Selecting and Breeding for Cold Resistance in Eucalyptus

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(Received for publication August 14, 1956)

Importance in the Northern Hemisphere

The widespread use of Eucalyptus in countries where hardwoods are deficient is one of the promising practical ways by which this shortage may be reduced in a relatively few years. Eucalyptus has great potential value in this regard and the extent of the possibilities is far from fully known, still less is it put into effect. Australia is not a cold country judged from the Northern Hemisphere, and when a comparison is made between two localities which are similar in latitude and in other general respects, such as altitude and distance from the coast, it will be found usually that the Northern Hemisphere station is colder than that of the Southern. This is particularly so with regard to the departure of the extreme minima from the mean minimum temperatures. A species introduced, therefore, and known to stand the mean minimum temperature of a locality, may fail in one of the colder years which the locality regularly but infrequently experiences, and therefore some consideration must be given (if it is to be successful) to the incorporation of cold resistance additional to that of the "normal" species. In addition to this, there are great land areas in the Northern Hemisphere extending into a climate much colder than any part of Australia. The northern limits to which Eucalyptus can be cultivated successfully as a timber-producing tree could have great consequence in local economy, and for this reason cold resistant forms have particular value. Likewise some degree of frost resistance in a species like E. citriodora, which though much more frost sensitive than many other species may have special importance in areas where it is grown if this feature can be introduced. For reasons of this kind careful attention to selecting and breeding for cold resistance in Eucalyptus is likely to have very worth while benefits.

Eucalyptus as a Genus

Eucalyptus, through its many species, is the principal tree of the forests and woodlands of Australia. As a genus it therefore occupies a very wide range of climate and soil. There are some 500 described species together with an additional 150 described varieties. The systematic treatment of the genus is contained largely in the works of MUELLER (1879), BENTHAM (1864), MAIDEN (1909), BLAKELY (1955), JACOBS (1935) and BLAKE (1953), BURBIDGE (1947) and CURTIS (1956).

It is obvious there is scope for further development of Eucalyptus systematics in spite of the fact that work already done is competent and includes the classic work of MAIDEN; the lengthy "*Critical* Revision of the Genus Eucalyptus". This is especially so if the results of research in genetics and ecology are to be applied to its taxonomy.

It is known that some of the described species are hybrids; probably more than 100. It is also clear that in some groups there has been "splitting"[1]) and on occasions several closely related species have been described which would be better understood if called subspecies, or alternatively merely as forms at particular points in clines within the one broad species. At the same time, when this "splitting" is done no name remains which can be used for the group as a whole. It is equally clear in some other species that variation of a similar pattern has not been recognized in any systematic description. In short, there is lack of uniformity in the systematic treatment of different sections of the genus. With this in mind, it is estimated that if all species (excluding hybrids) were treated uniformly, and geographic and edaphic subspecies counted as species, there might be well over 1000 species. On the other hand if species (again excluding hybrids) were counted only as species sensu lato, each of which embraced the subspecies, there may be as few as about 250.

One of the striking characteristics of the genus is that local small changes in habitat such as the ordinary topographic changes in aspect, or variations in soil, such as from alluvial to sedentary, are accompanied by a species change. Each species is closely linked to a particular ecological situation in any one locality. It is common to find in an area of no more than 100 acres six species of Eucalyptus and often there are several more. In addition to this, if an area say 100 miles distant but in a different altitude or latitude is considered and which presents ecological situations in the same pattern, related but nevertheless entirely distinct species often occupy each available habitat in a corresponding pattern. Further the same species may occupy a different ecological situation in different regions, e. g. E. viminalis is a woodland tree near Cooma on open undulating sites, but it is a gully species closely confined to the stream courses in some other localities.

There are some exceptions, of course. Large areas continuously occupied by one species or perhaps two at the most do occur. In such cases changes in ecological situation are reflected in the dimensions of the trees and the specific composition of the accompanying subordinate layers of plants in the stand. There are then changes in Forest Type with habitat in the sense of CAJANDER (1926). The most notable of these are the stands of E. *pauciflora*[2]) at high elevations on the mountains of south-eastern Australia, the E. camaldulensis stands along inland streams and the E. marginata — E. calophylla forests of the lateritic formations in south-western Australia.

[1]) Since BENTHAM, the major subdivisions of Eucalyptus have been founded on characters of the anthers, and while there are some anomalies it is clear that there are about five or six groups which are equivalent to subgenera, principally the Renantherae, Porantheriodeae-Terminales, Macrantherae-Normales, *Corymbosae* and Eudesmiae. The first two groups are clearly separated on anther characters, the latter three are not. Within these major groups there are other groups of species which are frequently referred to by the Australian colloquial name for the group, such as "Stringybark", "Ash", "Box", "Ironbark" or "Bloodwood". It is common practice to say, for example, that there has been taxonomic "splitting" in the "Stringybarks". While such expressions lack precision in the sense of the international botanical rules, to those familiar with the genus within Australia they are quite precise in their meaning.

[2]) Nomenclature throughout as in BLAKELY "*A* Key to the *Eucalypts*" 1955.

The more common situation, however,is that each species occurs in relatively small stands often with one or two other species codominant, separated from the next similar sand by a distinct space occupied by other species in combinations. It is likely that such separate stands are largely reproductively isolated. In many cases there are phenotypic differences between them which, though often subtle, are nevertheless distinct, and there is evidence that these are perhaps always accompanied by genotypic differences with which they are no doubt largely correlated. As the distance between any such pair of stands increases, and especially if there is an ecological gradient associated with increasing distance so, as a rule, the differences increase and it is a consequence of this that in different regions stands can sometimes be grouped to comprise subspecies. The phenotypic variation between these separate stands is also usually in a graded sequence (though perhaps in small steps as described by HUXLEY (1942), that is, there is a cline. Such clines are general in most species and are related to some regular habitat change such as that which corresponds with changing altitude or latitude. It is common to find that closely related "species" as described in some taxonomic works are merely individuals from different positions in these clines at which a type has been selected for description. The location of this point has often been a matter of chance depending on such things as accident of exploration, collecting chance or prejudice.

At the same time there is also evidence in continuous stands of a marked selective environmental effect with the result that the population in one zone is genetically distinct from that in another zone even though the species is continuous in distribution. In such cases clinal variation is continuous and not in steps. However, whatever standards are adopted with regard to *Eucalyptus* classification and nomenclature, it is clear that by comparison with many plant genera, especially those in which the species are principally trees, *Eucalyptus* is a large genus in which there are many species. It is also clear that most species have a very distinct ecological specificity so that they occur in general as rather small stands, even though such a stand may be repeated very many times when the situation on each occasion is favourable.

