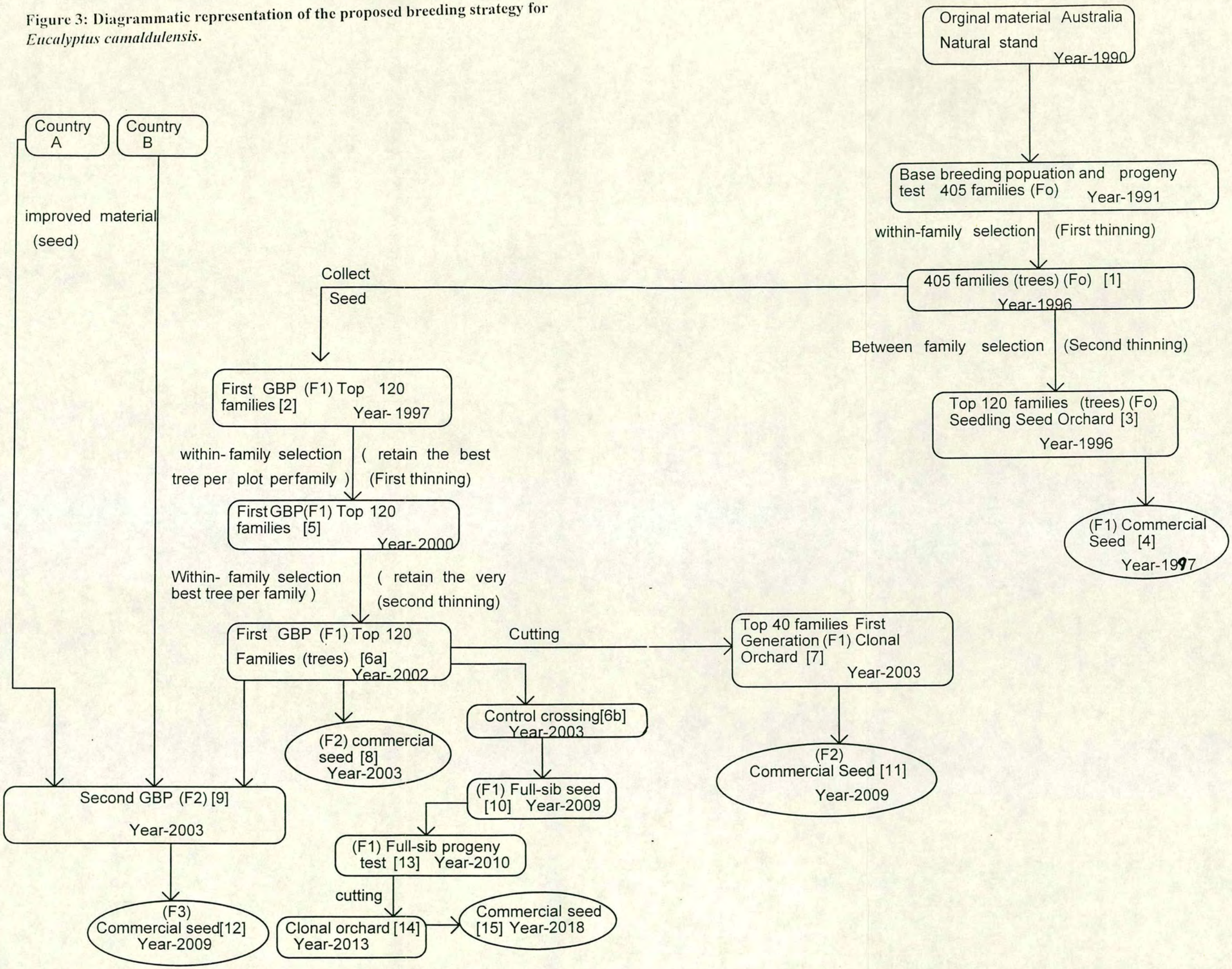
Secondly, the result from the second stage or first generation breeding population will be ready at the end of 10-years and this result is more reliable than the first one, and due to more screening it is expected genetic gain will be maximised for the selected individuals.

Thirdly, a facility will be developed for rooting of cuttings and it is more practical to establish clonal seed orchards at the latter stage (Fig. 3).

Table 6.1 : Proposed breeding strategies for *E. camaldulensis* in Ethiopia.

Year	Stage	Activities
1990	0	Selection of **base population** from Australia (405 families).
1991	1a	Raising of seedling and establishment of **progeny trial (F_0).**
1994	1b	Estimation of genetic parameters and family ranking.
1995	1c	Selection within-families to retain the very best individual tree for each family (405 trees).
1996	1d	Selection between families to retain the top 120 families (trees).
1996	2a	Collect open-pollinated seed from the top 120 families from stage 1c, by maintaining family identity to raise the seedlings.
1997	2b	Establish **first-generation (F_1) breeding population** and progeny trial.
1997	2c	Collect bulk open-pollinated seed for commercial purposes from stage 1d
2000	2d	Retain the best individual trees per plot for each family from stage 2b, based on the result of the progeny trial.
2002	2e	Retain the very best individual trees for each family stage 2d.
2002	2f	Collect cutting for rooting from the top 40 individuals (families) from stage 2e.
2003	2g	Collect open-pollinated seed from stage 2e by maintaining family identity and raise the seedlings.
2003	2h	production of open-pollinated seed from stage 2e for commercial purposes.
2003	2i	Establish **clonal seed orchard** using rooted cuttings from stage 2f.
2003	2j	Establish **second generation (F_2) breeding population** by using seedling from stage 2g.
2003	2k	Control crossing of superior individuals from stage 2b.
2009	3a	Production of open-pollinated seed from stage 2i for commercial purposes.
2009	3b	Production of open-pollinated seed from stage 2j for commercial purposes.
2009	3c	Production of **full-sib seed** from stage 2k and raise full-sib seedlings.
2009	3d	Establish **full-sib progeny test** from stage 3c
2013	3e	Establish **clonal seed orchard** using rooted cutting from stage 3d.
2018	3f	production of open-pollinated seed from stage 3e for commercial purposes.

Figure 3: Diagrammatic representation of the proposed breeding strategy for *Eucalyptus camaldulensis*.



CHAPTER 7

Conclusion and Recommendation

This thesis presents an investigation into the genetic variation between 405 open-pollinated families of *E. camaldulensis* from Australia (Queensland) for tree height, diameter and stem straightness, the selection method used to exploit this variation and the future breeding strategy designed for regeneration of the successive breeding populations. Published results from different countries has been reviewed and most of the provenance studies indicated that there is great genetic diversity between different seed origins; the northern provenances - such as Petford from Queensland and Katherine from the Northern Territory are the most suitable provenances in the tropical and sub-tropical climate, whereas the Southern provenances - such as Lake Albacutya from Victoria is well suited to the Mediterranean climate.

E. camaldulensis was introduced into Ethiopia at the turn of this century. Wide spread plantings, using seed collected from the first plantation (local seedlots) and their progeny continued until now and it is one of the best-adapted species at lower altitudes (1000 to 1500 m) in Ethiopia and widely planted for production of short poles and fuel wood. However, its low volume production and poor stem form restricts its use for a commercial plantation. The seed origin of the initial introduction is not clear and it appears that it consists of a few grams of seed and is suspected of having a narrow genetic base.

It has been decided that genetic improvement of this species should be carried out with known seed origins and in 1991 a combined provenance/progeny trial was established by using seed from 405 open-pollinated families taken from six provenances. All the provenances were from Queensland state, particularly Petford region. The decision to use provenances from Queensland was based on their early success in most tropical and sub-tropical countries.

The major objective of the trial was to identify superior provenances and families within-provenances, with vigorous growth and straight stem for use in the breeding and seed production population. Genetic variation for tree height, diameter and stem straightness between provenances mean and families-within-provenances were detected by using the analysis of variance and the results indicated that there was significant variation between the provenances and families within-provenances for all the traits studied. There were also significant variation between replications and significant family x replication interactions, suggesting that the performance of individual families varied in different blocks.

Generally, there were minor differences between the provenances mean for the three traits studied; the best families yielding twice as much as the worst family for height and two-half times for diameter and stem straightness. The top ranking families for all the traits derive from the full range of provenances, suggesting that family selection should be done for future breeding without considering provenance identity.

The calculation of the variance components showed that the greatest proportion of the observed variation is accounted for by differences between trees within plot (σ^2w), replication × family interaction variance (σ^2_{Rf}) and then by family variance (σ^2f). Narrow-sense family heritability values show that stem straightness is under most additive genetic control (0.56) followed by height (0.46) and then by diameter (0.32), suggesting family selection based on phenotypic appearance for stem straightness provides substantial genetic gain compared to the height and diameter growth.

