

EUCALYPT BREEDING

A Review

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SUMMARY

The general steps involved in tree breeding are outlined together with special problems which are associated with breeding eucalypts. A brief review of eucalypt breeding overseas and in Australia is given, with final emphasis on breeding in Western Australia

Introduction

Eucalypts form the dominant tree cover over much of Australia and as such, eucalpt forests are an important component of Australia's hardwood resource. Comprising some 500 recognised species, the genus encompassess considerable diversity. This enables it to exist in a wide range of environments, from the cold mountainous regions of Tasmania and south eastern Australia, north to the wet tropical regions of northern Queensland and throughout the arid regions of central and Western Australia.

Since European settlement of Australia, extensive areas of eucalyt forest have been cleared and the remaining forest exploited to a large extent as a source of timber. Such activities have led over the long term to depletion of the gene pool, by complete loss of some provenances of some species. The significance of these losses is unknown (Sheperd 1977).

Although eucalypt forests are the main source of Australian hardwood, eucalypts are not extensively planted in Australia. The majority of our eucalypt forests are regenerated naturally. The greater proportion of eucalypt planting occurs overseas in the establishment of exotic plantations. For example Sheperd (1977) at time of writing noted that Brazil had 1 000 000 ha. of eucalypt plantation with annual plantings of 70 000 ha. In contrast Australia had only 30 000 ha. of eucalypt plantations. South Africa has a large number of

private plantations and commercially eucalypts are becoming increasingly important. At present over 500 000 ha of eucalypt plantation have been established (Poynton 1981).

Owing to the relatively low priority which eucalypt planting in Australia has had in the past, as compared to exotic conifer establishment, relatively little progress has been made in eucalypt breeding. In the last decade there has been a resurgence of interest in planting eucalypts for purposes such as rehabilitation and conservation as well as production of timber and pulp. As a result, interest in breeding eucalypts has also grown.

The value of tree breeding in plantation wood production is high. Tree breeding plays an important role in producing trees with desirable traits and in obtaining higher yields from eucalypt plantations. This is achieved through the provision of genetically improved seed from the best provenances of eucalypts. (Eldridge 1978a). The gains achieved can be impressive. Ades and Burgess (1982) showed that the average relative volume of the open pollinated progenies of 20 plus trees of *Eucalyptus grandis* Hill ex Maiden, selected in plantations near Coffs Harbour, N.S.W., was 54% larger than that of a local routine seed lot collected from a natural stand. Davidson (1981) notes that early stands of eucalypts in the Congo produced about 12 m³/ha/yr to age 6 years. Selection of good provenances of *Eucalyptus urophylla* S.T. Blake has raised

production to over 25m³/ha/yr. In Brazil it is claimed that a 100% increase has been obtained in the volume growth of eucalypt plantations over the last decade, through selection of improved genetic material from Australian and other provenance sources, combined with intensive cultural treatments (Davidson 1981, Brune and Zobel 1981).

BASIC STEPS IN TREE BREEDING.

Eucalypt breeding, while similar in principle to breeding of cereal crops, is complicated by the long generation span of most species. It is important therefore, that much thought and deliberation should go into planning a tree breeding program, since errors of judgement may have long lasting effects. Prior to becoming involved in an expensive tree breeding program for a given species or number of species, a review of production objectives is necessary and several questions must be answered. These include (1) How important are the species in question to achieving the desired objectives? (2) Are there alternative species better suited to the job? (3) Is a breeding program economically or biologically justifiable? i.e. does the genetic gain which can be obtained in a species warrant the time and expense of a breeding program? (4) Could objectives be met simply by defining a good seed source?

A tree improvement program can be divided into two

3.

broad stages. The first being an investigation and information gathering stage and the second incorporating the actual tree breeding. In order to answer the above questions the first stage investigations are initiated. Within this stage, trials aimed at determining the best species and provenances for use in a breeding program are established. Details of sexual reproduction, genetic factors such as heritability of traits, juvenile - adult correlation, genotype x environmental interaction and gain from selection are established (Wilcox 1980). It is also necessary to have knowledge on the feasibilities of different breeding techniques such as grafting or controlled pollination.

Such information is also used in choosing an optimum breeding strategy. The breeding strategy is a scheme for efficiently managing the various parts of a breeding program within available financial, staff and biological constraints. With the initial stage completed, the second stage of tree breeding can begin. Outlined below are the various stages which may be involved in initiating a tree breeding program.

Species Trials

Basic to any forest plantation scheme is the selection and trial of potential plantation species, in the environmental conditions in which the new plantation is to be established.

The primary objective of these trials is to eliminate species which show little promise, in order that more comprehensive testing on a reduced number of species can be carried out. This second phase usually involves the establishment of provenance trials, in which a wider range of provenances are tested on several sites, for each species (Turnbull 1978).

Care must be taken in the selection of seed for primary species trials. If for example seed was collected from only one locality, it may prove to be a very poor indication of the potential of the species. Ideally, for an unknown species, several provenances should be tried. Turnbull (1978) lists three categories of provenance which should be included. (1) Where the species reaches its finest development, (2) part of the range which matches the new conditions, (3) marginal sites.

Provenance Trials

Where there is some indication from species trials that a species may be of value on a particular site, but the full extent of variation within that species is unknown, range wide provenance trials may be established. Such trials should include many seed sources widely scattered throughout the existing range.

The system of sampling which is used to choose

localities depends largely on the natural distribution of the species and any existing knowledge about variation patterns.

When a species is being sampled for the first time 'Coarse Grid' sampling (Turnbull 1978) or sampling at widely spaced intervals can be used. The aim is to determine the major features of distribution patterns by exposing genetic differences between populations. Delineation of provenance in eucalypts may often be difficult. Boland (1978) observes that in natural stands, eucalypts often occupy distinct ecological sites. If all sites are small and discontinuous, then the term provenance may be synonymous with site and defined naturally. Defining provenances of eucalypts with a continuous distribution is difficult and may be arbitrary.

Sampling schemes should include populations on the outer limits of a populations range. It is likely that in these situations a species may be subject to extremes of temperature rainfall and edaphic conditions and hence possess genotypes of considerable potential in some environments, despite the likelihood of these stands being phenotypically poor. Once a particular provenance or set of provenances are proven to be most suited for planting in a given area, then selection for superior or plus trees to be incorporated into a breeding program can be done.

Selection of Seed Stands for Provenance Trials

The stand from which seed is to be obtained should be sufficiently large to allow adequate cross pollination, while being isolated as far as possible from related species, to minimise the risks of hybridisation. The history of the stand may be of considerable importance in determining whether the stand is representative of the provenance. For example, if a stand has been selectively thinned to remove the best phenotypes for sawlogs, then it may be inadequate for seed collection purposes. Ideally the stand selected should have a good chance of remaining untouched, so that it can be used for future seed collections if the provenance proves to be of value.

Selection of Individual Seed Trees

Individual trees for seed collection are selected within the seed stands. Turnbull (1978) lists three main factors to consider.

(1) The number of trees to be selected. It must be determined for each provenance how many trees are going to form a representative sample. This will depend on the range of the species and the size of a provenance. If a species has a very wide range, then it may not be feasible to collect from a large number of trees per provenance.

(2) Type of Trees. Turnbull (1978) does not recommend that trees of better than average phenotype be selected for provenance trials as the sample would be biased and represent only a proportion of the variability. It would be better for seed to be collected from a wide variety of trees representing the whole range of phenotypic expression on a site.

An opposing view however, is that considerable time may be saved by selecting the best trees in a provenance to collect seed from. This will still give an indication as to which provenance or provenances are superior. If family identity is maintained in the trial, individual parent trees from each provenance can be ranked for progeny performance. Selection of plus trees for inclusion in a seed orchard is then simply a matter of picking the best trees from the best provenances, according to the ranking indicated by data obtained from the trial. Two problems which may arise are 1) A superior phenotype in its home environment may not perform well in a new environment. ii) There may be difficulties in selecting superior genotypes in unevenaged forests.

(3) Distance between trees to be sampled. This is important in avoiding selfed or half sib seed, the collection of which, would not give a good representation of genetic variability within a provenance.

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(4) Time of collection of seed is also of importance. It is desirable to collect seed when there is a good seed crop on the majority of trees. The advantages of this include (a) less chance of inbreeding (b) viability of seeds is likely to be high (c) a wide choice of trees to select from (d) shorter and more efficient collecting time. Even in a good year however, a species may not produce good seed crops throughout its entire range. In this case it may be necessary to store seed until a complete collection can be made. Maintenance of the identity of individual trees permits study of genetic variation within and between populations.