Variation in Eucalyptus Populations

The general characteristics of clinal variation in species populations is displayed as prominently in the colder parts of the country as anywhere else. This clinal variation may take place in many characters and may be occurring in different directions in these characters at the one place. The study of clinal variation in *Eucalyptus* populations is complicated somewhat by the rather difficult and still incompletely developed *Eucalyptus* taxonomy. For example, *E. Johnstoni, E. subcrenulata* and perhaps *E. vernicosa* pass insensibly from one to the other. The limits of each species are quite obscure. *E. Johnstoni* and *E. vernicosa* are extreme forms near either end of the cline and *E. subcrenulata* is near the centre. There is no doubt that physiological characters show similar clinal variation often corresponding with morphological characters and in a few cases this has been established by test. The existence of this kind of variation is extremely important to any programme for selecting *Eucalyptus* for cold resistance, because it means that the precise habitat of origin (that is the provenance) of the seed is likely to determine in a substantial degree the relative resistance of the population. A rather detailed study has been made of *E. pauciflora* in this connection, and as it has a rather complicated pattern a description of it illustrates well this feature in *Eucalyptus.*

Eucalyptus pauciflora

This is widespread in south-eastern Australia and Tasmania, growing generally above 2,000 feet elevation, but at times descending to lower elevations, especially on the south coast of Victoria. Two described "species", *E. niphophila* and *E. de Beuzevillei,* are connected in clinal sequence within the broad species population. There are several other distinct forms (if considered dissociated from their clinal positions) which could be regarded as of similar rank, but they have not been taxonomically described. *E. pauciflora* occurs in general in two ways. It forms large pure stands above about 4,000 feet elevation, at latitude 35° S or at comparable elevations in relation to latitude. It also occurs scattered over a wide area at lower elevations in disjunct stands. Progeny raised from trees in stands at different elevations but within the large area continuously occupied by the same species show differences which are consistent within the progeny itself but distinct from each other. The height of the mature parent trees is closely related to altitude of the habitat — the higher the elevation the smaller the tree *(Fig. 1),* and *Plates I (a—e).* By growing progeny from these

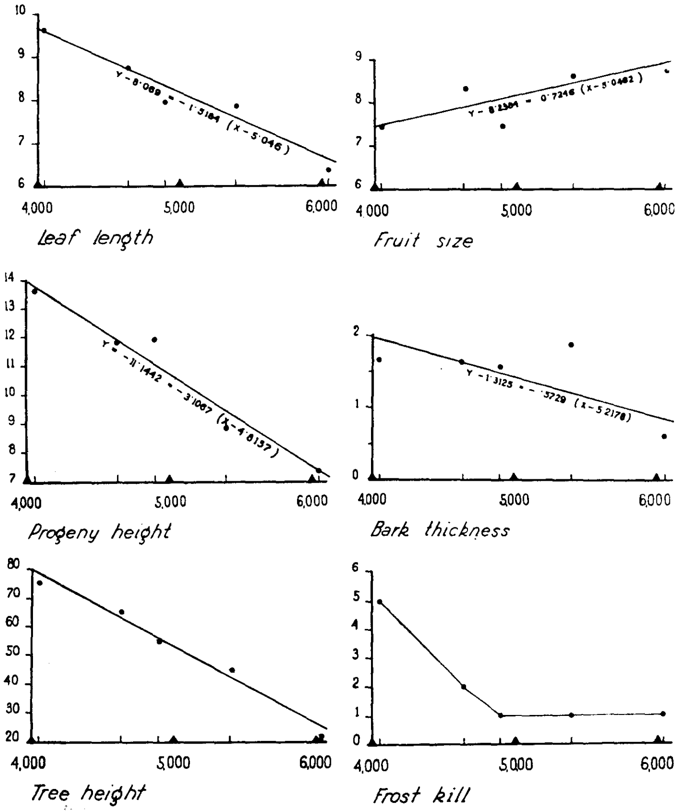

Fig. 1. — Relationship of leaf length, fruit size, progeny height and bark thickness of *E. pauciflora* to altitude at which the parent stand was growing is shown. The figures for leaf length, fruit size and bark thickness are the means of ten measurements each on five different trees in each stand. The diagram, "Tree Height", shows the maximum height of the stand at different elevations related to altitude, and winter "Frost Kill" shows the number of plants killed in a small trial of five plants only from each elevation examined when all were planted together at 6,000 feet.

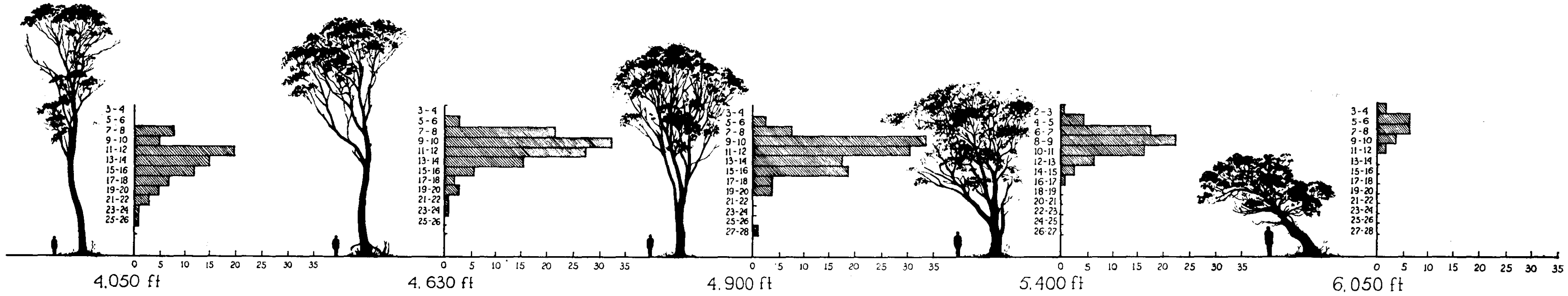

Fig. 2. — Shows the form of *E. pauciflora* at different elevations and a histogram of the progeny at each site showing the height in inches at 12 months of plants raised from seed from five different trees at each station.

Plate I (a), (b), (c), (d), (e). — *E. pauciflora* at 4,050 feet, 4,630 feet, 4,900 feet, 5,400 feet and 6,050 feet. The photographs are approximately to the same scale but that at 6,050 feet is a little larger and that at 4,050 feet somewhat smaller than the scale of the remainder.

together in an essentially uniform environment it is apparent that rate of growth, at least in the first six years of growth over which trials have extended, is closely associated with the elevation of origin of the seed: the higher the altitude the slower the rate of growth *(Fig. 2)*. Thus the varying phenotypic character of mature height is seen to have genotypic specificity closely associated with it. It is also apparent from similar experiment that resistance to low temperatures is greater in seedlings from plants which come from the higher elevations. Other features are found with similar correlation, such as leaf length and fruit diameter. Examination shows in addition that there is no discontinuity in the variation of several characters of trees from near the tree line at about 6,000 feet to those from about 4,000 feet. Highly significant linear correlations are obtained between altitude of origin and the morphological characters as illustrated by *Fig. 1*. It is clear from this that there are marked heritable differences in different stands even within a large area continuously occupied by a single species and that if seed is taken from such stands many of these differences are preserved in the progeny. Where a comparison has been made between progenies from disjunct stands similar differences are found. This, of course, is closely similar to many well-known examples in trees other than *Eucalyptus* in other countries.

It is clear, therefore, that characters such as rate of growth and resistance to low temperatures are genetically controlled in *E. pauciflora* and vary through the species population in accordance with habitat, their degree being closely related to the precise habitat in which the trees are growing. It is likely, in this and many other species, that very great benefits can be obtained by the selection of seed carefully from natural habitats within Australia. Such habitats are often relatively inaccessible but they can be expected to provide material adapted to distinctly colder conditions than that from habitats selected perhaps because of ease of access but without such discrimination.