The Australian families included in the Ethiopian progeny trial grow slowly when compared with similar experiments from Thailand. In Thailand 351 families which were included in the Ethiopian progeny trial are growing five times faster than their Ethiopian relatives at the same age. It was also observed that the Ethiopian land race which was planted three miles away in the neighbouring plantations were growing twice as fast as the Australian families. It is not yet clear why the growth of the Australian families in Ethiopia is poor. It is suspected the difference in elevation

between the experimental site (high elevation) and the seed origin in Australia (low elevation) might be the possible reason.

Results from genetic gain calculation shows that the higher the selection intensity (the fewer selected from the top), the bigger the selection differential and the higher the genetic gain or, *vice versa.* Aiming for maximum genetic gain narrows the genetic base of the breeding population and results in inbreeding. To compromise the conflict between maximum gain and broad genetic base it has been decided to select the top 120 families (first generation (F_1) breeding population) from the original test, and subsequently to select the top 40 families (seed production population) from the first generation breeding population as the possible optimum family number to be included in the next generation.

It is observed from the genetic gain calculation that using either height or diameter for selection provides almost similar gain for the two traits, suggesting either height or diameter can be used as a selection criteria when the objective of selection is to maximise growth traits. This is because there is a strong genetic correlation between the two traits. On the other hand selecting either for height or diameter results in loss of the genetic gain for stem straightness or *vice versa.* It can be concluded that single-trait selection for either height or diameter, or stem straightness independently does not provide maximise gain for the three traits simultaneous.

The multiple-trait index selection was found to be the most efficient in optimising the gain for height, diameter and stem straightness simultaneously. Result from the multiple-trait selection index shows that out of the total of 18 indices used 6 produces optimum genetic gain for height, diameter and stem straightness and can be used for selection programme. However, index 1 which was constructed on equal economic weightings for height, diameter and stem straightness is more suitable to reflect the present market conditions for *E. camaldulensis* wood in Ethiopia and the one most suitable for use in the selection programme.

The open-pollinated breeding method was chosen to regenerate the successive breeding populations. The main criteria used in choosing the breeding method was skilled manpower, finance and the urgency for the improved material. The open-

pollinated breeding method is based on the principle of the recurrent selection methods, i.e. the next breeding population will be forward selected based on the results of the progeny test until the desired genetic gain is reached.

The progeny test should be converted to a seedling seed orchard by roguing the inferior families and the selection of superior families will be based on multiple-trait selection index. Between family and within-family selection method will be used to identify superior individuals for inclusion in successive breeding populations. Figure 3, presents different stages of selection and the proposed breeding method to establish the successive breeding and seed production populations. For referring to stages in the breeding programme identification numbers are used both in the text below and within each box in figure 3.

Selection within-families will be applied to retain the best trees per family regardless of their family averages in the original test or base breeding population (Fo). In this case it is assumed all the 405 families will contribute pollen to the next breeding population [1]. Thereafter, seed will be collected from the top 120 families by maintaining family identity. This seed will be used to establish the first generation (F_1) breeding population [2].

Second stage thinning will be done between families in the original test to retain the top 120 families (trees) [3] and these will provide first generation improved seed for commercial purposes [4].

The first generation breeding population (top 120) [2] will be progeny tested and based on the results, the progeny test will be thinned to the very best trees within each family [6a]. Out of these the top 40 families (trees) will be selected to provide rooted cutting material for establishment of a clonal seed orchard [7].

The top 120 families (trees) [6a] which were retained from the first generation breeding population will be used to provide second generation seed for commercial purposes [8] and to regenerate of the second generation breeding population [9]. To broaden the genetic base of the second generation breeding population these top 120 families will be supplemented or enriched by improved material from other countries.

Since family identity is kept in all stages artificial crosses can be made between the best families to obtain maximum gain and this will be done in the first generation breeding population for the top 120 families [6a]. Full-sib seed will be collected from crossed families (trees) [10] for progeny testing to identify superior individuals [13]. Thereafter, cutting material for rooting can be collected for establishing clonal orchard [14] which will be managed for production of commercial seed [15]. Control crossing of individuals for production of full-sib seed for commercial purposes is expensive and little emphasis will be given for breeding of *E. camaldulensis* at present condition, and it will be considered for the long-term programme if budget and technical skill permit.

The seedling seed orchard [3] which was converted from the progeny trial [1] through roguing will continue to provide seed until improved seed is available from the clonal seed orchard [11]. Once the genetically improved seed is available from the first generation breeding population [6a] and clonal orchard [11] the progeny test will no longer be used for seed collection. It will be managed for the purpose of *ex-situ* gene conservation.

The life cycle or years required for the seedling to flower and produce abundant seed is five to six-years for *E. camaldulensis*. This duration is used as an interval between two subsequent generations for production of improved seed for commercial purposes.

(i) the first generation improved seed will be produced from the rogued progeny test (base breeding population (Fo)) at the end of 6- years [4];

(ii) the second generation improved seed will be produced from the first generation (F_1) breeding population at the end of 12-years [8]; and;

(iii) the second generation (F_2) improved seed will also be produced from the clonal orchard at the end of 18- years [11].

It can be concluded that sound genetic information has been generated from the *E. camaldulensis* progeny test in Ethiopia. However, the results from this progeny test should be interpreted with great caution due to the following points:

(1) The progeny trial is too young, the environment therefore would still be very much overriding any genetic effects that may be present.

(2) There might be selection errors, especially for height and diameter if we rely on this result, because growth traits are affected by site factors and there is no guarantee that the early winners will continue to be the best for the whole rotation.

(3) The progeny test was established on one test site and it does not provide information on genotype x environmental interaction. Thus, the estimated genetic parameters might not be reliable and the applicability of the result is limited.

(4) There was significant variation between blocks and this results in high value of family x replication interaction variance which in turn, results in low value of heritability. It is likely the true genetic variance is over masked.

(5) The lack of local land race as a control in the progeny test restricts further discussion whether the Australian families are genetically inferior to the already adapted local land race.

Based on the result of the progeny trial the growth of the Australian families was poor when compared to what has been achieved at age 34 months from the existing plantation in Ethiopia on the same planting site. The possible reasons are listed above. The uncertainty listed under 1 and 2 are time related ones and waiting for the whole rotation might probably indicate if there is a change in ranking of individual families. Points 3 and 4 will require more than one planting sites (testing sites) to obtain reliable results, and 5 requires Genetic Gain Trials (GGT) with the inclusion of land race. Therefore it is recommended that further trials should be done to confirm the results already obtained and to generate additional information.

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Appendix 1: Ranking of the top 40 families by mean height.

OBS	FAMILY	HEIGHT	DIAM	Form (straightness)
1	232	437.292	4.05000	2.91667
2	103	425.208	3.76087	3.45833
3	28	417.500	3.61304	3.41667
4	3	409.167	4.05714	3.12500
5	314	402.857	3.43000	4.04762
6	101	397.708	3.92273	4.50000
7	114	396.875	3.35000	4.58333
8	168	396.667	3.60435	3.25000
9	279	395.083	3.94167	3.29167
10	344	393.318	3.95000	2.82609
11	244	392.917	3.40455	3.29167
12	153	392.500	3.33810	3.00000
13	134	392.143	3.36190	3.04762
14	161	390.435	3.71905	3.21739
15	343	384.167	3.61250	3.66667
16	317	382.609	3.27273	3.47826
17	240	382.174	3.60000	3.95652
18	404	381.667	3.39565	3.45833
19	30	380.833	3.11667	3.83333
20	99	379.348	3.47500	3.04348
21	303	379.167	4.20556	3.45833
22	276	378.958	3.64762	3.41667
23	247	378.542	3.26957	3.37500
24	13	377.857	3.36000	2.80952
25	136	377.609	3.31429	3.34783
26	258	377.273	2.73500	3.04545
27	329	376.667	3.56500	4.33333
28	57	374.130	3.23043	3.39130
29	160	373.958	3.08696	3.29167
30	299	373.958	3.27727	3.34783
31	370	373.478	3.25455	3.26087
32	113	372.727	3.15789	3.09091
33	348	372.708	3.05714	3.45833
34	170	372.500	3.07391	3.54167
35	246	371.522	3.04545	3.30435
36	386	371.250	3.62273	3.95833
37	360	371.087	3.16190	2.95652
38	150	370.417	3.09583	3.08333
39	364	370.417	3.33043	3.20833
40	115	369.167	2.86250	3.83333

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	385.3464574	15.7946381	369.1666667	437.2916667
DIAM	40	3.4332494	0.3383133	2.7350000	4.2055556
FORM	40	3.4230390	0.4256890	2.8095238	4.5833333

Appendix 2: Ranking of the top 40 families by mean diameter.