Once the provenance trials have been measured for rate of growth, form and height, the data can be analysed and superior provenances determined. Following this, the second or major stage of the program can begin. This stage involves the selection of plus trees followed by their incorporation into the breeding program.

Phenotypic Expression.

Phenotypic variation observed in the field may be caused by three main factors. These include genetic differences between individuals, environmental differences and occasionally genotype x environment interaction. The breakdown of observed variation into its components is often done by analysis of variance. Thus observed Phenotypic variance (V_P) is composed

of three main sources of variation: genotypic (V_G), environmental (V_E) and interaction (V_{GE})

$$\text{i.e. } V_P = V_G + V_E + V_{GE} \quad (\text{Equations taken}$$

from Strickberger 1976.)

V_E The environmental variance may include growth in different localities or different years, variation in soil fertility, soil structure, drainage, ashbed effects, disease and insect attack. Transient factors may include fire, flood, and drought. Overhead competition from older trees can result in poor phenotypic expression from an otherwise good genotype, particularly in crown sensitive species.

V_{GE} Genotype x environment interactions occur when genotypes act differently in different environments. In practice this may be expressed as different ranking of families when they are grown in different environment.

V_G Genotypic variance may be caused by genes producing additive effects (V_A), dominance effects (V_D), or genes producing epistatic or interaction effects (V_I). (See glossary).

$$\text{i.e. } V_G = V_A + V_D + V_I$$

$$\text{and } V_P = V_A + V_D + V_I + V_E + V_{GE}$$

Most breeding programs are concerned with selection for traits which result from the additive effects of genes. Selection for non - additive traits caused by dominance or epistatic effects is difficult.

The genes which comprise a tree's genotype are responsible through various reactions, for organising and directing materials obtained from the environment into the growth of the tree. Hence a tree's phenotype is the result of interaction between its genotype and the environment.

It should not be assumed therefore that a given phenotype whether good or average is purely the product of its genotype. The environmental variation that exists and changes which have occurred over time all influence the phenotypic appearance of a tree. Genotype x environment interaction is also an important factor which is often overlooked or ignored.

Selection of Plus Trees

Once the best provenances of a particular species are chosen, either seed may be collected and used to create a new base population or the provenances themselves may be used as a

base population. It is within the base population that plus trees are selected. This is an important job since the trees selected, start the pedigreed lines of selection over several future generations. Plus trees are selected for their superiority over neighbouring trees, usually in several characters such as stem straightness, branching, height, frost tolerance and disease resistance. The characters used in selection are dependant on the objectives of the breeding program.

By necessity, plus trees are selected on the basis of their superior phenotype. The genotype of plus trees is not known until they have been subjected to progeny testing, to establish their value as parents for a breeding program. It is usually better to carry out plus tree selection in even aged forests e.g. plantations, where every individual has had the same silvicultural treatment and similar levels of competition. Plus tree selection in wild or unevenaged forests is complicated by factors such as those discussed under environmental variance and for those reasons may be less desirable. However, in the initial stages of a breeding program the only option may be to make selections from wild stands. Subsequent generations of plus trees may be selected from plantations or breeding populations produced from the original plus trees.

It is necessary to know prior to starting the selection, exactly what character or characters are to be selected for. It is the usual practice in forestry to select

for more than one trait at a time i.e. multiple trait selection. This can slow the progress made in a breeding program since increasing the number of characters selected for, decreases the efficiency of the selection (Eldridge 1978a). It is worthwhile at this point to examine the principles underlying selection.

The aim of most breeding programs is to maximise genetic gain. The general formula for genetic gain is $\text{Gain} = \text{Selection differential} \times \text{heritability}$ (Wright 1976). To increase gain a breeder must increase one or both components. Heritability is dependant on how closely the phenotype resembles the genotype and hence how closely off spring will resemble the parents. This is difficult to manipulate so efforts are generally concentrated on increasing selection differential (S.D.).

S.D. is the difference between average and selected trees, families or clones. For example if a stand has an average height of 20m and selected trees are 22m tall, the S.D. is 2m or 10%. S.D. is often expressed in terms of standard deviation. The idea in selection of plus trees is to achieve the highest S.D. practicable. S.D. is a function of the number of trees selected and the number of trees from which selections are made. The greater the ratio of trees observed to trees selected, the higher the selection differential. The nature of this relationship is essentially logarithmic. To increase the

S.D. becomes increasingly more costly in practice, as the area or number of trees to be searched increases in dimension logarithmically for a given amount of increase in S.D. (Shepherd 1978). See figure 1.

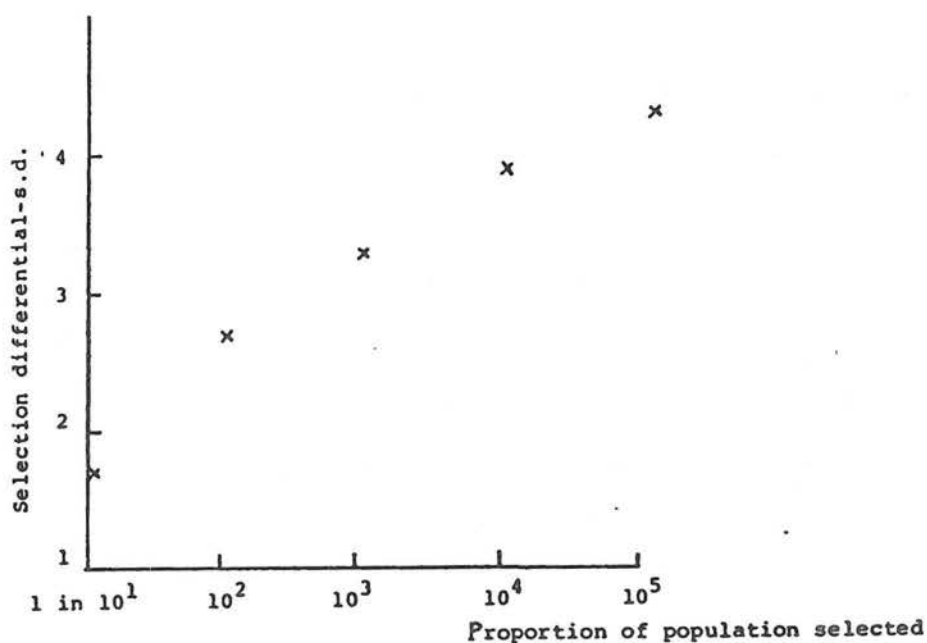


Fig. 1 Showing relative gain in selection differential with proportion of population selected. (Taken from Sheperd 1978)

Thus there is a practical limit to the size of the S.D. If, as already pointed out, selection is to be based on more than one character at a time, the issue becomes complicated with regard to S.D. for each trait. In order to maintain the same efficiency or standard of selection, the number of trees to

be examined in an infinite population is multiplied many times as each additional character is added to the program. In a finite population however, it is not possible to increase the number of trees examined, and the S.D. for each trait will decrease, since the number of trees searched relative to the number of characters selected for does not increase.

Eldridge (1978a) gives an example of how the efficiency of selection falls with each additional character specified;

If the standard of selection is the best 1 percent

For <u>one</u> character	100 trees need to be examined
When <u>two</u> unrelated characters are sought together	10 000 trees need to be examined
<u>three</u> unrelated characters are sought together	1 000 000 trees need to be examined
<u>four</u> unrelated characters are sought together	1 000 000 000 trees need to be examined

There are three main methods which may be used for the purposes of multiple trait selection as listed by Eldridge (1978a):

(1) Tandem Selection This involves the improvement of one

character at a time over successive breeding generations. This method is unsuitable for forest trees owing to their long generation intervals.

(2) Independent Culling Levels Here a level of merit for each character is established. A candidate tree not meeting requirements in one character is rejected regardless of the suitability of other characters.

(3) Selection Index This provides an objective method which weighs characters in a systematic manner, taking into account 1) the relative economic value of each character, 2) Genotypic and phenotypic variances of each character, 3) Genotypic and phenotypic variances between each pair of characters considered. This method is often difficult to use owing to lack of knowledge of economic weights and genetic parameters. A point score system is a more commonly used method of constructing a selection index. In such a system, each character being assessed is awarded a score out of 5 for example, and a trees merit recorded relative to other trees on the same site. The weakness of such scoring systems is that points are allocated by subjective decision.