The Breeding System of Eucalyptus

In many ways *Eucalyptus* as a genus is comparable with *Quercus*. They are similar in having within the genus a large number of species. Likewise, the degree of variation within the species populations and the rather frequent occurrence of hybrids at the junction zones of species areas is similar (Pryor, 1953 b). The latter two characteristics might lead to the thought that *Eucalyptus*, as *Quercus*, is fully self-sterile and regularly outcrossed. Krug and Alves (1949) support this view by reporting that all of seven species planted in Brazil which they examined, viz., *E. alba, E. robusta, E. citriodora, E. umbellata, E. maculata, E. grandis* and *E. punctata,* were self-sterile. Likewise, Penfold, Morrison, McKern and Willis (1950) state that with *E. citriodora* this view is supported by their experiments which indicated a high degree of self-incompatibility. On the other hand, experiments in Canberra (Pryor, 1951 b, 1956 b) have shown that several species, including *E. Maideni, E. bicostata, E. cinerea, E. Blakelyi, E. rubida, E. polyanthemos, E. macrorrhyncha, E. caesia* and *E. pulverulenta,* are fully self-fertile and manipulated selfings of these species set viable seed. Of some dozens of individuals tried among the species last listed, only one tree within one species, namely *E. bicostata,* has been found under conditions of manipulated pollination tobe fully self-incompatible. The possibility that this particular individual might be self-sterile was first noticed in 1949. The particular tree has subsequently been examined each year, with one exception, until 1955 and evidence that it is fully self-incompatible in five different seasons has been obtained. It was thought at first the pollen from this tree was inactive, but later experiment has established that it is capable of setting seed on other trees of the same species and also that it will germinate *in vitro*.

Later examination of more trees of *E. bicostata* gives an indication of varying degress of self-incompatibility which may be part of a genetically controlled self-incompatibility system. There is need for much more experiment along these lines by an adequate mating programme to investigate the matter fully, but it seems on general grounds that there must be rather a high amount of intraspecific outcrossing, whatever the precise mechanism, to maintain the genetic diversity which *Eucalyptus* species usually show.

The experimental technique for manipulated pollination is quite simple. Numerous trials have shown that *Eucalyptus* is not, in any degree, wind pollinated. Emasculation alone is sufficient to prevent most pollination and bagging of emasculated flowers with a fabric sufficient to exclude insects completely prevents pollination. Emasculation is easy simply by cutting the calyx tube just below the staminal ring shortly before the operculum is due to fall. At this stage the anthers as a rule have not dehisced. In most species the anthers and operculum can easily be lifted free of the stigma. For critical experiment pollen may be taken from buds just before opening, which are split and allowed to dry for a few hours, to free the pollen which is thereupon used for pollination. There is no doubt that selfing can occur in many species while on the other hand there is at least in the genus the possibility of self-incompatibility in some individuals which would lead to obligatory outcrossing in these cases. There may be in still other species, as claimed by Krug and Alves (ibid), general self-incompatibility, but this remains to be established clearly experimentally and it is certainly not a universal condition of the genus.

The question of the proportion of selfing to inter-specific crossing in the natural state remains to be solved. It must vary a great deal from season to season according to varying flowering times and also there may be preferential benefit to some pollen when lots from different sources are on the stigma at the one time. There is some evidence that the amount of interspecific crossing between trees separated by 100 yards is about 1%. Even if there were no higher rate, this no doubt would be sufficient to maintain hybrids at the zone of contact of two species and to enable substantial gene exchange between species which can interbreed.

It may be that the amount of intraspecific outcrossing in fully self-fertile species is also of this order but it may be much higher. Adequate assessment has not yet been made, but by the discovery of individual trees with suitable dominant marker genes, the effects of which can be observed at an early stage in the growth of the resultant seedlings, this could be resolved.

The position is somewhat easier to elucidate experimentally with interspecific outcrossing. The opportunity was taken, therefore, to examine this in the case of *E. fastigata* and *E. Robertsonii*. In January 1953 these two species flowered heavily and with a large time overlap on the Brindabella Range in the Australian Capital Territory. They set a heavy crop of fruit. A series of pairs of trees, one of each species, were chosen, each separated from one another by varying distances. Open pollinated seed was collected, and a progeny of 200 plants raised from each parent. The juvenile leaves[3]) of the two species are quite distinct and the phenotype of the F_1 hybrid can be fairly certainly deduced in the juvenile stage. In most of the progenies the large majority of seedlings was true to the parent type, but some plants corresponding with the assumed form of the F_1 hybrid were found, the number differing broadly according to the distance by which the two parent species were separated and ranging from 1% to 25% at distances of separation of 100 yards to 5 yards. This represents the maximum possible rate of outcrossing at the time of experiment. The actual rate may be somewhat less because a reduction would be necessary to eliminate the hybrid forms which would result following selfing from any heterozygosity in a parent. Until the results of controlled selfing are applied to the figures they must be regarded only as an upper limit of interspecific outcrossing.

It appears therefore that *Eucalyptus* differs from *Quercus* in that the individual trees in *Eucalyptus* are in many cases capable of selfing.

Hybridism

The idea that species of *Eucalyptus* may hybridize and that natural hybrids may occur in the field was first put forward as early as 1810 by Caley, but Wools in 1867 thought that hybridization was unlikely. A series of opinions has subsequently been presented, both for and against the occurrence of hybrids in *Eucalyptus,* with Mueller (1879) and Baker and Smith (1920) taking a definite negative view and Maiden (1904) taking a positive view. With all this discussion, however any attempt to verify the position experimentally was conspicuously lacking until the work of Brett (1937) in Tasmania. A considerable amount of direct experimental evidence is now available to show that not only do *Eucalyptus* hybrids occur, Martin and Gilbert (unpub.); Barber, (unpub.) (Pryor, 1951 b, 1955, 1956 b), but they can be synthesised with relatively little effort.

The occurrence of hybrids is not haphazard nor apparently is crossing possible, at least under field conditions, between all species or groups of species. The characteristic of *Eucalyptus,* described above, by which species occur each confined to its own particular ecological situation often of quite small extent, leads to a common pattern of distribution in which the area occupied by one species is sharply demarcated in relation to those species with which it can interbreed, and often a very brief transition zone separates two such species. At such species junction zones in the field hybrids can usually be found. This situation is comparable with that described for *Quercus* (Stebbins 1950).

The frequency of interspecific hybrids at such places, however, differs a good deal and apparently depends upon several factors such as the abruptness of the habitat change, the degree of genetic isolation of the species and the viability of the hybrid. Hybrid viability differs widely. In one or two cases positive heterosis has been observed in F_1 hybrids between closely related species whereas early mortality or very inferior growth has been observed in wide crosses. In some cases also hybrids are much more frequent in one part of the common range of two species than in others and the general habitat conditions seem to favour the survival of hybrids in some areas more than in others.

Field evidence, supported by all the experimental trials so far made, shows that certain groups of species approximately subgenus status do not interbreed with other groups of species within the genus, whereas species within those groups frequently interbreed easily and many hybrids are found. For example, no species of the group *Renantherae* has yet been artificially combined or found in hybrid combination with a species of any other group although between such species within the group hybrids are very common. This is associated with an interesting characteristic of natural stands, which is especially true of those of colder areas in Australia, in which the same ecological situation is generally occupied by a pair of *Eucalyptus* species. In short, the natural stands are seldom pure stands but a pair or three *Eucalyptus* species mingle together as codominants to make up the stand. Where such species occur in this way they belong to different systematic groups which do not interbreed. There is reason to think there may be biological significance and sylvicultural benefit in such mixtures. This position has been described in some detail for stands characteristic of south-eastern Australia (Pryor, 1953 b).