OBS	FAMILY	HEIGHT	DIAM	Form (straightness)
1	303	379.167	4.20556	3.45833
2	3	409.167	4.05714	3.12500
3	232	437.292	4.05000	2.91667
4	344	393.318	3.95000	2.82609
5	279	395.083	3.94167	3.29167
6	101	397.708	3.92273	4.50000
7	243	368.125	3.79250	3.70833
8	103	425.208	3.76087	3.45833
9	161	390.435	3.71905	3.21739
10	368	347.083	3.70455	2.95833
11	77	364.783	3.69474	3.26087
12	276	378.958	3.64762	3.41667
13	185	351.957	3.63529	3.17391
14	386	371.250	3.62273	3.95833
15	28	417.500	3.61304	3.41667
16	343	384.167	3.61250	3.66667
17	168	396.667	3.60435	3.25000
18	240	382.174	3.60000	3.95652
19	329	376.667	3.56500	4.33333
20	392	360.652	3.53500	3.91304
21	308	366.875	3.51500	2.62500
22	80	366.875	3.49545	3.12500
23	140	319.318	3.48235	3.86364
24	99	379.348	3.47500	3.04348
25	294	363.500	3.46111	3.10000
26	188	366.000	3.45000	3.85000
27	6	343.542	3.43043	3.00000
28	314	402.857	3.43000	4.04762
29	135	353.958	3.41429	3.50000
30	244	392.917	3.40455	3.29167
31	404	381.667	3.39565	3.45833
32	388	325.217	3.38824	2.73913
33	134	392.143	3.36190	3.04762
34	13	377.857	3.36000	2.80952
35	114	396.875	3.35000	4.58333
36	153	392.500	3.33810	3.00000
37	364	370.417	3.33043	3.20833
38	42	349.792	3.32917	4.00000
39	274	338.478	3.32000	2.78261
40	53	333.958	3.31500	2.75000

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	376.0363413	26.0303491	319.3181818	437.2916667
DIAM	40	3.5820249	0.2305435	3.3150000	4.2055556
FORM	40	3.3907860	0.4985439	2.6250000	4.5833333

Appendix 3: Ranking of the top 40 families by mean stem straightness.

OBS	FAMILY	HEIGHT	DIAM	Form (straightness)
1	127	319.167	2.55833	4.70833
2	114	396.875	3.35000	4.58333
3	101	397.708	3.92273	4.50000
4	126	339.773	3.09048	4.36364
5	329	376.667	3.56500	4.33333
6	43	329.524	2.62000	4.19048
7	128	292.143	2.64737	4.14286
8	256	353.478	2.92174	4.13043
9	27	326.875	2.75455	4.12500
10	210	248.043	2.11111	4.08696
11	12	340.625	3.19565	4.08333
12	48	354.792	2.83125	4.08333
13	76	331.458	3.03696	4.08333
14	314	402.857	3.43000	4.04762
15	42	349.792	3.32917	4.00000
16	333	287.917	2.26087	4.00000
17	386	371.250	3.62273	3.95833
18	397	292.083	2.54286	3.95833
19	240	382.174	3.60000	3.95652
20	130	367.500	3.19545	3.95455
21	201	341.042	2.78261	3.91667
22	255	330.417	2.37917	3.91667
23	269	342.292	2.87083	3.91667
24	400	313.333	2.70000	3.91667
25	392	360.652	3.53500	3.91304
26	396	349.130	2.98696	3.91304
27	149	340.714	2.78571	3.90476
28	120	327.917	2.52500	3.87500
29	140	319.318	3.48235	3.86364
30	188	366.000	3.45000	3.85000
31	30	380.833	3.11667	3.83333
32	115	369.167	2.86250	3.83333
33	147	354.375	2.92500	3.83333
34	59	356.522	2.97727	3.82609
35	245	341.304	2.99000	3.82609
36	81	296.136	2.39000	3.81818
37	2	340.417	3.15217	3.79167
38	10	306.875	2.68182	3.79167
39	212	312.174	2.53913	3.78261
40	146	336.667	2.57222	3.76190

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	341.1496324	32.7130028	248.0434783	402.8571429
DIAM	40	2.9572663	0.4210607	2.1111111	3.9227273
FORM	40	4.0093517	0.2227799	3.7619048	4.7083333

Appendix 4: Input data for RESI (Restricted selection index)

Genetic parameters			
	Height	Diameter	Straightness
Family Heritability	0.4577	0.3246	0.5557
Phenotypic Variance	7760.34	1.27	1.16
Phenotypic Correlation			
Height	1.000		
Diameter	0.870	1.000	
Straightness	0.360	0.350	1.000
Genetic Correlation			
Height	1.000		
Diameter	0.790	1.000	
Straightness	0.390	0.410	1.000

Sets of Economic weights						
	Height		Diameter		Straightness	Remark
INDEX 1	0.0100	(1)	0.8800	(1)	0.9300 (1)	Equal weight
INDEX 2	0.1000	(10)	0.8800	(1)	0.9300 (1)	
INDEX 3	0.0100	(1)	8.8000	(10)	0.9300 (1)	
INDEX 4	0.0100	(1)	0.8800	(1)	9.3000 (10)	
INDEX 5	0.1000	(10)	0.8800	(1)	9.3000 (10)	
INDEX 6	0.0100	(1)	8.8000	(10)	9.3000 (10)	
INDEX 7	0.1000	(10)	8.8000	(10)	18.6000 (20)	
INDEX 8	0.0100	(1)	8.8000	(10)	18.6000 (20)	
INDEX 9	0.1000	(10)	0.8800	(1)	18.6000 (20)	
INDEX10	0.1000	(10)	8.8000	(10)	0.93000 (1)	
INDX 11	0.1000	(10)	17.6000	(20)	18.6000 (20)	
INDEX12	0.1000	(10)	17.6000	(20)	46.5000 (50)	
INDEX 13	0.1000	(10)	44.0000	(50)	46.5000 (50)	
INDEX 14	0.2000	(20)	17.6000	(20)	46.5000 (50)	
INDEX 15	0.2000	(20)	0. 8800	(1)	46.5000 (50)	
1NDEX 16	0.0100	(1)	17.6000	(20)	46.5000 (50)	
INDEX 17	0.5000	(50)	17.6000	(20)	46.5000 (50)	
INDEX 18	0.2000	(20)	44.0000	(50)	46.5000 (50)	

Note : The numbers in the parenthesis represent relative economic weights.

Appendix 5: Index coefficients, or 'b' values.

	Calculated 'b' values for each trait			
List of indices	Height	Diameter	Straightness	Remark
Index 1	0.0093	-0.1644	0.6236	
Index 2	0.0796	-2.9327	1.0160	
Index 3	0.0171	1.7031	1.1552	
Index 4	0.0153	-0.7435	5.3121	
Index 5	0.0855	-3.5119	5.7045	
Index 6	0.0230	1.1239	5.8437	
Index 7	0.0999	-2.2878	11.4455	
Index 8	0.0296	0.4805	11.0531	
Index 9	0.0921	-4.1553	10.9139	
Index 10	0.0873	-1.0653	1.5476	
Index 11	0.1084	-0.2128	12.0361	
Index 12	0.1282	-2.1432	27.6644	
Index 13	0.1540	4.0818	29.4363	
Index 14	0.2063	-5.2191	28.1004	
Index 15	0.1900	-9.1616	26.9781	
Index 16	0.0580	0.6251	27.2720	
Index 17	0.4406	-14.4468	29.4083	
Index 18	0.2326	1.1238	29.9059	

Appendix 6: SAS program for family ranking

```
option linesize=80;
data progeny;
infile 'fey3';
input block family tree height diam form;
if tree=1 then plot+1;
height1=b1*height;
diam1= b2*diam;
form1=b3*form;
index= height1+diam1+form1;
proc sort;
by family;
proc means noprint;
var height diam form height1 diam1 form1 index;
by family;
output mean= height diam form height1 diam1 form1 index1;
proc rank descending out= temp1;
var index;
ranks indexr;
proc sort data= temp1;
by indexr;
data temp2;
set temp1;
proc print;
var family height diam form index;
proc means;
var height diam form index;
run;
```

Appendix 7: Ranking of the top 40 families by index 1 (best for all the three traits).