Progeny Testing

As discussed earlier, phenotype is the expression of the interaction of genotype x environment. Simple observation of a phenotype gives no true indication of the relative influences exerted on the phenotype by the genotype, as compared to the influence exerted by environmental or site conditions. For example, a tree of superior phenotype within a stand of trees may be the only individual to have germinated in an ashbed and reaped the beneficial effects. Obviously in considering a plus tree for use in a tree breeding program, the tree breeder wishes to know what proportion of the phenotype is due to inheritable genetic characters as against non-inheritable site factors.

The way in which this is determined is to test the performance of the progeny of each plus tree, in an environment in which all provenances are grown under the same conditions. The higher the proportion of the phenotypic variance that is due to genetic variance rather than environmental variance, the higher the heritability, and the more the progeny resemble their parents.

i.e. heritability = $h^2 = V_A/V_P$ (from Strickberger 1976)

If progeny of a given plus tree perform poorly, it is a good indication that the superior phenotype of the parent was largely due to local environmental factors and not good genotype. Such

trees would be dropped from a breeding program.

The advantage of basing plus tree selection on progeny performance (family selection) as against simple selection based on phenotype (i.e. simple mass selection) are demonstrated in the following diagrams taken from Wright (1976).

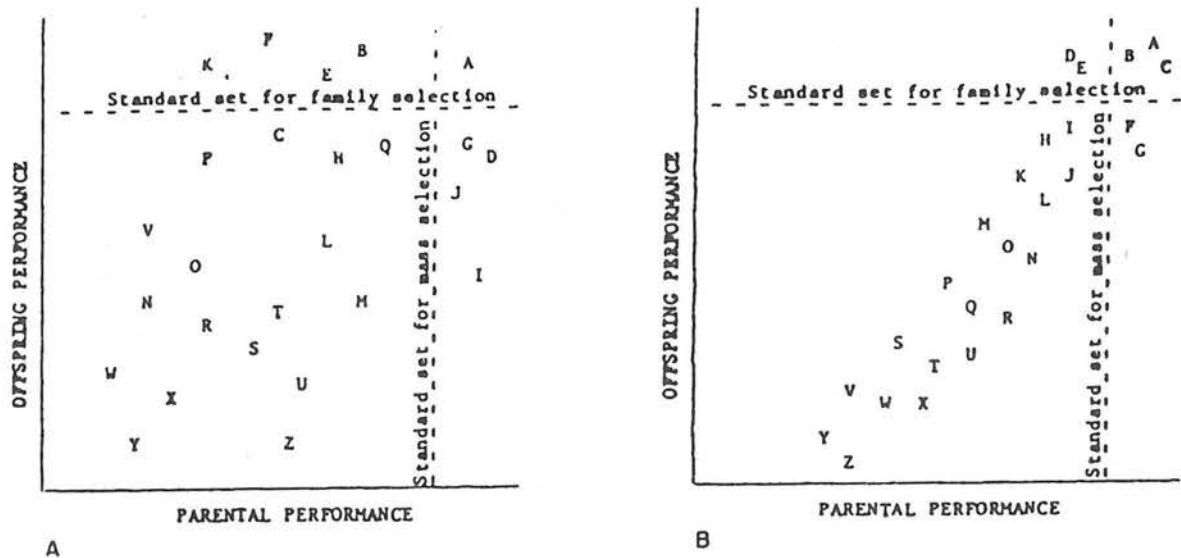


Fig. 2 Differences between mass and family selection with low heritability (A) and high heritability (B). Taken from Wright 1976.

Figure 2A illustrates a situation in which heritability is low. There is little correlation between parental performance and offspring performance. If the tree breeder was selecting purely on the basis of phenotype (i.e. mass

selection), he would choose parents A D G I and J as being to the right of the dashed line marked 'standard set for mass selection'. A slight improvement would be obtained, as the offspring of these parents are slightly above average. If the breeder selected on the basis of offspring performance, he would choose parents A, B, E, F and K as being above the line marked standard set for family selection. The gain would be much greater.

In figure 2B it is assumed that heritability is high and there is a very strong correlation between parent and offspring. A breeder practicing mass selection would choose parents A B C F and G. If selection was made on the basis of progeny performance, parents A B C D and E would be chosen. There would be relatively little difference between the two selection methods.

Types of Progeny Test

There are two basic types of progeny tests (Matheson 1978).

1. Open Pollinated Tests In these tests the female parent is known but the male parent is unknown. The resulting progeny may be any one of, or a mixture of full sibs (i.e. with the same parents), half sibs (only one parent the same) or the result of self pollination (selfing). Open pollinated progeny tests are

used as relatively cheap, quick tests from which a reasonably accurate estimate of general combining ability (G.C.A.) can be made. G.C.A. is the ability of a superior parent tree to produce superior offspring when mated with average trees. G.C.A. effects are due to the additive effects of genes. Once the G.C.A. for plus trees is determined they can be ranked in order of decreasing G.C.A. This ranking is a valuable tool in selecting trees for use in breeding programs, since maximum gain is achieved by mating together trees with the highest G.C.A. for desired characters.

Some caution is required when using open pollinated progeny tests to estimate G.C.A.'s. This is due to uncertainty as to the identity of male parents. Shelbourne (1969) notes that it must be assumed that the progeny are half sibs or the number of pollen parents is infinite, and that for different parent trees located in different parts of the forest, the same pollen spectrum is being sampled. The larger the number of male parents that pollinate the female flowers on the parent trees, the better the chance that the pollen will be a good genetic sample of the population. Thus because of possible differences in pollen spectra and numbers of male parents represented, the use of open pollinated seed is liable to induce bias into G.C.A. estimates.

Control Pollinated Progeny Tests - or full sib tests. These are better for estimating genetic parameters because the male

parent of each progeny group is known. A disadvantage of control pollinated tests is that they are more expensive than open pollinated progeny tests owing to the size required and the necessity of controlled pollination. Accurate estimates of G.C.A. and specific combining ability i.e. a trees ability to transmit superiority to its offspring when crossed with a22.

specific tree rather than with trees in general, can be made. In addition, estimates of heritability and genetic gain expected for selection between the plus trees can be made. These parameters are important in designing an efficient tree breeding strategy.

Breeding Methods

The breeding method is the means by which a breeding strategy is implemented. The method chosen may be dependant on a number of factors, for example, economic constraints, availability of skilled staff, characteristics of the species being bred. Breeding methods may be planned to continue for several generations or only one. A simple method may be chosen initially and then displaced by a more complex one. Brown (1978) lists three main categories of breeding methods. These include (1) Selection with regeneration through seed (2) Selection with mass clonal propagation (3) Hybridisation of

species or provenances. These broad categories can be further subdivided.

1.0 Selection of Plus Trees with Regeneration Through Seed

1.1 Simple Mass Selection

With this method, desirable individual trees are chosen and their open pollinated seed collected and bulked, without a progeny test, to produce the following generation. Selection is thus based on female parent phenotype only. The original superior (plus) trees are harvested for seed continually. This method is somewhat dead ended as it leaves no room for further improvement of stock.

1.2 Recurrent Mass Selection

This involves the same principle as Simple Mass Selection except that subsequent selection and seed collection is eventually carried out within the progeny of each generation of superior trees. This method is cheap and can be quite effective where the selection differential is large and phenotypic selection is accurate i.e. phenotype corresponds closely to genotype. The method has proved ineffective in areas where heritability is low (Shelbourne 1969).

1.3 Selection and Simple Progeny Testing

Recurrent Mass Selection combined with progeny testing can help overcome some of the deficiencies of Recurrent Mass Selection alone. Here open pollinated progenies of select trees are grown in a progeny test and later, on the basis of the measurements in the test, only the best trees in the best families are retained and seed is collected from them. Such a process involves family selection i.e. removal of poorer families.

1.4 Simple Recurrent Selection (Shelbourne 1969)

Desirable genotypes are selected on the basis of their own phenotype and are intercrossed without restriction to produce populations for the second cycle of selection. This process is different from Recurrent Mass Selection in that both male and female parentage is select. For given intensities of selection the genetic improvement expected will be double that for Recurrent Mass Selection.

Using this method, plus trees are selected and propagated in a clonal seed orchard. The harvest of the seed represents a single cycle of Simple Recurrent Selection. Within the clonal seed orchard, clones are allowed to inter-pollinate randomly in the seed orchard and the seed produced is used to

establish plantations from which the next cycle of selection is made. As with Recurrent Mass Selection, no test crosses are made, so Simple Recurrent Selection is only efficient for characters with heritability high enough to make accurate selection for a superior genotype from phenotypic evaluation.