As far as is known the groups which can interbreed easily, follow in some degree the systematic scheme of Blakely (1955) which is the most recent *Eucalyptus* classification. For example, the 140 species of the *Renantherae* are genetically isolated from the rest of the genus but freely interbreed amongst themselves. The same also seems true of the combined group *Porantheroidae-Terminales.* It is clear on the other hand that there are some inconsistencies between ability to cross and systematic groups to which the species belong. It is likely that systematic treatment will be improved by taking into account, when assessing affinity of species, their capacity to cross one with the other, in the way described by Duffield (1952) for *Pinus.*

The reason for incompatibility in those inter-specific combinations which do not cross is not yet known. There is no gross cytological difference in the different groups, the haploid chromosome number being 11 for all of the 40 or so species examined in the complete range of systematic groups of the genus (Smith White, 1948) (McAulay and Cruickshank 1937). It may well be that an experimental means of producing such hybrids can ultimately be found, as has been the case with the pear-apple cross (Brock 1954). If this were so, the possibility of combination of characters from widely separated groups within the genus would be greatly extended. Nevertheless, within the limits as they are known to exist at present, there are numerous combinations which are possible.

Many of these, of course, occur naturally. In any two species which may be thought on general grounds to interbreed, but which do not usually occur side by side naturally, careful field study can sometimes lead to the discovery of somewhat exceptional physiographic circumstances where they are growing side by side. At that spot often a hybrid may be located. On the other hand, at least in three cases, a hybrid has been synthesised (between

[3]) Many *Eucalyptus* species have juvenile foliage which often persists for two or three years and which is quite distinct from the mature foliage. Species which are similar in many respects are often quite distinctly separated by the form of the juvenile foliage e. g., *E. viminalis* and *E. Dalrympleana.*

E. cinerea and *E. robusta, E. pulverulenta* and *E. caesia* and *E. pulverulenta* and *E. grandis)* which could not occur naturally because the two species are much too widely geographically separated in their natural distribution.

Under field conditions, where two interbreeding species meet and particularly following the extensive regeneration after disturbance by felling or burning, segregating hybrid swarms between pairs of interbreeding species can often be found. It has been suggested that the frequency of these swarms may have been increased by some factor associated with the settlement of Australia, such as the introduction of the honeybee, but it seems unnecessary to require more than the original reservoir of hybrid trees along the species-area boundaries, coupled with the "hybridization" of the habitat as described by ANDERSON (1949), to permit the present situation to develop.

Inheritance of Characters

Most of the information available concerning the inheritance of various characters in *Eucalyptus* has been derived from a study of open pollinated progeny from selected parents. Only a small number of F_1 hybrids has been produced and there are only two known F_2 progenies — *E. cordata* × *E. globulus* raised by MARTIN in Tasmania (unpub.), and *E. Maideni* × *E. rubida* raised in Canberra. Both of these are in the early juvenile stages. It has been possible from the few F_1 hybrid combinations which have been raised to get some indication of dominance, especially in the juvenile stage, where it is seen that features such as petiolate leaf and the square stem in the juvenile condition of some species are expressed in the F_1 in a way that suggests they are at least partially dominant. On the other hand characters such as leaf shape and glaucousness are intermediate in the juveniles of some F_1's. The study of the inflorescence in the F_1 hybrid between *E. Maideni* and *E. rubida* has special interest because of the diagnostic importance of the three-budded flower cluster in many species. In this combination *E. Maideni* has a sevenflowered inflorescence and *E. rubida* three-flowered. In the F_1 hybrid there is sequence of flower clusters from three to seven flowered, depending on the position of each on the flowering shoot, the first basal ones tend to be three and the later ones seven or nearer seven (PRYOR, 1954). The general conclusion from the study of progeny of various species combinations is that most morphological characters are determined by multiple factors and that segregation and recombination are possible in most cases. It is noticed, however, that there is a tendency for individuals in a segregating progeny which already resemble in some degree one parent in one character to have several other characters approaching the same parent in a similar degree. For example, leaf venation pattern often corresponds with leaf thickness and oil components. It is not known at present whether this is the result of close linkage to which exceptions are relatively few, or whether there is selection at some stage after the zygote is formed which favours the combinations which approach the parent rather than those which are thoroughly mixed. The large number of ovules in the fruit of many species compared with the number of seed set might well be associated with some kind of selective mechanism. Recombination of characters is demonstrated by a study of *Eucalyptus* oil which has been examined in the segregating progeny raised from a naturally occurring hybrid between *E. Macarthuri* and *E. cinerea*. *E. Macarthuri* contains geranyl acetate, which is an oil found rarely in the genus, whereas *E. cinerea* has a high cineole content. In one segregate the leaf shape and colour approaches the distinctive form of *E. cinerea,* which is orbicular and glaucous, but the characteristically *E. Macarthuri* oil constituent, geranyl acetate, is present in the oil (PRYOR and BRYANT, unpub.). A similar striking example of recombination is that of a segregate from a naturally occurring hybrid of *E. Robertsoni* × *E. gigantea*. *E. Robertsoni,* in common with the great majority of *Eucalyptus* species, develops prominent lignotubers[4]). *E. gigantea* does not develop lignotubers at any time. In such progenies occasionally a segregate is recovered which very closely resembles *E. gigantea* in its general phenotypic characters, but which has prominent lignotubers.

A study of the inheritance of wood and bark characters (PRYOR, CHATTAWAY and KLOOT, 1956) between *E. Robertsoni* and *E. Rossii,* also displays recombination and the multiple factor type of inheritance of the various characters of the wood and bark of these two species.

Resistance to leaf-eating insects has been similarly shown to be a heritable character, and this has particular importance in Australia where leaf-eating beetles especially can be so severe in many cases as to make re-establishment of some species impracticable in areas now cleared but where they have previously grown naturally. Similar study also has shown that anther shape (in those combinations where species from different anther groups can hybridize, as between the groups *Porantheroideae* and *Terminales)* follows the same pattern of inheritance.

Vegetative Propagation

There is still much opportunity for investigation into effective means of vegetative propagation. Much breeding work for quick and effective application must be coupled with vegetative propagation and therefore substantial efforts in improvement in this way are warranted. *Eucalyptus* must be regarded as one of the groups of plants vegetatively hard to propagate. Nevertheless, over a long period there are sporadic records of successful vegetative propagation, and bottle grafting at least is found to be a method by which a quite high percentage of success can be obtained. It is, of course, a relatively expensive method and while suitable for experimental or horticultural work is one which is not sufficiently cheap for ordinary plantation work.

Records of Vegetative Propagation

MAIDEN records certain work on the vegetative propagation of *Eucalyptus* in France soon after 1871, and also the propagation of *E. calophylla* var. *rosea* of desirable flower colour in the Canary Islands, in both cases mainly by approach grafting.

Natural grafts, particularly between branches on the same tree, are found commonly enough in the field, and every Australian forester can recall having seen them. MAIDEN also quotes WESTON in recording the grafting of

4) A lignotuber is a distinct organ in *Eucalyptus*. It is a mass of woody tissue which develops in the axils of the cotyledons and sometimes in the primary and secondary pairs of leaves. It contains numbers of buds and food storage tissue. It is an organ which greatly aids survival of the plant. If the top is destroyed by any means, vigorous shoots come from the lignotubers and these can recur very many times. A very few species within the genus, perhaps 30 or so, do not develop lignotubers and have at the same time rather distinctive sylvicultural characteristics.

very young *Eucalyptus* seedlings by pressing them together when at the cotyledonary stage.