OBS	FAMILY	HEIGHT	DIAM	FORM	INDEX
1	101	397.708	3.92273	4.50000	6.11007
2	329	376.667	3.56500	4.33333	6.05636
3	114	396.875	3.35000	4.58333	5.99836
4	314	402.857	3.43000	4.04762	5.81517
5	303	379.167	4.20556	3.45833	5.72497
6	103	425.208	3.76087	3.45833	5.62337
7	240	382.174	3.60000	3.95652	5.61240
8	386	371.250	3.62273	3.95833	5.58972
9	28	417.500	3.61304	3.41667	5.54171
10	245	341.304	2.99000	3.82609	5.53601
11	188	366.000	3.45000	3.85000	5.51805
12	3	409.167	4.05714	3.12500	5.48726
13	127	319.167	2.55833	4.70833	5.48378
14	276	378.958	3.64762	3.41667	5.47108
15	126	339.773	3.09048	4.36364	5.44567
16	275	338.750	2.65714	3.62500	5.44099
17	30	380.833	3.11667	3.83333	5.41984
18	392	360.652	3.53500	3.91304	5.39323
19	244	392.917	3.40455	3.29167	5.39064
20	43	329.524	2.62000	4.19048	5.38950
21	185	351.957	3.63529	3.17391	5.38572
22	256	353.478	2.92174	4.13043	5.38275
23	48	354.792	2.83125	4.08333	5.38047
24	146	336.667	2.57222	3.76190	5.37197
25	344	393.318	3.95000	2.82609	5.36784
26	140	319.318	3.48235	3.86364	5.36676
27	348	372.708	3.05714	3.45833	5.36483
28	130	367.500	3.19545	3.95455	5.35847
29	27	326.875	2.75455	4.12500	5.35336
30	115	369.167	2.86250	3.83333	5.35312
31	317	382.609	3.27273	3.47826	5.34218
32	12	340.625	3.19565	4.08333	5.34140
33	113	372.727	3.15789	3.09091	5.31406
34	75	362.391	3.21364	3.73913	5.30004
35	265	349.167	3.03182	3.62500	5.29698
36	161	390.435	3.71905	3.21739	5.29536
37	374	342.083	3.18095	3.66667	5.27908
38	136	377.609	3.31429	3.34783	5.27776
39	168	396.667	3.60435	3.25000	5.26771
40	76	331.458	3.03696	4.08333	5.26641

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	367.4500253	27.3102690	319.1666667	425.2083333
DIAM	40	3.3046667	0.4134195	2.5583333	4.2055556
FORM	40	3.7662022	0.4381124	2.8260870	4.7083333
INDEX	40	5.4678619	0.2097733	5.2664070	6.1100673

Appendix 8: Ranking of the top 40 families by index 10 (best for height).

OBS	FAMILY	HEIGHT	DIAM	FORM	INDEX
1	103	425.208	3.76087	3.45833	39.4193
2	3	409.167	4.05714	3.12500	39.2996
3	101	397.708	3.92273	4.50000	39.2655
4	329	376.667	3.56500	4.33333	39.1777
5	303	379.167	4.20556	3.45833	39.0045
6	28	417.500	3.61304	3.41667	38.7693
7	314	402.857	3.43000	4.04762	38.5715
8	232	437.292	4.05000	2.91667	38.3749
9	114	396.875	3.35000	4.58333	38.1716
10	344	393.318	3.95000	2.82609	37.9223
11	244	392.917	3.40455	3.29167	37.3537
12	113	372.727	3.15789	3.09091	37.3411
13	276	378.958	3.64762	3.41667	37.3115
14	240	382.174	3.60000	3.95652	36.9749
15	99	379.348	3.47500	3.04348	36.7597
16	168	396.667	3.60435	3.25000	36.7548
17	161	390.435	3.71905	3.21739	36.7214
18	185	351.957	3.63529	3.17391	36.5888
19	317	382.609	3.27273	3.47826	36.4443
20	348	372.708	3.05714	3.45833	36.4421
21	386	371.250	3.62273	3.95833	36.3907
22	136	377.609	3.31429	3.34783	36.3628
23	188	366.000	3.45000	3.85000	36.2226
24	258	377.273	2.73500	3.04545	36.1195
25	30	380.833	3.11667	3.83333	35.8590
26	77	364.783	3.69474	3.26087	35.8085
27	404	381.667	3.39565	3.45833	35.7936
28	392	360.652	3.53500	3.91304	35.7374
29	153	392.500	3.33810	3.00000	35.7176
30	299	373.958	3.27727	3.34783	35.7108
31	308	366.875	3.51500	2.62500	35.7052
32	360	371.087	3.16190	2.95652	35.4896
33	247	378.542	3.26957	3.37500	35.4517
34	279	395.083	3.94167	3.29167	35.3859
35	134	392.143	3.36190	3.04762	35.3691
36	343	384.167	3.61250	3.66667	35.3639
37	245	341.304	2.99000	3.82609	35.3101
38	370	373.478	3.25455	3.26087	35.3093
39	170	372.500	3.07391	3.54167	35.2737
40	275	338.750	2.65714	3.62500	35.1203

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	382.4177824	19.7094070	338.7500000	437.2916667
DIAM	40	3.4698884	0.3422561	2.6571429	4.2055556
FORM	40	3.4568408	0.4424235	2.6250000	4.5833333
INDEX	40	36.7542491	1.3531984	35.1203171	39.4192891

Appendix 9: Ranking of the top 40 families by index 3 (best for diameter).

OBS	FAMILY	HEIGHT	DIAM	FORM	INDEX
1	101	397.708	3.92273	4.50000	19.1410
2	303	379.167	4.20556	3.45833	18.9937
3	329	376.667	3.56500	4.33333	18.3237
4	3	409.167	4.05714	3.12500	18.2538
5	103	425.208	3.76087	3.45833	17.9120
6	344	393.318	3.95000	2.82609	17.8198
7	114	396.875	3.35000	4.58333	17.7866
8	232	437.292	4.05000	2.91667	17.7446
9	314	402.857	3.43000	4.04762	17.6061
10	386	371.250	3.62273	3.95833	17.5783
11	240	382.174	3.60000	3.95652	17.5737
12	28	417.500	3.61304	3.41667	17.4650
13	276	378.958	3.64762	3.41667	17.4061
14	279	395.083	3.94167	3.29167	17.2715
15	185	351.957	3.63529	3.17391	17.2242
16	161	390.435	3.71905	3.21739	17.2242
17	188	366.000	3.45000	3.85000	17.0990
18	392	360.652	3.53500	3.91304	17.0387
19	243	368.125	3.79250	3.70833	17.0378
20	77	364.783	3.69474	3.26087	17.0373
21	343	384.167	3.61250	3.66667	16.9574
22	168	396.667	3.60435	3.25000	16.9426
23	140	319.318	3.48235	3.86364	16.8862
24	244	392.917	3.40455	3.29167	16.7689
25	99	379.348	3.47500	3.04348	16.5703
26	135	353.958	3.41429	3.50000	16.4895
27	404	381.667	3.39565	3.45833	16.4665
28	317	382.609	3.27273	3.47826	16.4162
29	136	377.609	3.31429	3.34783	16.3801
30	130	367.500	3.19545	3.95455	16.2947
31	80	366.875	3.49545	3.12500	16.2939
32	42	349.792	3.32917	4.00000	16.2721
33	12	340.625	3.19565	4.08333	16.2660
34	30	380.833	3.11667	3.83333	16.2485
35	126	339.773	3.09048	4.36364	16.2482
36	75	362.391	3.21364	3.73913	16.2226
37	245	341.304	2.99000	3.82609	16.2113
38	113	372.727	3.15789	3.09091	16.1318
39	374	342.083	3.18095	3.66667	16.1188
40	308	366.875	3.51500	2.62500	16.0994

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	376.6053177	24.4419818	319.3181818	437.2916667
DIAM	40	3.5249745	0.2883729	2.9900000	4.2055556
FORM	40	3.5904905	0.4600183	2.6250000	4.5833333
INDEX	40	17.0455522	0.7904160	16.0994315	19.1409968

Appendix 10: Ranking of the top 40 families by index 4 (best for stem straightness).