1.5 Recurrent Selection for General Combining Ability (Shelbourne 1969)

In this method, superior trees are selected on the basis of phenotype in the forest, and propagated vegetatively in an orchard or clone bank and progeny testing then carried out. Seed for progeny tests is collected from the open pollinated selected parent trees or alternatively from controlled crossing in the orchard to generate half sib families, or a group of full sib families from which G.C.A. can be estimated. As previously discussed, problems arise in using open pollinated seed for estimates of G.C.A., so controlled pollination is the better alternative. On the basis of progeny test results, the best clones can be retained in the orchard with the remainder being removed. Alternatively a new orchard containing only the best clones can be established.

Selection of a breeding method for eucalypts will depend in part on the finance available. Breeding methods which involve controlled pollination may be unsuitable owing to the

difficulties and expense of emasculating flowers. Davidson (1981) suggests that the difficult and laborious methods required for controlled pollination of eucalypts and the present scarcity of information on genetic parameters, are likely reasons for the lack of establishment of control pollinated seed orchards in most eucalypt breeding programs throughout the world. Of the above methods, perhaps method 1.5 using only the open pollinated seed for progeny testing would be suitable for most budgets.

2.0 Selection, With Mass Clonal Propagation and Clonal Testing

This method involves phenotypic selection of plus trees combined with progeny testing. Trees of superior genotype can be cloned en masse for commercial use. This is a high gain procedure but may lead to a dead end in terms of increased gain unless a crossing program is included to produce new selection material.

Cloning by use of cuttings of genetically improved and other desirable individuals on a commercial scale, has only become possible in recent years due to advances made in the production of Eucalypt cuttings. Davidson (1981) observed that in the Congo over 3 000 ha of plantation area had been established with cuttings by 1980. At Aracruz in Brazil, one

million cuttings had been planted in 1979 and five million in 1980.

Tissue culture offers an alternative method of vegetatively propagating eucalypts and has several advantages over cuttings, (1) the multiplication rate is usually greater, (2) pests and diseases are not a problem during culture and (3) the techniques are more reliable as greater control of physical and chemical factors can be achieved (Hartney and Barker 1980). The cost of this method of propagation is not necessarily greater than the cost of propagation by cuttings. Hartney and Barker (1980) suggest four reasons (1) the cost of the media is small (2) once the cultures are established, virtually no maintenance is required between sub-culturing (3) a large number of cultures can be maintained in a small area (4) the cultures can be grown in simple controlled environment facilities such as a shaded glasshouse or a low light intensity room.

Techniques for tissue culturing Jarrah (*Eucalyptus marginata* Donn ex Smith) have been developed by Bennett and McComb (1982).

3.0 Hybridisation of Species or provenances

Hybridisation occurs naturally between some species of eucalypt within the same subgenus. Examples of this include the

hybrid found by Pryor and Johnson (1962) between *E.marginata* and *E.megacarpa* F. Muell (Bullich). Hybridisations of this nature may result in offspring which have desirable attributes of both parents, a feature known as hybrid vigour. If a hybrid between *E.marginata* and another species could be developed, which incorporates the desirable attributes of *E.marginata* together with resistance to the 'dieback' fungus *Phytophthora cinnamomi* Rands, it may have considerable potential for use in rehabilitation of areas badly affected by dieback. Until the recent development of mass production techniques, the use of superior hybrids in plantations has been minimal. The reasons for this are that the progeny of hybrids often display characters which range between the character means of the two species involved in the cross. Such hybrid breakdown is usually accompanied by some genetic degrade.

Basic Outline of a Tree Breeding Program

The type of breeding program in which one of the above breeding methods may be incorporated are generally of an ongoing nature. Initially a base population is selected, from which the breeder picks plus trees. These individuals are used to generate an expanded breeding population in which both genetic recombination and population size are maximised, to afford the greatest potential selection differential for the next round of selection (Brown 1978). An immediate gain may be achieved by

cloning these plus trees to form production populations until superior lines can be generated for the next generation. The basic features of such a breeding program are illustrated in figure 3.

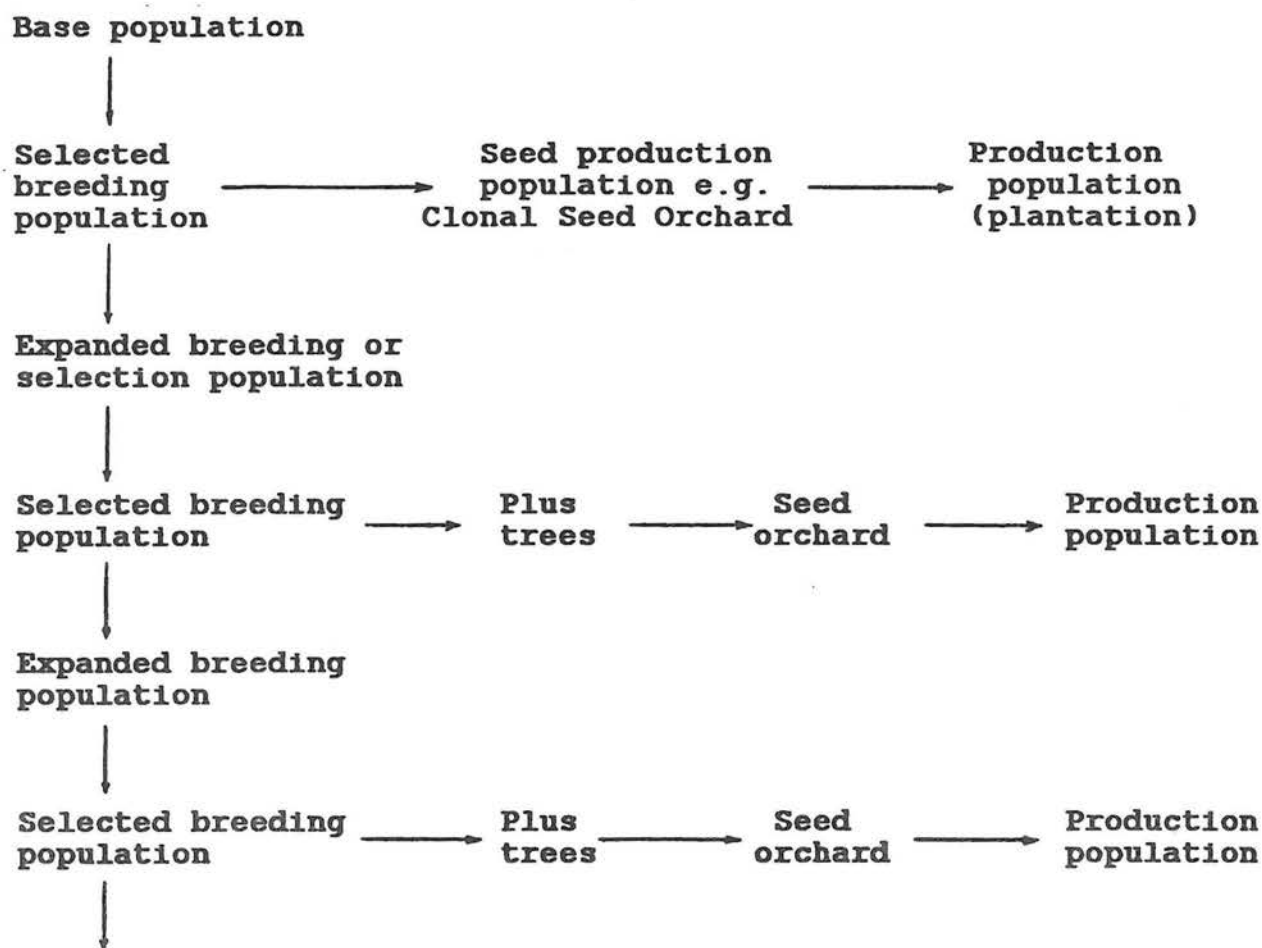


Fig. 3 Basic features of a breeding program. (Adapted from Brown 1978).

A more complex program incorporating the use of clones is presented by Nikles 1974 (from Brown 1978) in figure 4.