It has also been a matter of common observation that green stakes (tent poles or small pegs) driven into moist, warm ground, will often sprout and even form callus, but no authentic case of rooting of such material is known. In India (Champion and Pant, 1932) a method was developed for "stump" planting in which the root was cut off a few inches below the lignotuber, and the stem a few inches above, then the resulting stump split into four or more pieces which were planted and would grow successfully. This technique has been successfully repeated in Canberra. Layering of *E. camaldulensis* in sandy river courses, in Central Australia and elsewhere, is a common feature (Jacobs, 1955). Maiden also records some successful budding in Palestine in 1893 of *E. globulus* and *E. resinifera.*

Nevertheless, by the standards on which ease of propagation in plants is generally judged, *Eucalyptus* has remained an intractable genus and little success has been achieved in vegetative propagation. Successful results have been so erratic, in fact, that it has been a subject of debate, led by Willis and Fielding (1948 b) as to whether *Eucalyptus* can be grown from cuttings or not. It has been shown that several Tasmanian species can be readily propagated from cuttings under certain conditions and Fielding (1948 b) records successful "bottle grafting" of a number of species and success with cuttings of shoots from very young seedlings. Success by cuttings is also recorded by Ivaschenko (1939) in the U. S. S. R. with *E. urnigera, E. tereticornis, E. cinerea* and *E. rudis.*

Vegetative propagation is so important to a breeding programme in *Eucalyptus* that continued effort to find a means of propagating species by one or other vegetative means is very necessary, and some progress and encouraging results in this field are recorded below without yet disclosing a successful technique which could be widely adopted for sylvicultural use.

Stem Cuttings

A number of trials has been made with stem cuttings of different species taken at different times of the year, with different rooting media, such as standard potting soil, sand, sand and peat mixed, and vermiculite, with only very slight success. It is found, however, that *E. Gunnii* strikes fairly readily, giving up to 30—40% success if cuttings made from ripe wood still carrying juvenile leaves and of weak growth are used.

A few other species, especially *E. pauciflora* and *E. polyanthemos,* have struck this way, again when the juvenile material which is growing weakly is used. However, figures have been very low, only one or two cuttings having struck, of the order of 1% of those taken, and these only in the juvenile stage. Trials with indole acetic acid have so far given negative results, but such trials have been by no means exhaustive.

The fact that some cuttings can be rooted even though the percentage is very low, suggests that the conditions under which rooting takes place can be found by adequate experiment, and a means of propagating from stem cuttings may yet be developed. Experiment is warranted in this field.

Stem Cuttings with a Heel of Lignotuber

If stem cuttings are taken from shoots from a lignotuber, made with a small heel of the tuber tissue, both bark and wood, and the cuttings placed in a mixture of sand and peat with bottom heat, rooting is readily obtained in a number of species tried. About 50—75% of cuttings made have been successful by this means. Species from diverse systematic groups with which there has been success in this way are: —

E. microcarpa, E. dealbata, E. albens,
E. Bridgesiana, E. stellulata, E. Blakelyi.

This technique would lead to the substantial vegetative multiplication from a particular lignotuber. If the quality of the particular individual could be assessed it may have some application, for example, in the propagation of desirable oil-bearing combination where a test might be made at a comparatively early stage, and selected individuals for propagation taken from a progeny. While this has some uses, and particularly some experimental uses, it has obvious limitations as a really successful method of vegetative propagation for plantation work.

Budding and Layering

Budding has been tried on a number of species, but so far success has been achieved only with *E. Blakelyi* to itself when about one in ten buds took. In other cases, the shield of tissue has been successfully grafted, but the bud has been lost and has not sprouted subsequently. The result, therefore is not encouraging with this method, although again, the fact that a few have been successful suggests that more thorough trial is warranted.

A number of layers of young plants in their first year have been made, and success, again at a very low figure, has been obtained with one or two. *E. pauciflora* particularly, rooted in this way in a few months after being pinned into an adjoining pot.

Grafting

Two methods have given considerable success. First, *approach grafting* of a mature shoot from a large tree on to a seedling in a pot has resulted in a limited amount of success, and one or two grafts of *E. bicostata* have been made in this way, which are now growing in their second year.

Inarch grafting between seedlings of the same age gives a fairly high percentage of success, but again has obviously limited application.

Bottle grafting as described by Fielding (1948 a) is, up to the present, the most promising method tried. The base of the scion is left free in water in a tube and the best results so far have been found by cutting off the top of the stock a little above the point of graft *(Plate II).* About 75% success is achieved with this method and several species have been grafted on seedlings of the same species or other species, in particular: — *E. Blakelyi* on *E. Blakelyi; E. ovata* on *E. Blakelyi; E. bicostata* on *E. bicostata; E. dives* on *E. Lindleyana; E. ficifolia* on *E. ficifolia; E. maculosa* on *E. bicostata,* and Fielding records success with thirteen species, namely: —

E. bicostata, E. Blakelyi, E. Dalrympleana,
E. globulus, E. grandis, E. maculosa,
E. viminalis, E. dives, E. Robertsoni,
E. bosistoana, E. Stuartiana,
E. macrorrhyncha and *E. racemosa.*

It is noticed in this method that callusing sometimes takes place at the base of the scion, and roots may develop in the free water and there is a possibility that a scion may be established as has been done on a few occasions with *E. Blakelyi,* on its own roots, after a period of support by the stock through the graft. For experimental purposes, and for the propagation of a limited number of grafts for special purposes where the cost of the grafting is not a material factor, this method is fully feasible, and with some refinement it may be used with advantage.

Grafts have been successfully made, especially with *E. bicostata,* using scions from mature trees carrying buds *(Plate III).* These have been carried on in the glasshouse until flowering, whereupon they were pollinated and carried through successfully to produce ripe capsules and viable seed. In this case it was noted that a much larger number of viable seed was produced per capsule than is normally the case. The possibility, then, of carrying out hybridization on the bench comparable with the way in which it has been done with *Larix* and *Pinus,* is open for development.