OBS	FAMILY	HEIGHT	DIAM	FORM	INDEX
1	101	397.708	3.92273	4.50000	28.0687
2	127	319.167	2.55833	4.70833	27.9923
3	114	396.875	3.35000	4.58333	27.9286
4	329	376.667	3.56500	4.33333	27.5651
5	126	339.773	3.09048	4.36364	26.2746
6	43	329.524	2.62000	4.19048	26.0578
7	27	326.875	2.75455	4.12500	26.0126
8	245	341.304	2.99000	3.82609	25.6952
9	210	248.043	2.11111	4.08696	25.5422
10	314	402.857	3.43000	4.04762	25.5177
11	12	340.625	3.19565	4.08333	25.3523
12	128	292.143	2.64737	4.14286	25.3445
13	76	331.458	3.03696	4.08333	25.3040
14	386	371.250	3.62273	3.95833	25.2115
15	256	353.478	2.92174	4.13043	25.1772
16	48	354.792	2.83125	4.08333	25.0144
17	240	382.174	3.60000	3.95652	24.8792
18	275	338.750	2.65714	3.62500	24.8391
19	129	275.000	2.20526	3.75000	24.7902
20	81	296.136	2.39000	3.81818	24.6997
21	397	292.083	2.54286	3.95833	24.6140
22	188	366.000	3.45000	3.85000	24.5908
23	140	319.318	3.48235	3.86364	24.5787
24	146	336.667	2.57222	3.76190	24.5276
25	45	295.870	2.16875	3.52174	24.4151
26	10	306.875	2.68182	3.79167	24.3850
27	201	341.042	2.78261	3.91667	24.2603
28	130	367.500	3.19545	3.95455	24.2539
29	42	349.792	3.32917	4.00000	24.1250
30	303	379.167	4.20556	3.45833	24.0976
31	131	259.130	2.46111	3.60870	24.0954
32	255	330.417	2.37917	3.91667	24.0922
33	32	328.261	2.79048	3.69565	24.0717
34	400	313.333	2.70000	3.91667	23.9859
35	250	348.125	2.76087	3.75000	23.9277
36	269	342.292	2.87083	3.91667	23.9083
37	396	349.130	2.98696	3.91304	23.9074
38	149	340.714	2.78571	3.90476	23.8842
39	115	369.167	2.86250	3.83333	23.8830
40	30	380.833	3.11667	3.83333	23.8726

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	40	338.2578751	36.3668899	248.0434783	402.8571429
DIAM	40	2.9406343	0.4758687	2.1111111	4.2055556
FORM	40	3.9690437	0.2661409	3.4583333	4.7083333
INDEX	40	25.0185843	1.1752474	23.8725583	28.0687341

Appendix 11: Ranking of the top 200 families by index 1.

OBS	FAMILY	HEIGHT	DIAM	FORM	INDEX
1	101	397.708	3.92273	4.50000	6.11007
2	329	376.667	3.56500	4.33333	6.05636
3	114	396.875	3.35000	4.58333	5.99836
4	314	402.857	3.43000	4.04762	5.81517
5	303	379.167	4.20556	3.45833	5.72497
6	103	425.208	3.76087	3.45833	5.62337
7	240	382.174	3.60000	3.95652	5.61240
8	386	371.250	3.62273	3.95833	5.58972
9	28	417.500	3.61304	3.41667	5.54171
10	245	341.304	2.99000	3.82609	5.53601
11	188	366.000	3.45000	3.85000	5.51805
12	3	409.167	4.05714	3.12500	5.48726
13	127	319.167	2.55833	4.70833	5.48378
14	276	378.958	3.64762	3.41667	5.47108
15	126	339.773	3.09048	4.36364	5.44567
16	275	338.750	2.65714	3.62500	5.44099
17	30	380.833	3.11667	3.83333	5.41984
18	392	360.652	3.53500	3.91304	5.39323
19	244	392.917	3.40455	3.29167	5.39064
20	43	329.524	2.62000	4.19048	5.38950
Mean of top 20		375.32	3.41	3.89	5.60
21	185	351.957	3.63529	3.17391	5.38572
22	256	353.478	2.92174	4.13043	5.38275
23	48	354.792	2.83125	4.08333	5.38047
24	146	336.667	2.57222	3.76190	5.37197
25	344	393.318	3.95000	2.82609	5.36784
26	140	319.318	3.48235	3.86364	5.36676
27	348	372.708	3.05714	3.45833	5.36483
28	130	367.500	3.19545	3.95455	5.35847
29	27	326.875	2.75455	4.12500	5.35336
30	115	369.167	2.86250	3.83333	5.35312
31	317	382.609	3.27273	3.47826	5.34218
32	12	340.625	3.19565	4.08333	5.34140
33	113	372.727	3.15789	3.09091	5.31406
34	75	362.391	3.21364	3.73913	5.30004
35	265	349.167	3.03182	3.62500	5.29698
36	161	390.435	3.71905	3.21739	5.29536
37	374	342.083	3.18095	3.66667	5.27908
38	136	377.609	3.31429	3.34783	5.27776
39	168	396.667	3.60435	3.25000	5.26771
40	76	331.458	3.03696	4.08333	5.26641
Mean of top 40		367.45	3.30	3.77	5.47
41	343	384.167	3.61250	3.66667	5.26539
42	59	356.522	2.97727	3.82609	5.25771
43	250	348.125	2.76087	3.75000	5.25663
44	201	341.042	2.78261	3.91667	5.23854
45	404	381.667	3.39565	3.45833	5.23578
46	135	353.958	3.41429	3.50000	5.22732
47	336	339.792	3.21905	3.54167	5.22007
48	77	364.783	3.69474	3.26087	5.22004
49	232	437.292	4.05000	2.91667	5.21983

50	170	372.500	3.07391	3.54167	5.21672
51	99	379.348	3.47500	3.04348	5.20701
52	45	295.870	2.16875	3.52174	5.20566
53	147	354.375	2.92500	3.83333	5.20528
54	42	349.792	3.32917	4.00000	5.20015
55	258	377.273	2.73500	3.04545	5.19942
56	396	349.130	2.98696	3.91304	5.19603
57	247	378.542	3.26957	3.37500	5.16589
58	299	373.958	3.27727	3.34783	5.15955
59	269	342.292	2.87083	3.91667	5.15378
60	209	343.542	3.02727	3.62500	5.15139
61	149	340.714	2.78571	3.90476	5.14568
62	370	373.478	3.25455	3.26087	5.13879
63	32	328.261	2.79048	3.69565	5.13695
64	165	346.957	2.97500	3.39130	5.13356
65	7	345.833	3.27000	3.41667	5.12458
66	255	330.417	2.37917	3.91667	5.12417
67	243	368.125	3.79250	3.70833	5.11259
68	211	303.125	2.83529	3.20833	5.10534
69	345	368.864	3.10476	3.38095	5.10315
70	186	346.458	2.84348	3.66667	5.10225
71	160	373.958	3.08696	3.29167	5.09720
72	2	340.417	3.15217	3.79167	5.08634
73	279	395.083	3.94167	3.29167	5.07895
74	166	348.750	3.06364	3.41667	5.07767
75	162	367.391	3.11591	3.26087	5.07281
76	393	348.043	2.95000	3.34783	5.07257
77	346	348.542	3.02045	3.29167	5.07208
78	57	374.130	3.23043	3.39130	5.06315
79	128	292.143	2.64737	4.14286	5.05978
80	246	371.522	3.04545	3.30435	5.05729
Mean of top 80		361.68	3.21	3.65	5.31
81	153	392.500	3.33810	3.00000	5.05491
82	10	306.875	2.68182	3.79167	5.05363
83	400	313.333	2.70000	3.91667	5.05313
84	120	327.917	2.52500	3.87500	5.05097
85	207	306.905	2.38889	3.61905	5.04713
86	295	357.292	2.83913	3.29167	5.04661
87	49	360.000	3.17619	3.31818	5.04048
88	360	371.087	3.16190	2.95652	5.03959
89	80	366.875	3.49545	3.12500	5.03404
90	293	332.826	2.99050	3.21739	5.03199
91	379	361.458	3.08571	3.04167	5.03179
92	79	355.714	3.10476	3.57143	5.02486
93	397	292.083	2.54286	3.95833	5.02317
94	81	296.136	2.39000	3.81818	5.01894
95	148	357.083	2.80000	3.45833	5.01717
96	203	321.458	2.89048	3.50000	5.01632
97	142	299.348	2.57647	3.26087	5.01547
98	364	370.417	3.33043	3.20833	5.01389
99	361	307.045	2.40526	3.63636	5.01322
100	112	336.304	2.22609	3.60870	5.01204
101	129	275.000	2.20526	3.75000	5.00708
102	172	351.875	3.03810	3.04167	5.00510
103	134	392.143	3.36190	3.04762	4.99473
104	395	319.375	2.59048	3.54167	4.98280
105	109	313.182	2.75263	3.36364	4.97757
106	347	319.348	2.81111	3.21739	4.97181
107	226	359.545	3.15714	3.18182	4.96872
108	300	348.043	3.21905	3.26087	4.96661
109	387	314.091	2.97500	2.95455	4.95074
110	121	351.667	3.00000	3.33333	4.94940
111	190	323.636	2.99000	3.54545	4.94056
112	8	356.957	3.06087	3.39130	4.93131

Appendix 11 continued...