Size of Base Population

The size of the base population and the number of plus trees selected from it is of great importance. The use of seed from one or a small number of plus trees is undesirable for several reasons:

- 1) Many useful alleles in the base population may not have been included in the sample taken. Hence the sample may not be a suitable population from which to establish a tree improvement program (Eldridge 1978b).
- 2) Plantations with a narrow genetic base are likely to be more susceptible to pests and disease than one based on a large number of unrelated parents. This may be a problem with plantations produced by mass clonal propagation using only a few clones as the base population.
- 3) The quality of tree produced from successive breeding populations of closely related individuals may be significantly reduced in terms of form and vigour, due to the effects of inbreeding depression. A classic example of this situation occurred in Brazil (Brune and Zobel 1981). Here, eucalypt seed from what is known as the 'Brazil Source' was used for seed production areas and seed orchards. Stands derived from this source have many problems stemming from hybridisation and resultant 'hybrid

breakdown' and from inbreeding, since the original stands contained a limited number of parents.

As to the actual size of the base population Brown (1978) suggests that it should contain more than 10 000 individuals while the selected breeding population should consist of at least 50 effective unrelated individuals. This is quite a small number however and 300 unrelated individuals would be better.

Multiple Populations

One of the problems confronting tree breeders in any of the above classical approaches to tree improvement is that they do lead to a narrowing of the genetic base within only a few generations. It is therefore necessary to have a program for introduction of new genetic material in the form of clones or seed. The problem with this is that the introduction of unimproved genes to a breeding population, may result in a temporary lowering in the performance of the improved population .

An alternative to the classical scheme is the use of a multiple population breeding strategy (Barnes 1984). In this strategy, separate populations are maintained or created to grow in different environments or to produce trees with different

combinations of traits. Such a system could be set up using empirical data on genotype x environment interaction (G.E.I.) from provenance trials and species trials. A primary objective is to maintain or create diversity between the populations while applying heavy selection pressure within them.

The major advantages of such a system are (1) genetic variability may be replenished easily by crossing between populations, without having to accept the large reductions in performance, which may result from crossing with unimproved gene pools. (2) The system facilitates full exploitation of G.E.I. for maximum gain in a range of environments. (3) Potentially valuable genes with no immediate priority may be conserved in separate populations for future use.

THE EFFECT OF EUCALYPT BREEDING SYSTEMS ON BREEDING PROGRAMS

Selfing

In the past, breeding programs have been planned on the assumption that eucalypts are predominantly out-crossing and that levels of inbreeding are similar to those found in pines. In many species of the Pinaceae, self fertilisation is only 5 to 10% and abortion of selfed zygotes is 90% due to high levels of embryonic lethals. Selfed seedlings suffer severe inbreeding

depression (Eldridge 1978b). The implication of this is that selfing in these members of the Pinaceae can largely be ignored when planning a breeding strategy. Recent research by several authors (e.g. Phillips and Brown 1977, Moran and Brown 1980, Hodgson 1976) have yielded estimates of selfing in nine different eucalypt species, at an average of around 30%. In addition there is evidence that selfed zygotes and seedlings have higher survival rates than those of conifers. Considerable variation in levels of self fertility between individuals of a species was found by Griffin (1980a). Compounding this, is an indication of significant variation between parents, in the inbreeding depression displayed by their progeny.

These finds have implications of great importance in tree breeding strategies.

(1) In planning an optimal tree breeding strategy it is necessary to have accurate estimates of genetic parameters (e.g. additive and non additive genetic variance, phenotypic and genotypic correlations between characters selected) in order to predict gain from alternative strategies and hence to choose the best strategy (Eldridge 1978b). Thus if high levels of inbreeding exist in eucalypts, then it is obviously inappropriate to ignore it as can be done with some of the conifers. This is because high levels of inbreeding will yield inflated estimates of genetic gain. It follows that such estimates may lead to the erroneous selection of sub optimal breeding strategies.

(2) Variable levels of inbreeding may cause problems in interpreting family variation data (Griffin 1980a). This may be counteracted to some degree by using seed collected from a large number of parent trees per provenance.

(3) High levels of inbreeding will influence choice of breeding population size and seed orchard design (Eldridge and Griffin 1983). The size of the breeding population may need to be increased in order to achieve levels of gain predicted from smaller populations in which no inbreeding occurs. If selfing is prevalent in seed orchards, the plus trees may have reduced opportunity to display the high general combining ability they were selected for.

(4) Further problems arise in the nursery, where conditions are maintained to ensure minimum seedling mortality. Such procedures also ensure that a large proportion of the selfs which may otherwise be selected against in the field, survive to be planted in a plantation situation (Eldridge and Griffin 1983). Attempts to eliminate selfed seedlings by heavy culling in the nursery may not be very effective. Observations by several authors (Eldridge and Griffin 1983, Hodgson 1976 and van Wyk 1981) indicate that inbreeding depression is expressed only gradually over several years. For example, Eldridge and Griffin (1983) found only slight differences between selfed and outcrossed families of *E. regnans* F. Muell in the first two years of growth. It was after five years growth that highly

significant differences between families in survival, height and diameter were recorded. This is an important management problem. If a species is important and seedlings are being raised in any number as are for example *E. diversicolor* F. Muell (Karri) and *E. wandoo* Blakely (Wandoo), it is necessary to know if nursery culling is effective in eliminating some of the selfed seedlings. Further work is required in this area.

(5) Another problem arising from selfing is that of lowered seed yields. Loneragan (1979) found that artificial selfing of karri flowers gave an average yield of 0.67 seeds per capsule, while on the same tree, outcrossing of flowers yielded an average of 0.96 seeds per capsule. Artificial outcrossing of flowers on a separate tree yielded an average of 4.03 seeds per capsule.

Factors Affecting Levels of Selfing

Individual Flower Development

Eucalyt flowers are hermaphroditic and usually occur as members of an inflorescence. Considering their hermaphroditic nature, it might be expected that a high degree of self pollination of individual flowers would occur. Eucalyt flowers however, are generally considered to be protandrous (Pryor 1976), which would tend to minimise the chances of self

pollination. For example, Griffin and Hand (1979) found that in *E. regnans*, pollen was shed from the day of operculum opening, while stigmas are not fully receptive until ten or more days later. Although protandry may minimise such self pollination, it must be ineffective against pollination between flowers on the same tree (geitonogamous pollination). Griffin (1980a) observed that flowers within single inflorescences of *E. regnans* may open over a size day period and those on the same branch over fourteen days, allowing ample opportunity for pollination to occur. Pollination ecology is likely to play an important role here. Eucalypts in general have relatively unspecialised flowers (Moran and Griffin 1980) and are vector pollinated. It is likely that insects, birds and small mammals may all act as pollen vectors (Griffin 1982). Griffin (1980a) observes that *E. regnans* is in the main insect pollinated and suggests that vector behaviour pattern is likely to result in a high frequency of geitonogamous pollination.

Phenology

When considering the effects phenology may have on levels of selfing within a species, the factor of major interest is the synchronisation of flowering times. The greater the synchronisation of flowering times between individual trees, the greater the potential for interbreeding. Different species of eucalypts show considerable variation in flowering times (Moran and Griffin 1980). In some species the peak flowering season

may be regular, whereas in other species, flowering occurs intermittently throughout the greater part of the year.

Observations by Ashton (1975) showed that the flowering season in a population of *E. regnans* at Wallaby Creek (Victoria) varies from 2.5 to 4.5 months with as much as 3 to 4 weeks fluctuation in starting and finishing times. Griffin (1980b) showed that within a stand of *E. regnans*, the population tended to be divided into groups of trees with similar flowering times. Within this stand it was found that even in a heavy flowering year 15% of the trees were excluded from the breeding population as they did not flower at all, and 8.2% of potential crosses between flowering trees could not have occurred because of complete temporal isolation.

The main problem arising from this for tree breeders is that of creating a seed orchard in which all trees have closely synchronised flowering peaks. This may prove difficult since trees involved may have originated from widely separated provenances and potentially have considerable phenological variation. Out of phase flowering in a seed orchard means that the number of possible intercross combinations will be reduced and the relative proportion of selfing will be increased. Careful selection of trees with regard to flowering times may be a necessary step towards reducing this problem.

Means of Reducing Selfing Effects

(1) Reduce the proportion of fertilisations by related gametes. This may be achieved by using seedling or clinal seed orchards comprised of many unrelated individuals. Inbreeding effects are minimised by ensuring each between tree vector flight occurs between non-relatives. It may be necessary to ensure that a pollen vector is present. This can be done by introducing bees to a seed orchard at time of flowering.