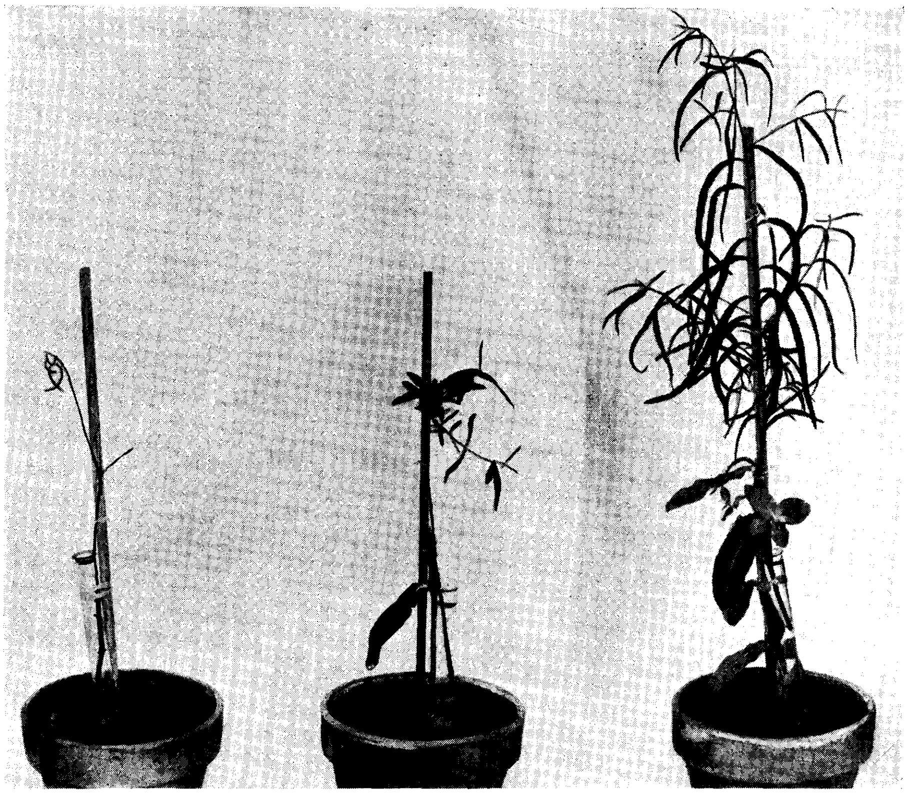

Plate II. — *Left:* Control: Scion in water but not grafted. — *Centre:* Scion of *E. maculosa* grafted on *E. bicostata* stock but the top of the stock not cut off until six weeks after grafting. — *Right: E. maculosa* grafted on to *E. bicostata,* the top of the stock cut off at the time of grafting. Photographed 11 weeks after grafting.

Plate III. — *E. bicostata* scion from a mature tree carrying buds at the time of grafting. The graft was successful and the buds subsequently flowered and set good seed.

A Breeding Programme

There are many ways in which investigation of *Eucalyptus* to improve the cold resistance of various species can proceed, some of which will depend upon the results of more general research as has been indicated above. Improved cold resistance in quite sensitive species such as *E. citriodora* may be of importance at times, but the main interest lies in taking already resistant species and developing still more resistant forms from them. In this latter case especially there are some obvious ways of approach which can be put immediately into effect and which will produce useful results.

1. Species Trials. Cold resistance of *Eucalyptus* species in the Northern Hemisphere does not always correspond with the indications of their limits of endurance as deduced from their natural habitat of occurrence in Australia. For example, *E. parvifolia* is known to be one of the very frost-resistant species but its natural occurrence would not at first sight imply that it would survive the extremes it does. Adequate assessment of the various species which are available is an important first step and this can be gained only by planting in different localities a replicated collection of species. The most important species which are likely to contain the most frost resistant are set out in *Table I.*

2. Provenance Tests within Species. In a somewhat similar way provenance tests should be carried out within species by first selecting stands which are growing in the apparent coldest physiographic locality available, and secondly by taking trees of the best form from within a

Table I.

RENANTHERAE *)				*MACRANTHERAE-NORMALES*			
Well-drained soils		Swampy Soils		Well-drained Soils		Swampy Soils	
Possible timber trees	Small trees	Possible timber trees	Small trees	Possible timber trees	Small trees	Possible timber trees	Small trees
				Gunnii	*vernicosa*		
pauciflora	*Kybeanensis*	*stellulata*		*Dalrympleana*	*Perriniana*		*parvifolia*
	Moorei var.						
coccifera	*latiuscula*			*urnigera*	*pulverulenta*	*camphora*	*neglecta*
Mitchelliana				*glaucescens*		*aggregata*	
gigantea			*Moorei*	*subcrenulata*			
salicifolia				*nitens*			
Robertsoni				*viminalis*			
				Johnstoni			
fastigata				*rubida*			

*) It is believed the *Renantherae* mostly require a specific mycorrhizal fungus for thrifty growth, and tests with this group should take account of this probable need also.

The species are arranged horizontally in approximate order of cold resistance — the most resistant are at the top of the table.

cold resistant species. For example, *E. pauciflora* occurs as a small shrubby tree on the edges of high altitude frost hollows, and it also appears as a tall forest tree of 90 feet. The same applies to *E. coccifera*. There are at least two distinct races of *E. gigantea*[5]), one of which is likely to be more cold resistant than the other, and there are some sites which *E. gigantea* penetrates which are certainly colder than many of the more easily accessible ones. At the same time, *E. Gunnii*, while often a small straggling species, occasionally occurs in better stands and it is likely that seed can be obtained from stands with a form very distinctly better than that which has been the common source of seed which is now in use outside Australia. The same applies to *E. camphora*. On the other hand *E. Dalrympleana* occurs over quite a wide area and more cold resistance might be found in some stands from isolated high altitude frost hollow pockets than is the common case. However, as has been said before it is very likely that heritable characters will be found in stands sought from particular localities in this way, and the trials can embrace not only a search for extreme sites for the good timber producing species but also better forms of cold resistant trees which are normally not timber producers.

3. *Tests with Progeny from Natural Hybrids.* The opportunity for raising segregating populations offers the chance of testing combinations which could not otherwise be reached, assuming favourable conditions for the production of seed, for 10 years. *Table II* sets out some of the hybrids which are known to occur naturally, seed from which could possibly produce recombinants of particular value in some localities. The combination of swamp resistant species with those of good form offers especial promise, such as *E. Dalrympleana* × *E. camphora*. Or the incorporation of considerably greater resistance to cold in a first-class timber producing tree such as *E. gigantea* in the combination *E. pauciflora* × *E. gigantea* could be of special value.

Table II. — Some known Natural Hybrids of Potential Value for Selection of Recombinants

Macrantherae	*Renantherae*
Dalrympleana × *camphora*	*pauciflora* × *gigantea*
Dalrympleana × *viminalis*	*pauciflora* × *Robertsonii*
Dalrympleana × *Gunnii*	*gigantea* × *Robertsonii*
Dalrympleana × *glaucescens*	*gigantea* × *coccifera*
Johnstoni × *globulus*	*gigantea* × *salicifolia*
nitens × *viminalis*	*stellulata* × *Robertsonii*
parvifolia × *viminalis*	*Robertsonii* × *fastigata*
aggregata × *rubida*	*fastigata* × *obliqua*

4. *Artificial Hybridizing.* There are very many combinations which potentially could lead to valuable results. Much hybridizing work may show its full benefits when F_2 or backcross generations can be produced. The more obvious lines to follow in detailed experiment are the synthetic production of potentially reasonably good timber producing trees by using a shrubby species of superior cold resistance with known good timber producers, as shown in columns *(a)* and *(b)* of *Table III*. A further set of combinations by perhaps extending experimental work into less certain fields is represented by a series of crossings that might be made between species of the group *Transversae*[6]) and species of the group *Macrantherae-Normales*[6]). Several naturally occurring combi-

Table III. — Artificial Hybrids

(a) RENANTHERAE		*(b) MACRANTHERAE-NORMALES*		*(c) TRANSVERSAE × MACRANTHERAE-NORMALES*	
Good Timber Trees	*More Cold Resistant but less good timber species*	*Good Timber Trees*	*More Cold Resistant but less good timber species*	*Good Timber Trees*	*More Cold Resistant but relatively less good timber species*
gigantea	*pauciflora*	*Dalrympleana*	*vernicosa*	*saligna*	*Gunnii*
regnans	*Kybeanensis*	*subcrenulata*	*parvifolia*	*botryoides*	*Dalrympleana*
obliqua	*coccifera*	*nitens*	*neglecta*	*grandis*	*vernicosa*
fastigata	*stellulata*	*bicostata*	*Perriniana*	*robusta*	*Perriniana*
pilularis	*Mitchelliana*	*globulus*	*Gunnii*	*resinifera*	*glaucescens*
Sieberianae		*quadrangulata*	*pulverulanta*	*diversicolor*	*neglecta*
oreades		*viminalis*		*propinqua*	*parvifolia*
Andrewsii		*camaldulensis*			
microcorys					

[5]) *E. gigantea* Hook f. is the name used by Blakely. The name *E. Delegatensis* Baker and Smith has priority according to the International Rules and is widely known.