113	294	363.500	3.46111	3.10000	4.92575
114	249	300.909	2.64737	3.52381	4.92102
115	175	340.870	2.82727	3.34783	4.91909
116	288	328.542	2.61429	3.37500	4.91677
117	287	318.500	2.83333	2.70000	4.91675
118	152	337.500	3.03889	3.00000	4.91143
119	308	366.875	3.51500	2.62500	4.90914
120	118	269.091	2.15714	3.00000	4.90302
Mean of top 120		352.65	3.09	3.54	5.20
121	388	325.217	3.38824	2.73913	4.90199
122	52	329.792	2.75833	3.66667	4.90013
123	123	270.870	2.42941	3.21739	4.89643
124	341	316.458	2.84211	3.33333	4.88931
125	235	342.292	2.57143	2.87500	4.87980
126	332	306.818	2.68095	3.72727	4.87101
127	138	298.696	2.44737	3.43478	4.86623
128	362	318.333	2.56364	3.54167	4.86569
129	194	316.522	2.48409	3.52174	4.86273
130	154	335.000	2.97083	3.58333	4.86166
131	342	346.667	2.76087	3.16667	4.85885
132	150	370.417	3.09583	3.08333	4.85869
133	13	377.857	3.36000	2.80952	4.85748
134	278	331.957	3.28421	3.21739	4.85522
135	220	350.714	3.18235	2.68182	4.85314
136	316	326.458	2.44783	3.37500	4.84977
137	212	312.174	2.53913	3.78261	4.84462
138	210	248.043	2.11111	4.08696	4.84295
139	349	337.826	2.68696	3.43478	4.84198
140	357	295.000	3.01765	2.86957	4.83836
141	171	298.750	2.81000	3.37500	4.83668
142	252	319.783	2.48095	3.21739	4.83462
143	338	335.000	2.50417	3.41667	4.83445
144	26	318.125	2.92609	3.62500	4.83393
145	267	351.875	3.15000	3.33333	4.83324
146	82	318.696	2.65909	3.59091	4.83309
147	117	322.000	2.88824	3.05000	4.82618
148	164	330.000	2.67826	3.52174	4.82485
149	377	321.875	2.45833	3.58333	4.82385
150	372	358.958	3.00000	2.75000	4.82320
151	399	334.167	2.50000	3.20833	4.82170
152	193	329.958	3.18000	3.00000	4.82026
153	95	305.476	2.77778	3.23810	4.81924
154	133	289.565	2.40526	3.39130	4.81686
155	315	310.000	3.21875	2.90476	4.81014
156	333	287.917	2.26087	4.00000	4.80473
157	40	355.217	2.76087	3.13043	4.80177
158	257	316.875	2.48571	3.29167	4.79176
159	104	347.500	3.21818	2.95833	4.79168
160	219	314.773	2.61053	3.36364	4.79033
Mean of top 160		345.26	3.01	3.48	5.11
161	131	259.130	2.46111	3.60870	4.78785
162	221	296.316	2.25882	3.42105	4.78757
163	259	309.773	2.09500	3.36364	4.78670
164	98	329.167	2.64167	3.45833	4.78358
165	196	304.864	2.81579	3.50000	4.77872
166	233	364.792	2.83043	2.87500	4.77810
167	119	340.625	2.96087	3.16667	4.77745
168	200	333.750	3.14091	3.20833	4.77615
169	182	302.500	2.74706	2.95833	4.77554
170	231	293.125	3.15714	2.50000	4.76756
171	312	283.125	2.46500	3.45833	4.75443
172	229	336.667	2.45417	3.25000	4.75424

Appendix 11 continued...

173	335	311.042	2.31190	3.16667	4.75391
174	124	322.500	2.64545	3.20833	4.75279
175	398	326.136	3.12500	3.13636	4.75031
176	41	316.087	2.64762	3.17391	4.74652
177	375	302.083	2.32105	2.87500	4.74536
178	298	312.708	2.42381	3.20833	4.74476
179	297	328.750	2.67727	3.04167	4.73899
180	274	338.478	3.32000	2.78261	4.73249
181	36	328.043	2.63478	3.39130	4.73246
182	385	315.208	2.92000	3.25000	4.73053
183	31	345.000	3.03529	2.60000	4.73010
184	184	317.917	2.60000	3.12500	4.72871
185	54	328.478	2.42000	3.00000	4.71276
186	214	291.667	2.21500	3.16667	4.70843
187	22	309.318	2.68500	3.31818	4.70830
188	334	247.174	1.97857	3.17391	4.70788
189	167	331.739	3.07000	2.95652	4.70533
190	29	348.333	3.14545	2.95833	4.70380
191	350	332.917	2.28261	3.00000	4.69963
192	318	314.565	2.68571	3.26087	4.69949
193	169	322.391	2.78182	3.21739	4.69780
194	238	327.917	2.72609	3.29167	4.69760
195	403	290.870	2.84000	3.45455	4.69552
196	4	322.708	2.99583	3.50000	4.69127
197	176	347.273	2.59048	2.90909	4.68261
198	51	326.957	2.75909	3.17391	4.68164
199	271	323.958	2.80000	3.25000	4.68126
200	368	347.083	3.70455	2.95833	4.67915

Variable	N	Mean	Std Dev	Minimum	Maximum
HEIGHT	200	339.8611986	32.4867946	247.1739130	437.2916667
DIAM	200	2.9519407	0.4268802	1.9785714	4.2055556
FORM	200	3.4180910	0.3907743	2.5000000	4.7083333
INDEX	200	5.0375309	0.2774818	4.6791455	6.1100673

Appendix 12: Ranking of the 405 families by mean height (cm), diameter (cm) and mean stem straightness (points).

Family	Height	Family	Diameter	Family	Straightness
232	437.292	303	4.20556	127	4.70833
103	425.208	3	4.05714	114	4.58333
28	417.500	232	4.05000	101	4.50000
3	409.167	344	3.95000	126	4.36364
314	402.857	279	3.94167	329	4.33333
101	397.708	101	3.92273	43	4.19048
114	396.875	243	3.79250	128	4.14286
168	396.667	103	3.76087	256	4.13043
279	395.083	161	3.71905	27	4.12500
344	393.318	368	3.70455	210	4.08696
244	392.917	77	3.69474	12	4.08333
153	392.500	276	3.64762	48	4.08333
134	392.143	185	3.63529	76	4.08333
161	390.435	386	3.62273	314	4.04762
343	384.167	28	3.61304	42	4.00000
317	382.609	343	3.61250	333	4.00000
240	382.174	168	3.60435	386	3.95833
404	381.667	240	3.60000	397	3.95833
30	380.833	329	3.56500	240	3.95652
99	379.348	392	3.53500	130	3.95455
303	379.167	308	3.51500	201	3.91667
276	378.958	80	3.49545	255	3.91667
247	378.542	140	3.48235	269	3.91667
13	377.857	99	3.47500	400	3.91667
136	377.609	294	3.46111	392	3.91304
258	377.273	188	3.45000	396	3.91304
329	376.667	6	3.43043	149	3.90476
57	374.130	314	3.43000	120	3.87500
160	373.958	135	3.41429	140	3.86364
299	373.958	244	3.40455	188	3.85000
370	373.478	404	3.39565	30	3.83333
113	372.727	388	3.38824	115	3.83333
348	372.708	134	3.36190	147	3.83333
170	372.500	13	3.36000	59	3.82609
246	371.522	114	3.35000	245	3.82609
386	371.250	153	3.33810	81	3.81818
360	371.087	364	3.33043	2	3.79167
150	370.417	42	3.32917	10	3.79167
364	370.417	274	3.32000	212	3.78261
115	369.167	53	3.31500	146	3.76190
345	368.864	136	3.31429	129	3.75000
243	368.125	339	3.30000	250	3.75000
130	367.500	330	3.29545	75	3.73913
162	367.391	278	3.28421	332	3.72727
80	366.875	299	3.27727	243	3.70833
308	366.875	317	3.27273	32	3.69565
188	366.000	7	3.27000	52	3.66667
233	364.792	247	3.26957	186	3.66667
77	364.783	370	3.25455	343	3.66667
294	363.500	57	3.23043	374	3.66667
75	362.391	300	3.21905	361	3.63636
379	361.458	336	3.21905	26	3.62500
392	360.652	315	3.21875	105	3.62500
49	360.000	104	3.21818	209	3.62500
226	359.545	75	3.21364	265	3.62500
372	358.958	353	3.20526	275	3.62500
295	357.292	12	3.19565	207	3.61905
148	357.083	130	3.19545	112	3.60870
8	356.957	220	3.18235	131	3.60870
59	356.522	374	3.18095	21	3.59091
79	355.714	193	3.18000	82	3.59091
40	355.217	49	3.17619	365	3.59091
48	354.792	360	3.16190	87	3.58333
147	354.375	113	3.15789	125	3.58333
135	353.958	226	3.15714	154	3.58333
256	353.478	231	3.15714	377	3.58333

Appendix 12 continued...