(2) Selection of self incompatible trees for use in seed orchards. The work of Griffin (1980a) and Eldridge and Griffin (1983) indicates that it is possible to screen a tree for its self fertility and hence select trees for use in seed orchards which have low levels of self fertility.

(3) Collection of seed following years of heavy flowering, since seed from trees flowering in spatial or temporal isolation is bound to have the greatest proportion of self fertilised seed. (4) Delayed collection of seed. Data on levels of outcrossing in seed collected from three successive crops in *E. delegatensis* R. Baker indicated variation from 66% in the youngest crop, increasing to 85% in the oldest crop (Moran and Brown 1980). One theory ventured forward to explain this was differential viability of inbred as opposed to outcrossed seed since fertilisation events in the oldest crop i.e. the inbred more homozygous seed may have a lower viability than

the more heterozygous outcrossed seed and hence be selected against while still within the seed capsule. Thus collection of seed from older crops may result in a higher proportion of outcrossed individuals being collected while minimising the change of obtaining inbred seed.

EUCALYPT BREEDING OVERSEAS

The natural occurrence of eucalyptus species over a wide range of habitats, combined with rapid growth, good form, favourably woody properties and generally good fuel wood characteristics, makes many species of eucalypt attractive for growth in exotic plantations. Eucalypts are currently planted in several countries including Brazil, U.S.A., Africa, Israel, France and New Zealand. In the majority of cases, plantations were established using seed from unknown and often inferior seed sources, with the result that attempts at improvement were often thwarted due to high levels of inbreeding and hybridism. This has to some extent set back the progress of tree breeding programs, with many countries still involved in the initial stages of species and provenance trials (Davidson 1981).

Objectives in different tree breeding programs may vary and hence the emphasis as to which characters are selected for, may vary from program to program. Selected characters common to many breeding programs include straightness, branching

character, vigour, woody quality - including wood density and grain straightness. Other more specialised characters which have been selected for include freedom from splitting, frost tolerance, salt tolerance and resistance to disease and pests. These will be reviewed briefly.

Freedom From Splitting

South African tree breeding programs were initiated, largely due to problems with low recovery from sawn boards. Freedom from end splitting on felling, as well as fast growth and stem straightness, were used as the main selection criteria (Van Wyk 1977). Plus tree selection involves visual phenotypic assessment as well as taking of wood samples of all selected trees for assessment of density and radial tangential and longitudinal shrinkage. Clones of selected trees are established in tree banks for experimental purposes and in seed production orchards.

Frost Tolerance

Frost tolerance is an important character in many countries where plantations may be subject to repeated, or intermittent but nonetheless lethal frosts. Extensive provenance testing of different species has been carried out

within different countries to establish the best species and provenances for use. Some species of interest include *Eucalyptus nitens* (Deane and Maiden) Maiden and *E. grandis* Hill ex Maiden in South Africa and Zimbabwe (Darrow and Roeder 1983, Nixon and Hogedorn 1983, Mullin et al 1983). Species undergoing trials in various parts of the U.S.A. include *E. camaldulensis* Denh., *E. dalrympleana* Maiden, *E. grandis* (Ludig 1983, Jahromi 1983, Hunt and Zobel 1978). Considerable work has been done in New Zealand by Wilcox et al (1980) on provenance variation with regard to frost tolerance of *E. regnans*. The outcome of these trials generally, has been to show up variation in frost tolerance between species and differences in tolerance between provenances within species. In France frost tolerance work has been taken a step further through the use of tissue culturing to mass propagate eucalypt clones selected for their wood yield and their cold resistance (Poissonier et al 1983).

Salt Tolerance

Breeding trees for salt tolerance is yet at the early species and provenance trial stage and there remains much work to be done. Kaplan 1983 outlined work of an exploratory nature carried out in Israel on the salt tolerances of *E. camaldulensis* and *E. occidentalis* Endl. Significant variation was found. For example *E. camaldulensis* provenances

from Lake Albacutya (Vic) tolerated twelve months of flooding in tap water containing 4 500 ppm NaCl whereas provenances from Katherine (N.T.) and Wyndham (W.A.) could only tolerate the same saline flooding treatment for four months each.

E. occidentalis was found to have a lower salt tolerance although this was greatly improved by the presence of CaCO₃.

Disease Resistance

Breeding for disease resistance overseas has to date received relatively little attention, possibly due to a lack of indigenous organisms and the appropriate environmental conditions to enable disease to become a problem on eucalypts planted as exotics. However, in Brazil susceptibility of *E. grandis* to canker caused by *Diaporthe cubensis* has been recognised as a limiting factor in effective establishment of the species (Silva and Justo 1983). Heritabilities for resistance of 0.65 and 0.77 in two localities (Borges and Brune 1983) indicated that a breeding program to develop resistance trees is justifiable.

Breeding for resistance in eucalypts may present problems in the long term owing to the longevity of the crop and the nature of many host-pathogen relationships. Research on Canker caused by *Cryphonectria cubensis* (Bruner) Hodges on *Eucalyptus* spp. (Alfenas et al 1983) showed the existence of

host specific pathogenicity for *C. cubensis* isolates on Eucalyptus spp. and variation in levels of resistance of the Eucalypts to isolates of *C. cubensis*. In such a case, it may only be a matter of time before a pathogen with the genes to overcome the hosts resistance may develop and cause an epidemic situation in a plantation - especially if the trees are closely related. This is because the frequency of parasite or pathogen races with matching host specific pathogenicity, rises in response to selection by resistant character (Alfenas et al 1983). Ideally, breeding for resistance in forest trees should be based on polygenic non specific, or horizontal resistance in which individual trees display resistance to a wide range of pathogen races, rather than resistance to a specific pathogen race as found in vertical resistance. It was suggested (Alfenas et al 1983) that despite the variability in virulence of *C. cubensis*, breeding for resistance may reduce losses from the disease on a long term basis. Currently however the use of resistant or less susceptible species in plantations is the only means of reducing losses to disease.

Insect Pests

Little on variation in resistance to insect pests has been done to date. Susceptibility of several species of eucalyptus to Orthopteran *stiphra* spp in Brazil has been

examined, with *E. alba* Reinw ex Blume, showing significant variation (Moraes et al 1983).

EUCALYPT BREEDING IN AUSTRALIA

Eucalypt Breeding in the Eastern States

In the past, Australian efforts in the field of tree breeding have largely concentrated on improvement of exotic plantation species. Increasing demands for eucalypt pulpwood and a range of other hardwood products, combined with a general lack of knowledge on eucalypt biology and the extent of genetic variation in numerous desirable characters, has stimulated further research in these areas. Thus eucalypt breeding for most species is at the data accumulation stage. Provenance trials and progeny trials have been established for a number of species and studies of some eucalypt breeding systems carried out as already noted.

Measurements of trials have been for growth, form, pulping and wood qualities, tolerance to frost, salt or insects as well as morphological allozyme characteristics. Species on which such work has been carried out on include *E. regnans*, *E. obliqua* L'Herit, *E. delegatensis* R. Baker, *E. nitens*, *E. globulus*, *E. grandis*, *E. saligna* Sm., *E. camaldulensis*, *E. fastigata* Deune and Maiden, *E. viminalis* Labill,

E. cloeiziana F.Muell. and *E. pauciflora* Sieb ex spreng.
 Seeds orchards have been established for *E. globulus*,
E. nitens, *E. grandis /saligna*, *E. polybractea* R.T.Baker.,
E. regnans, (Nikles 1984).

Natural Variation in Morphology

There are numerous examples of studies which have been carried out on different species to establish natural variation between provenances, in morphology and growth rate. Taking *E. nitens* for example, early provenance trials have indicated the presence of two main types (Pederick 1983). (1) A faster growing form with a relatively persistent juvenile foliage (typical of the central Victorian highlands) and (2) A slower growing form with an early change from juvenile to mature foliage (from around Errinundra). Later trials to study variation in the Toorongu provenance, revealed populations of a fast growing, juvenile persistent form, particularly good in terms of growth rate straightness and branch size. Pederick (1976) reviews provenance trials of several Victorian species in which significant differences in growth rate have been observed between provenances. The results of such studies indicate the existence of considerable genetic variation within the gene pools of species tested, and hence great potential for harnessing and incorporating superior or desirable genes into tree improvement programs. Selection of more specialised

characters such as frost tolerance, salt tolerance and disease resistance as well as for fast growth and straightness are of importance in different areas.