[6]) The groups are given in Blakely's "*Key to the Eucalypts*", 1955.

nations of this general nature are known to occur and two of these have been made synthetically, leading to the production of rather vigorous F_1 hybrids, namely *E. pulverulenta* × *E. grandis* and *E. cinerea* × *E. robusta* (PRYOR, 1955). It seems therefore that continued experiment in combinations of this kind would be very well justified in view of the highly desirable sylvicultural and timber qualities which many of the species of the *Transversae* carry.

Summary

Improvement of resistance to low temperatures is important in the Northern Hemisphere because in localities where the mean minimum temperature is similar to corresponding localities in Australia the extreme minimum is often considerably lower. Many *Eucalyptus* species are widespread and display regularly clinal variation corresponding with changes in habitat such as those that accompany altitude or latitude, and physiological behaviour corresponds closely with clinal sequences. Careful attention to seed provenance would lead to great improvements, firstly by selecting more cold resistant forms of species being used, and secondly by taking trees of the best form from within a cold resistant species. *Eucalyptus* hybrids occur frequently in Australia where interbreeding species meet in a common boundary in the field. These hybrids can be especially valuable in providing a source of seed to raise segregating progenies from which more cold resistant recombinants can be selected. Some groups of *Eucalyptus* species do not hybridize naturally but a great many do, and careful field search often discloses localities where two species meet, even though this may occur rarely. Some hybrids have been synthesized between species which never occur naturally side by side. It is certain at the moment that manipulated hybridizing would be successful between many species of the *Transversae* and the *Macrantherae-Normales*. In the latter group some of the most cold resistant species of the genus are found, while in the former many good though relatively cold sensitive timber trees exist. Vegetative propagation is possible, but no technique which is satisfactory for large-scale production has yet been worked out. It is likely that experiment would lead to the development of a successful method. It is concluded that a breeding programme should follow four main lines: (1) an accurate assessment of cold resistance of various species; (2) provenance tests with seed from within species; (3) tests with progeny from natural hybrids; (4) artificial hybridizing and the development of vegetative propagation.

Résumé

Titre de l'article: *Sélection et amélioration des Eucalyptus pour la résistance au froid.* —

L'amélioration pour la résistance aux basses températures est importante dans l'hémisphère Nord parce que, dans les stations où les moyennes des températures minima sont analogues à celles des localités correspondantes en Australie, les minima absolus sont souvent beaucoup plus bas.

Beaucoup d'espèces d'*Eucalyptus* ont une aire de répartition étendue et manifestent une variation clinale régulière correspondant avec les variations d'habitat en latitude et en altitude, et leur comportement physiologique correspond parfaitement à ces variations clinales. Le choix de la provenance des graines pourrait permettre d'aboutir à une amélioration considérable, en premier lieu en sélectionnant des types plus résistants aux froids dans les espèces utilisées actuellement et en second lieu en prenant des arbres de la meilleure forme possible parmi les espèces résistantes au froid.

Des hybrides existent fréquemment en Australie dans les stations où interfèrent deux espèces susceptibles de s'hybrider. Ces hybrides présentent un intérêt particulier : les descendants issus de leurs graines peuvent permettre de sélectionner, grâce à la ségrégation, puis à la recombinaison des caractères, des types plus résistants au froid. Certains groupes d'espèces ne s'hybrident pas naturellement, mais un grand nombre d'espèces en sont capables, et souvent une recherche soigneuse sur le terrain révèle des stations où deux espèces cohabitent, même si cela se produit rarement. Certains hybrides ont été réalisés artificiellement. Il et aujourd'hui certain que l'hybridation artificielle peut réussir entre de nombreuses espèces des *Transversae* et des *Macrantherae-Normales*. On trouve dans ce dernier groupe certaines des espèces les plus résistantes au froid du genre *Eucalyptus*, tandis que le premier groupe comprend beaucoup d'espèces économiquement intéressantes mais assez sensibles au froid.

La multiplication végétative est possible, mais aucune technique de multiplication en masse n'a encore été mise au point; mais il est probable qu'une recherche plus poussée permettrait d'aboutir dans ce domaine.

En conclusion, un programme d'amélioration devrait suivre quatre lignes principales: — (1) Evaluation précise de la résistance au froid des diverses espèces. — (2) Expériences de provenances avec des graines récoltées dans diverses régions de l'aire de ces espèces. — (3) Expériences comparatives sur les descendances des hybrides naturels. — (4) Hybridation artificielle et poursuite des recherches sur la multiplication végétative.

Zusammenfassung

Titel der Arbeit: *Kälteresistenz-Züchtung bei Eukalyptus.* —

Züchtung auf Frostresistenz dürfte für erfolgreichen Anbau von *Eucalyptus* in der, vom Herkunftsland Australien aus beurteilt, kühleren nördlich-gemäßigten Zone eine entscheidende Voraussetzung sein, vor allem wenn man an die zwar seltenen, aber regelmäßigen Kältejahre im Anbaugebiet denkt, die von der eingeführten Holzart eine übernormale, zusätzliche Frosthärte erfordern.

Die Gattung *Eucalyptus* ist artenreich; im klassischen Werk von BLAKELY sind 500 Arten und 150 Varietäten beschrieben. Eine kritische Durchsicht der Systematik, unter Berücksichtigung genetischer Erkenntnisse der neueren Zeit, würde wahrscheinlich jedoch mit 250 guten Arten auskommen (species sensu lato, die die geographischen und edaphischen sub-species jeweils mit umfassen).

Ökologisch interessant und genetisch offenbar entscheidend ist die Tatsache, daß die Arten streng standortspezifisch sind, d. h. Änderungen der ökologischen Situation selbst auf sehr kleiner Fläche sind von Änderungen in der Artenbestockung begleitet. Oder: ähnliche ökologische Situationen in jedoch unterschiedlicher Höhenlage oder geographischer Breite werden, selbst wenn nur 100 km entfernt, von zwar verwandten, aber deutlich verschiedenen Arten bestockt. Nur in wenigen Fällen nehmen eine oder zwei Arten ausgedehnte zusammenhängende Gebiete ein.