185	351.957
172	351.875
267	351.875
121	351.667
220	350.714
42	349.792
265	349.167
396	349.130
166	348.750
346	348.542
29	348.333
250	348.125
300	348.043
393	348.043
104	347.500
176	347.273
368	347.083
165	346.957
342	346.667
186	346.458
327	346.458
7	345.833
31	345.000
183	345.000
353	344.318
6	343.542
209	343.542
352	342.500
235	342.292
269	342.292
374	342.083
245	341.304
201	341.042
175	340.870
149	340.714
12	340.625
119	340.625
2	340.417
260	340.000
336	339.792
126	339.773
275	338.750
274	338.478
349	337.826
152	337.500
146	336.667
229	336.667
112	336.304
154	335.000
291	335.000
338	335.000
83	334.286
399	334.167
53	333.958
200	333.750
84	333.333
330	332.917
350	332.917
293	332.826
278	331.957
272	331.875
167	331.739
76	331.458
73	331.042
363	330.435
255	330.417
2	3.15217
267	3.15000
29	3.14545
200	3.14091
398	3.12500
30	3.11667
162	3.11591
9	3.11053
79	3.10476
345	3.10476
150	3.09583
126	3.09048
160	3.08696
379	3.08571
170	3.07391
167	3.07000
166	3.06364
8	3.06087
348	3.05714
390	3.04706
246	3.04545
152	3.03889
172	3.03810
76	3.03696
31	3.03529
265	3.03182
209	3.02727
346	3.02045
357	3.01765
121	3.00000
372	3.00000
4	2.99583
293	2.99050
190	2.99000
245	2.99000
396	2.98696
34	2.98421
59	2.97727
165	2.97500
387	2.97500
154	2.97083
119	2.96087
393	2.95000
17	2.93000
26	2.92609
147	2.92500
256	2.92174
385	2.92000
363	2.91429
266	2.91111
217	2.89545
376	2.89545
203	2.89048
117	2.88824
181	2.87368
64	2.87222
269	2.87083
273	2.86957
115	2.86250
132	2.85000
371	2.84500
186	2.84348
341	2.84211
403	2.84000
295	2.83913
211	2.83529
79	3.5714
190	3.5454
170	3.5416
336	3.5416
362	3.5416
395	3.5416
248	3.5238
249	3.5238
45	3.5217
164	3.5217
194	3.5217
4	3.5000
135	3.5000
196	3.5000
202	3.5000
203	3.5000
317	3.4782
98	3.4583
103	3.4583
148	3.4583
303	3.4583
312	3.4583
348	3.4583
404	3.4583
94	3.4545
156	3.4545
356	3.4545
403	3.4545
138	3.4347
349	3.4347
221	3.4210
7	3.4166
28	3.4166
166	3.4166
276	3.4166
338	3.4166
382	3.4166
67	3.4090
8	3.3913
36	3.3913
57	3.3913
133	3.3913
165	3.3913
296	3.3913
345	3.3809
35	3.3750
47	3.3750
171	3.3750
247	3.3750
288	3.3750
302	3.3750
316	3.3750
109	3.3636
219	3.3636
259	3.3636
136	3.3478
175	3.3478
299	3.3478
393	3.3478
121	3.3333
159	3.3333
267	3.3333
341	3.3333
380	3.3333
22	3.3181
49	3.3181

Appendix 12 continued...

164	330.000	234	2.83500	198	3.3043
268	330.000	11	2.83333	246	3.3043
193	329.958	287	2.83333	144	3.2916
52	329.792	48	2.83125	157	3.2916
43	329.524	233	2.83043	160	3.2916
98	329.167	401	2.83000	238	3.2916
376	329.167	175	2.82727	244	3.2916
297	328.750	155	2.82273	257	3.2916
139	328.542	196	2.81579	279	3.2916
288	328.542	347	2.81111	295	3.2916
54	328.478	171	2.81000	346	3.2916
32	328.261	327	2.80870	195	3.2777
36	328.043	83	2.80500	173	3.2727
120	327.917	272	2.80476	77	3.2608
238	327.917	148	2.80000	142	3.2608
9	327.174	271	2.80000	162	3.2608
237	327.174	242	2.79474	300	3.2608
51	326.957	32	2.79048	318	3.2608
27	326.875	268	2.78958	370	3.2608
253	326.667	149	2.78571	74	3.2500
143	326.458	201	2.78261	163	3.2500
316	326.458	169	2.78182	168	3.2500
398	326.136	95	2.77778	229	3.2500
390	325.870	143	2.76818	271	3.2500
388	325.217	206	2.76316	366	3.2500
33	324.783	40	2.76087	385	3.2500
206	324.000	250	2.76087	95	3.2381
271	323.958	342	2.76087	367	3.2381
331	323.958	381	2.76000	66	3.2272
50	323.750	51	2.75909	93	3.2272
190	323.636	225	2.75882	1	3.2173
371	323.409	52	2.75833	123	3.2173
11	322.955	402	2.75789	161	3.2173
4	322.708	27	2.75455	169	3.2173
254	322.609	109	2.75263	252	3.2173
102	322.500	182	2.74706	278	3.2173
124	322.500	331	2.73913	293	3.2173
169	322.391	258	2.73500	347	3.2173
117	322.000	33	2.73043	16	3.2083
377	321.875	238	2.72609	124	3.2083
203	321.458	264	2.72000	200	3.2083
242	321.304	304	2.71190	211	3.2083
68	321.087	157	2.70435	298	3.2083
252	319.783	400	2.70000	364	3.2083
395	319.375	68	2.69500	399	3.2083
347	319.348	349	2.68696	226	3.1818
140	319.318	318	2.68571	283	3.1818
127	319.167	22	2.68500	41	3.1739
273	318.958	187	2.68500	51	3.1739
82	318.696	10	2.68182	185	3.1739
287	318.500	332	2.68095	334	3.1739
362	318.333	164	2.67826	61	3.1666
26	318.125	297	2.67727	119	3.1666
110	318.125	84	2.67391	214	3.1666
184	317.917	139	2.67273	323	3.1666
132	317.826	340	2.67222	335	3.1666
325	317.292	352	2.66591	342	3.1666
78	317.083	82	2.65909	358	3.1666
257	316.875	275	2.65714	378	3.1666
381	316.875	41	2.64762	83	3.1428
194	316.522	128	2.64737	14	3.1363
25	316.458	249	2.64737	340	3.1363
341	316.458	310	2.64737	371	3.1363
41	316.087	25	2.64545	398	3.1363
234	316.087	124	2.64545	40	3.1304
17	315.652	106	2.64500	217	3.1304

Appendix 12 continued...