Frost Tolerance

Frost damage can reduce the chances of survival of young eucalypt seedlings in many parts of Australia. For this reason several species have been subject to provenance trials in an attempt to find the best provenances and/or families for incorporation into breeding programs. Evidence to date indicates, as found in overseas trials, significant genetic variation with respect to frost tolerance. Griffin et al (1982), in trials of 49 provenances throughout the natural range of *E. regnans* found considerable variation in growth rates and frost hardiness. The most frost hardy provenances were from high elevations in the central highlands and east Gippsland (Victoria) and from interior central and south east Tasmania. Paton (1972) found a similar pattern of increasing frost resistance with altitude in *E. viminalis*. Awe and Shepard (1975) found four provenances of *E. camaldulensis* to vary significantly in ability to withstand sudden frosts. The evidence suggests that more northerly provenances of the interior of Australia may be better able to withstand mild radiation forest in the unhardened state than are southern cool temperate provenances.

Salt Tolerance

Clearing of large tracts of forested land for agriculture has led to increases in soil salinity in many areas of the eastern states and W.A. Attempts to reclaim saline land by planting of trees have often failed owing to the low salt tolerance of many species. Sands (1981) showed significant levels of salt tolerance in two provenances of *E. camaldulensis* and suggests that further screening of the species is justifiable. The forests commission of Victoria is conducting glasshouse trials aimed at ranking the salt tolerance of some 100 species (Morris 1981). Blake (1983) outlined a method for rapid screening of eucalypts for salt tolerance using liquid culture techniques and produced a ranking of 52 species. Care must be taken however in applying such results to the field since salt tolerance is dependant to some extent on other environmental factors. Morris (1981) quoted some such factors as additional stress to a plant caused by elevated temperature, high light intensity and low atmospheric humidity. Disease, insect damage or senescence might also render a tree more susceptible to saline dieback. Edaphic conditions are also of importance, particularly soil aeration since water logging often occurs in conjunction with salting where rising water tables approach the surface.

Disease Resistance

The presence of disease in forests of commercial importance has been a topic of concern for some time. Perhaps the disease which has attracted the most interest in recent years is that of the dieback caused by *Phytophthora cinnamomi*. Many of the tree species most susceptible to the fungus are also of commercial importance. Regeneration of these forests with more resistant species may not be entirely desirable from a production point of view, since replacement species may not have the desirable attributes that the original species had. Ideally the diseased and dying stands would be replaced by members of the same species which are resistant to attack by *P. cinnamomi*. Limited exploration of variation in levels of resistance to *P. cinnamomi* among susceptible species has been done. Harris et al (1983) found significant differences in levels of resistance to *P. cinnamomi* among families of *E. regnans*. Pederick et al (1977) found variation between families of *E. muellerana* in tolerance to the dessication that accompanied root rot and suggested that this may be a form of resistance. It is likely then, that variation in levels of resistance to *P. cinnamomi* could occur in other species of disease sensitive eucalypts.

Eucalypt Breeding in Western Australia

Indigenous Species

Breeding of indigenous West Australian eucalypts is yet at a very early stage. Major provenance trials have been established on only three species to date namely Karri (*E. diversicolor*), Marri (*E. calophylla* R. Br.) and Wandoo (*E. wandoo*). Further trials of other species are planned for the future.

Karri

The majority of work has been with this species. Major provenance trials were established in 1972 and 1973. Seed was collected from throughout the main karri range and from major outlier populations. The trial was replicated on two sites within the main karri range. Early growth measurements (Schuster 1979) indicated that provenances from the higher rainfall, main range, exhibited superior height and diameter growth than outlier populations. An exception were families from the Porongorup range, which matched the best provenances for growth, despite lower rainfall. Further trials have been established, starting in 1979.

Seed orchard establishment is another important facet of the breeding program. Breidahl (1983) has shown that karri planted in areas outside the natural karri range, flower and set seed at an earlier age. As a result, experimental seed orchards are being established in several areas. Progeny trials of families from each seed orchard are established on natural karri sites. This enables the families which exhibit poor performance under normal operational conditions to be rogued from the orchards.

Marri

A Marri provenance trial was established in 1976 near Harvey. Eight provenances were planted. Early results indicated the existence of Marri provenances which exhibit superior growth characters. A further trial was established in 1980, unfortunately the pegs demarcating family plots were removed. Plots have yet to be relocated and measurements for provenance comparisons made. Perry (1974 unpublished) suggested that there may be potential for breeding Marri trees which were free from kino veins. His suggestions were based on observations of Marri logs put through sawmills, a number of which were virtually free of kino veins. It is possible that this character may be under genetic control and considerable potential for breeding kino free trees may exist.

Wandoo

Wandoo is an important species used in the restoration of the hydrological balance in areas east of the main Jarrah forest belt. Large scale clearing of land has resulted in the mobilisation of soil stored salt, rendering much land unusable. Field provenance trials have been established to examine variation in growth rates, tree form and frost tolerance. Glasshouse screening for salt tolerance has also been investigated (Butcher 1983a) with some success. Variation in salt tolerance of 64 Wandoo families ranged from 25 000 to 41 000 mg/l TDS to kill 50% of the seedlings.

A nursery assessment of provenances collected from the natural range showed pronounced differences in seedling morphology (Butcher 1983b). Wandoo seedlings from eastern wheatbelt provenances were found to be covered with stellate hairs and have numerous oil glands on the leaves. Leaves of eastern provenances are narrow lanceolate and greyish blue. Leaves from northern provenances are ovate lanceolate and bluish-grey. Southern provenances were found to be lanceolate and bluish green and Wandoo from the main range is lanceolate and glossy olive green.

Jarrah

Relatively little in the way of formal trials have been

established to examine any growth attributes of Jarrah. Loneragan (unpublished) established a small trial at Yallambee in 1977 using 10 seed sources from areas which included Yalambee, Gidgegannup, Kalamunda, Karragullen and Mandurah. Large differences in colour and shape of the mature leaves was observed. Variations included pendulous leaves and glaucousness in the eastern provenances. Another small trial was established at Inglehope in 1969 however this consisted of single tree plots with no replicates, so no definite inferences can be drawn from it.

In recent years there has been growing interest in the feasibility of developing lines of Jarrah which are resistant to, or tolerant of *Phytophthora cinnamomi*. There is some evidence of variation of Jarrah in degree of resistance to *P. cinnamomi*. (Podger 1972) found considerable differences between Jarrah provenances in degree of root rot, in a pot trial. Rockell (1977) showed significant differences in lesion development between Jarrah trees inoculated with *P. cinnamomi* on infected and non-infected sites. Davidson and McComb (unpublished) have shown that there are differences in the levels of *P. cinnamomi* infection and of seedling growth reduction for different seed sources of Jarrah. Thus, together with evidence of genetic variation in disease resistance of eastern states eucalypts, the indications are that it may be possible to breed Jarrah trees resistant or tolerant to *P. cinnamomi*.

Mazanec (1985) has demonstrated the existence of Jarrah trees which are resistant to the Jarrah Leaf Miner (*Perthida glyphopa* common.). It would be useful to screen such trees for resistance to *P. cinnamomi*, since the capacity to produce lines of Jarrah resistant to both of these pests, would be of great value for rehabilitation of forest areas prone to attack by either or both organisms.

Provenance Trial Design

This is an area of great importance when considering the information required from a trial. The Karri provenance trials were all established on a complete random block basis as were the Marri trials. This design is adequate in the situation where only a small number of families are to be tested and hence only a relatively small area is required. In the case of the 1972/73 Karri trials, in which a large number of families were planted over a relatively large area, some problems became evident. (1) The size of each replication was too large, and encompassed too much site variation. Ideally a block should be planted on as uniform a site as possible, so that any differences between families or provenances will not be masked by the effects of site variation. (2) The trial was planted over two years. This is undesirable because a years difference in growth makes comparisons of measurements difficult.

When using large numbers of provenances and families, a better provenance trial design, which gives more accurate information on intra and inter provenance variation, is the nested hierarchical design which makes use of incomplete blocks incorporated into a balanced lattice. This system provides greater opportunity to eliminate problems due to site variation. In addition these designs enable study of progeny from individual parents within populations and subsequently, stand growth of provenances.

Future eucalypt provenance trials will be largely based on this design. For example, the proposed design for an *E. accedens* W. Fitzg. trial to be planted in 1986 is a Nested hierarchical design (W.P. 33/84). For study of intra population variation, 10 families per provenance are completely randomised within the provenance plot. Family plots consists of a row of ten seedlings spaced at 4m x 2m. For inter-population studies the nine provenances in the study are planted in a 3x3 balanced lattice replicated four times. Thus in the early stages of growth, intra provenance, family variation can be examined and in later years, provenances may be compared using the provenance plots to represent stand performance.

The use of the nested hierarchical design is probably best suited to trials in which provenances of a species occur as discontinuous populations covering a wide range of environments. Where a species has a continuous range, and

provenances are defined artificially, large differences between 'provenances' or collection areas may not exist and the continuous random block design may be adequate. The nested design still has its advantages even in this situation. This is because each provenance is physically represented as a stand of trees. In the complete random block design, families from different provenances are grown at random throughout a block and consequently discrete provenance stands do not grow. This may result in some bias in results obtained. For example, if one family grows less vigorously than a family from another provenance, which is planted adjacent to it, then its growth may be further suppressed by competition with the more vigorous provenance and hence an inaccurate result obtained. This type of problem is minimised by using the nested hierarchical design since buffer zones between different provenances are incorporated into planting design to absorb any such competition effects. Buffer zones are not used in measurements for final analysis.

Choice of Parent Trees

The choice as to what class of parent trees should be selected for use in a provenance trial often varies, depending on time, money and objectives for the trial. For example, the 1972/73 Karri trial, although called a provenance trial, was in effect a family trial. This was largely owing to the continuous

distribution of Karri within its main range and the inherent difficulty in defining discrete provenances in such situations. Seed was collected only from high quality trees, with the intention of using the trial to identify the best trees for inclusion in seed orchards.

For the Wandoo trial there were three main objectives; (1) to select the best trees from each provenance for inclusion in a seed orchard (2) to identify the best areas for general seed collection (3) to determine whether there is any gain in collecting seed from trees of better phenotypic appearance rather than average trees. For this reason seed from four plus trees and one average tree was collected from each provenance for inclusion in the trial, thus allowing a comparison of performance to be made between the two classes of tree.

It is the objective of the proposed *E. accedens* trial to investigate the extent of variation existing within the population, and to establish how effective phenotypic selection is, in selecting superior trees for this species. To do this, seed from each provenance has been collected from six trees with plus phenotypes, three trees of better than average phenotype and one of average form for the collection area (WP 33/84). The performance of these families will enable an evaluation of how closely phenotype matches genotype and hence whether it is better to bias seed collection towards better quality trees for general planting operations.

Trial Layout

A factor of practical importance is that of precision in laying out a trial. Ideally the trial should be planted to a strictly geometric pattern and family locations marked with pegs. If the pegs are by chance removed, families can be relocated. If planting is somewhat haphazard, difficulty will arise in relocating families and any element of doubt will render the trial invalid. An event such as this occurred when vandals removed the family location pegs for the 1980 Marri trial. Owing to the regular layout of the planting, the trial will not be lost. Irregular planting may also give rise to uneven competition effects between trees within the trial and thus introduce bias into the results.

Exotic Species Trials in Western Australia

To date, major provenance trials of *E.maculata* and *E.resinifera* Smith have been established and trials of two more species, *E.camaldulensis* and *E.globulus* are to be established in 1985. The primary aim of these trials is to determine which provenances are best suited for planting in West Australian rehabilitation sites. Such sites include bauxite pits at Alcoa's Jarrahdale and Huntley mine sites and the Wellington Catchment.

E. maculata These trials were established in 1984, one at Jarrahdale minesite, one at Huntley minesite and the third in the Wellington catchment. Sixteen *E. maculata* provenances were planted in a balanced lattice design, with five replicates at each site (WP 38/82).

E. resinifera Family/provenance trials were established in 1984 at the Jarrahdale and Huntley minesites. Eighteen provenances comprising 145 families were planted in a 12 x 12 quadruple lattice design (WP 1/84). Data for the *E. maculata* and *E. resinifera* trials is yet to be collected.

E. camaldulensis Three trials are to be established in 1985, at the Jarrahdale and Huntley minesites and in the Wellington catchment. The trials will consist of twenty-five provenances collected from Victoria, New South Wales, South Australia and Western Australia in a 4 x 5 rectangular lattice design (WP 34/84).

E. globulus Family/provenance trials are to be established in 1985 in the Jarrahdale and Huntley minesites and in the Wellington catchment. The experiment design will be of a Nested Hierarchical design to enable intra and inter provenance

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performances to be examined (WP 32/84). Seed collections for these trials were made from a representative sample of the tree classes present in the collection areas.

In 1980, trials of 29 provenances of *E.globulus* were planted near Manjimup and in the Sunkslands. Data from these trials shows that provenances from Victoria and the Bass Strait Islands are superior for early height growth. Provenances from the south eastern and higher elevations of the species range, together with *E.globulus* seed collected from Portugal are also displaying good early height growth.

CONCLUSION

It is evident that eucalypt breeding in Australia and particularly Western Australia is in its infancy. It is crucial in this early stage of development, to seriously consider the direction in which future research should move. In W.A., shortcomings at the present time arise in three main areas.

(1) The Jarrah forest is at present under considerable pressure from bauxite mining, *P.cinnamomi*, and the Jarrah Leaf Miner, the latter two problems being further aggravated by timber production operations. Efforts to date in finding

species suitable for rehabilitation of bauxite pits, areas of forest affected by *P. cinnamomi* and catchment areas have largely been concentrated on eastern states eucalypts. The potential for greater use of indigenous West Australian species has yet to be fully explored. There is a great need for more investigative work on Jarrah, in terms of genetic variation and the possibilities for breeding lines which are resistant or tolerant to *P. cinnamomi*. The potential for simultaneously breeding for resistance to Jarrah Leaf Miner is further reason for this work to be done. Investigation of genetic variability in other West Australian species should also be carried out.

(2) There is an urgent need to establish the degree of selfing which can be expected from species currently involved in breeding programs, e.g. Karri, and the effectiveness of early nursery culling in eliminating selfed seedlings.

(3) A better understanding of eucalypt breeding systems will need to be developed in order to facilitate the design of efficient breeding programs.

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12.

GLOSSARY

Definitions taken from Wright (1976) unless stated otherwise.

Additive genes Factors affecting the same character in such a way that 1, 2, 3, 4, etc., genes have 1, 2, 3, 4, etc., units of effect on the phenotype.

Allele One of a pair (in a diploid individual) of genes located at the same locus in homologous chromosomes and controlling the same character. One of a pair of characters controlled by such genes and alternative to each other in inheritance.

Breeding The science or art of changing the genetic constitution of a population of plants or animals.

Clone All plants (ramets) reproduced asexually from a common ancestor (ortet) and having identical genotypes.

Combining ability The relative ability of an organism to transmit genetic superiority to its offspring.

Combining ability, general The relative ability of an organism to transmit genetic superiority to its offspring

when crossed with other organisms in general. High general combining ability usually implies the presence of genes with additive effects.

Combining ability, specific The relative ability of an organism to transmit genetic superiority to its offspring when crossed with specific other organisms. High specific combining ability usually implies the presence of dominance, overdominance, or epistasis.

Dominance Masking effects of one allele by another so that a heterozygote (Aa) and a homozygous dominant (AA) organism are phenotypically indistinguishable. Dominance may be complete or partial.

Epistasis Dominance exerted by nonallelic genes.

Family The offspring of a single tree after open pollination or of a single pair of trees after controlled pollination.

Geitonogamy Cross pollination between two flowers on the same plant. (Chambers 1974)

Gene The basic unit of most types of inheritance, occupying a fixed position on a chromosome and consisting of a portion a DNA molecule.

Genotype - environment interaction The situation in which genotype A performs better than genotype B at one place, but poorer than B at another place.

Heritability That portion of the total variance due to genetic factors. In a broad sense, that portion of the total variance due to all genetic factors. In a narrow sense, that portion of the total variance due to genes with additive effects and most indicative of the superiority that can be transmitted by seed.

Hybrid Offspring of organisms of dissimilar genotype, often the offspring of a cross between different species.

Inbreeding Mating between close relatives. Mating in a population consisting of a few individuals.

Lethal gene A gene in which the homozygous state causes death; usually a recessive gene.

Outbreeding Mating unrelated parents.

Pedigree Record of ancestry.

Phenology The study of the timing of periodic phenomena such as flowering.

Phenotype The visible characters of a plant. The product of a plants genotype and its environment.

Protandry Shedding of pollen prior to time of maximum receptivity of the flowers on the same tree.