301	315.652
385	315.208
219	314.773
318	314.565
58	314.130
387	314.091
367	314.048
401	313.636
400	313.333
217	313.261
109	313.182
155	313.125
298	312.708
145	312.500
212	312.174
335	311.042
315	310.000
159	309.792
156	309.773
259	309.773
187	309.375
22	309.318
1	309.130
38	309.091
16	308.333
356	308.182
306	307.609
34	307.174
137	307.083
66	307.045
361	307.045
174	306.957
207	306.905
10	306.875
107	306.875
122	306.875
332	306.818
85	306.739
313	305.625
95	305.476
163	305.417
179	305.208
328	305.208
196	304.864
384	304.783
280	304.583
222	304.318
248	303.571
106	303.333
211	303.125
208	303.043
285	303.043
192	302.955
292	302.826
151	302.708
339	302.609
182	302.500
375	302.083
321	301.957
389	301.042
249	300.909
378	300.833
202	300.625
286	300.217
88	300.208
157	300.000
98	2.64167
302	2.64091
36	2.63478
67	2.63158
292	2.63158
301	2.62727
43	2.62000
156	2.61818
198	2.61429
288	2.61429
219	2.61053
365	2.60476
184	2.60000
78	2.59565
394	2.59130
58	2.59048
176	2.59048
395	2.59048
222	2.58571
291	2.58182
253	2.57727
142	2.57647
146	2.57222
235	2.57143
248	2.57000
73	2.56667
213	2.56667
280	2.56500
362	2.56364
320	2.56190
127	2.55833
260	2.55652
91	2.55556
204	2.55000
208	2.55000
110	2.54783
306	2.54500
202	2.54348
397	2.54286
38	2.54000
212	2.53913
313	2.53636
122	2.52727
120	2.52500
321	2.51000
383	2.51000
323	2.50909
195	2.50556
66	2.50526
356	2.50476
338	2.50417
399	2.50000
257	2.48571
194	2.48409
15	2.48333
286	2.48235
252	2.48095
237	2.47727
191	2.47333
151	2.47273
183	2.47273
254	2.47143
312	2.46500
131	2.46111
377	2.45833
326	2.45714
3	3.125
80	3.125
90	3.125
184	3.125
223	3.125
405	3.125
294	3.100
111	3.095
113	3.090
62	3.086
70	3.086
25	3.083
50	3.083
60	3.083
108	3.083
150	3.083
117	3.050
134	3.047
38	3.045
199	3.045
258	3.045
99	3.043
306	3.043
37	3.041
172	3.041
181	3.041
241	3.041
297	3.041
313	3.041
379	3.041
389	3.041
6	3.000
11	3.000
46	3.000
54	3.000
71	3.000
72	3.000
118	3.000
145	3.000
152	3.000
153	3.000
158	3.000
193	3.000
225	3.000
262	3.000
264	3.000
266	3.000
268	3.000
301	3.000
350	3.000
369	3.000
394	3.000
29	2.9583
84	2.9583
104	2.9583
182	2.9583
273	2.9583
330	2.9583
368	2.9583
406	2.9583
33	2.9565
167	2.9565
227	2.9565
234	2.9565
270	2.9565
285	2.9565

Appendix 12 continued...

394	299.375
142	299.348
227	299.130
91	299.091
20	298.958
171	298.750
138	298.696
158	298.696
239	298.333
65	298.125
195	298.056
323	297.917
289	297.292
380	297.083
221	296.316
81	296.136
45	295.870
402	295.833
46	295.625
355	295.217
357	295.000
264	294.565
60	294.167
108	294.167
290	293.542
296	293.478
69	293.333
231	293.125
283	292.955
125	292.708
340	292.273
128	292.143
397	292.083
365	292.045
214	291.667
92	291.591
204	291.522
213	291.458
111	291.429
358	291.042
97	290.909
403	290.870
62	290.652
304	290.625
354	290.435
405	289.583
133	289.565
319	289.545
67	288.864
178	288.864
383	288.125
333	287.917
55	287.391
64	286.957
198	286.739
320	286.667
305	286.579
44	286.364
144	286.250
35	285.833
310	285.833
181	285.625
236	285.455
189	285.217
72	285.208
309	285.000
229	2.45417
316	2.44783
138	2.44737
16	2.43913
239	2.43000
367	2.43000
123	2.42941
241	2.42857
178	2.42778
355	2.42500
285	2.42429
298	2.42381
54	2.42000
85	2.41000
384	2.41000
133	2.40526
361	2.40526
328	2.40455
93	2.39524
81	2.39000
207	2.38889
236	2.38824
19	2.38632
406	2.38333
197	2.38235
255	2.37917
60	2.37826
92	2.37692
227	2.37000
389	2.36522
20	2.35789
192	2.35789
88	2.35714
145	2.35714
289	2.35500
189	2.35000
179	2.34783
102	2.34545
380	2.33913
325	2.33810
44	2.33750
50	2.33333
174	2.32381
107	2.32174
375	2.32105
405	2.31364
335	2.31190
35	2.31000
46	2.30952
116	2.30000
354	2.29474
281	2.28889
56	2.28421
350	2.28261
125	2.28043
70	2.28000
311	2.27500
108	2.27000
358	2.26957
86	2.26667
158	2.26667
296	2.26190
333	2.26087
163	2.25909
221	2.25882
144	2.25238
355	2.956
360	2.956
387	2.954
92	2.944
73	2.916
232	2.916
272	2.916
284	2.916
325	2.916
383	2.916
402	2.916
174	2.913
230	2.913
321	2.913
322	2.913
352	2.913
97	2.909
176	2.909
261	2.904
315	2.904
18	2.875
122	2.875
151	2.875
233	2.875
235	2.875
320	2.875
375	2.875
34	2.869
251	2.869
357	2.869
206	2.850
65	2.833
107	2.833
215	2.833
24	2.826
55	2.826
205	2.826
344	2.826
363	2.826
373	2.826
44	2.818
197	2.818
204	2.818
222	2.818
319	2.818
401	2.818
13	2.809
69	2.809
187	2.791
5	2.782
19	2.782
58	2.782
254	2.782
274	2.782
354	2.782
23	2.772
178	2.772
286	2.772
309	2.772
311	2.772
53	2.750
78	2.750
110	2.750
137	2.750
139	2.750
155	2.750

Appendix 12 continued...

281	284.783
18	284.375
302	283.958
382	283.333
39	283.261
312	283.125
21	282.727
251	282.174
116	282.045
15	281.739
105	281.667
197	281.364
199	281.136
19	281.087
241	280.542
277	280.417
87	279.792
284	279.583
5	279.348
266	278.462
86	277.826
47	277.083
225	276.957
24	276.304
93	276.136
322	275.217
223	275.208
129	275.000
37	273.542
141	273.333
366	273.333
23	272.955
307	272.917
311	272.273
373	271.957
74	271.250
123	270.870
90	270.625
191	270.217
369	269.792
406	269.375
118	269.091
61	268.333
56	267.708
70	267.609
230	267.609
205	267.391
215	266.042
173	264.545
94	263.864
96	263.043
351	262.826
326	260.652
216	259.792
263	259.783
359	259.773
131	259.130
228	259.130
337	259.091
407	257.826
270	256.435
180	256.087
218	253.913
324	253.913
177	250.625
262	248.913
159	2.25000
228	2.25000
378	2.25000
39	2.24706
1	2.23870
112	2.22609
214	2.21500
382	2.20870
129	2.20526
199	2.20526
223	2.20500
55	2.20455
24	2.20000
47	2.20000
69	2.20000
305	2.20000
324	2.19375
65	2.19048
97	2.17619
45	2.16875
137	2.16500
118	2.15714
105	2.15652
407	2.15294
111	2.15263
283	2.14762
62	2.14545
210	2.11111
173	2.11053
319	2.10000
259	2.09500
373	2.08947
74	2.08864
366	2.08636
290	2.08421
89	2.08125
18	2.07619
141	2.07391
277	2.07059
61	2.06900
307	2.06667
351	2.05789
37	2.05500
94	2.05000
72	2.04545
322	2.03500
21	2.02381
309	2.01111
261	2.00714
369	2.00476
230	2.00000
14	1.99286
71	1.99167
5	1.99091
63	1.98667
90	1.98500
96	1.98261
334	1.97857
251	1.96700
23	1.96111
215	1.94737
87	1.94167
177	1.93500
284	1.93000
359	1.90500
262	1.86471
260	2.750
281	2.750
327	2.750
372	2.750
381	2.750
15	2.739
242	2.739
263	2.739
388	2.739
236	2.727
337	2.727
20	2.708
331	2.708
287	2.700
132	2.695
180	2.695
390	2.695
220	2.681
56	2.666
141	2.666
213	2.666
289	2.666
304	2.666
68	2.652
208	2.652
237	2.652
359	2.636
177	2.625
239	2.625
277	2.625
308	2.625
310	2.625
183	2.608
189	2.608
324	2.608
328	2.608
31	2.600
63	2.600
91	2.590
353	2.590
143	2.583
89	2.565
116	2.545
88	2.541
102	2.541
290	2.541
192	2.523
17	2.521
231	2.500
326	2.478
351	2.478
106	2.458
280	2.458
376	2.458
100	2.450
9	2.434
339	2.434
407	2.434
305	2.421
64	2.409
86	2.391
218	2.391
228	2.391
282	2.391
253	2.375
191	2.347

Appendix 12 continued...

210	248.043	205	1.84500	292	2.347
334	247.174	263	1.84375	384	2.347
89	243.261	218	1.79412	179	2.333
14	241.136	270	1.79000	216	2.333
261	238.333	282	1.78750	291	2.227
63	237.750	100	1.74167	85	2.217
71	237.632	180	1.73810	307	2.166
100	232.000	216	1.71667	39	2.043
282	228.182	337	1.58000	96	1.956