Im Naturvorkommen ist also der Kleinbestand mit 2 oder 3 Arten offenbar die Regel. Er ist vom nächsten verwandten Kleinbestand räumlich durch Bestände anderer Artenkombination getrennt und wahrscheinlich genetisch isoliert. Mit wachsender räumlicher Trennung verwandter Bestände und noch mehr, wenn mit wechselnder Höhenlage oder geographischer Breite ein ökologischer Gradient auftritt, zeigen die Artenvertreter ausgeprägte phänotypische Unterschiede, die weitgehend genetisch festgelegt sind und so weit gehen können, daß man von sub-species sprechen muß. Diese Verschiedenheit des Phänotyps einer Art von Population zu Population verläuft in kleinen Stufen (bei räumlich getrennten Kleinbeständen), oder kontinuierlich (bei Wäldern mit durchlaufender Artenzusammensetzung) und wird als „cline" bezeichnet. Diese Clinal-Variation kommt bei den meisten species vor. Neben den morphologischen Merkmalen verschieben sich auch physiologische Merkmale, z. B. Wuchsleistung und Frostresistenz. In einigen Fällen, so bei *Euc. pauciflora,* ist die Erblichkeit einer ganzen Anzahl solcher morphologischer und physiologischer Merkmalsunterschiede sowie die lineare Korrelation zur Höhenlage des Herkunftsgebietes durch Versuche nachgewiesen. Für ein Züchtungsprogramm auf Frostresistenz bedeutet das, daß die Saatgut-Herkunft, ähnlich wie auch bei anderen Holzarten, Verhalten und Leistung der Nachkommenschafts-Population weitgehend bestimmen kann, und daß für den Erfolg des europäischen *Eucalyptus*anbaus die Saatgut-Auswahl in geeigneten Wuchsbezirken Australiens von entscheidender Bedeutung sein muß.

Im Gegensatz zur Gattung *Quercus*, mit der sich *Eucalyptus* in vieler Hinsicht vergleichen läßt, ist Selbststerilität für *Eucalyptus* nicht typisch. Bei vielen Arten kommt Selbstbestäubung vor, während bei anderen, zumindest für individuelle Bäume, Allogamie obligatorisch zu sein scheint. In solchen Fällen kann die Selbststerilität unterschiedlich scharf ausgeprägt sein (z. B. *Euc. bicostata*), was möglicherweise genetisch gesteuert ist. Intraspezifische Kreuzung muß schon deswegen vorkommen, um die genetische Vielfältigkeit zu erhalten, die für *Eucalyptus*arten so typisch ist. Der Anteil der Xenogamie bei völlig selbst-fertilen Arten läßt sich nur schwer nachweisen. Zeigen ließ sich aber (Versuche mit Baumpaaren von *Euc. fastigiata* und *E. Robertsonii*), daß interspezifische Kreuzung zwischen Freilandbäumen bei einer Entfernung von 100 m voneinander etwa 1% ausmacht und bei geringeren Entfernungen steigt, bis zu 25% bei 5 m. Selbst der geringe Anteil von 1% wäre genügend, um Bastardformen in den Grenzzonen zwischen zwei Artvorkommen aufrecht zu erhalten und erhebliche Gen-Verschiebungen zwischen kreuzungsfähigen Arten eintreten zu lassen.

Natürliche Artbastarde bei *Eucalyptus* kommen vor. Das Auftreten ist nicht gesetzlos; auch können nicht alle species oder Artengruppen, zumindest unter natürlichen Verhältnissen, miteinander bastardieren. Die kleinbestandsweise Verbreitung der Arten (s. oben) bringt es mit sich, daß bastardierungsfähige Arten räumlich meist scharf voneinander getrennt sind. Gelegentlich treffen sich solche Artenpaare aber auf Übergangsstandorten, und hier finden sich dann fast stets Artbastarde. Die Häufigkeit des Vorkommens von Artbastarden in solchen Zonen ist variabel und hängt, wie üblich, von mehreren Faktoren ab, z. B. der Schärfe des Standortunterschiedes, dem Grad der genetischen Isolierung der Arten und der Vitalität der Bastarde. Meist sind „entfernte" Bastarde wenig vital (frühe Sterblichkeit, geringer Wuchs), während an F_1-Bastarden nahe verwandter species in einigen Fällen Heterosis beobachtet werden konnte. Freilandbeobachtung und Versuch bestätigen übereinstimmend, daß gewisse Artengruppen innerhalb des genus, die etwa den Wert von Unter-Gattungen haben, nicht mit Artvertretern anderer solcher Gruppen (Unter-Gattungen) bastardieren, während innerhalb der Gruppen Bastardierung häufig ist. Z. B. wurde bisher kein Bastard zwischen species der *Renantherae*-Gruppe mit species irgendeiner anderen Gruppe gefunden. Dieser Komplex spiegelt sich in der Artenzusammensetzung natürlicher Bestände wider und hat sicher waldbauliche Bedeutung. Natürliche Bestände sind selten Reinbestände; vielmehr kommen zwei oder drei Arten in Mischung vor. Immer in solchen Fällen gehören die Mischholzarten zu Artengruppen, die kreuzungsunverträglich sind. Der Grund für die Unverträglichkeit ist nicht bekannt. Zytologisch zeigen die Artengruppen keine auffallenden Unterschiede.

Bezüglich der Vererbung von Merkmalen haben Nachkommenschaftsuntersuchungen bisher gezeigt, daß die meisten morphologischen Merkmale durch multiple Faktoren vererbt werden und daß Spaltung und Neukombination in den meisten Fällen möglich ist. Offensichtlich besteht aber eine Tendenz zu gekoppelter Merkmalsvererbung. Nachweisen ließ sich weiter, daß bei einigen Arten Resistenz gegen Blattinsekten erblich sein kann, ferner Rindeneigenschaften, Ölzusammensetzung und Form der Staubgefäße, welch letztere für die *Eucalyptus*-Systematik ja erhebliche Bedeutung hat.

Für die Züchtungsarbeit ist vegetative Vermehrbarkeit des Objektes immer erwünscht. *Eucalyptus* gehört zu den vegetativ schwer vermehrbaren Pflanzen. Es liegen aber Berichte über erfolgreiche Methoden vor; vor allem scheint Flaschen-Pfropfung ziemlich zuverlässig zu gelingen. Die Methode ist umständlich und kostspielig. Andere aussichtsreiche oder erprobenswerte Verfahren werden erwähnt, unter denen vor allem Stecklinge mit Lignotuber-Gewebe hervorgehoben werden.

Die Züchtung von *Eucalyptus* auf Kälteresistenz wird zunächst auf vorhandene, weitgehend frostharte Arten zurückgreifen und versuchen müssen, noch resistentere Formen daraus zu entwickeln. Das kann auf verschiedenen Wegen geschehen:

(a) durch Anbauversuche mit erfolgversprechenden Arten (s. *Tab. I*), wobei sich u. U. herausstellt, daß die eine oder andere Art weit tiefere Kältegrade verträgt als in ihrem Verbreitungsgebiet auftreten;

(b) durch Herkunftsversuche, die eingeleitet werden müßten durch Auswahl und Beerntung von Saatgutbeständen in den offensichtlichen Frostlagen des Ursprungslandes, ferner durch Selektion frostresistenter Lokalformen innerhalb der wertvollen Nutzholzarten, aber auch durch Selektion guter Nutzholzformen innerhalb bekannt frostharter Arten, die wegen geringen Holzwertes forstlich bisher unbeachtet geblieben sind;

(c) durch Anbauversuche mit Nachkommenschaften natürlicher Bastarde (s. *Tab. II*); aus Saatgut natürlicher Bastarde lassen sich in kürzester Zeit Nachkommenschaften heranziehen, unter denen Aufspaltung und Neukombination von Merkmalen zu erwarten ist, so daß dem Zuchtziel entsprechende Formen selektiert werden können;

(d) durch künstliche Kreuzung, wobei es vor allem um Einkreuzung größerer Frosthärte in wertvolle Holzarten geht *(Tab. III, a, b)*.

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Untersuchungen über Individualunterschiede im Schüttebefall bei Pinus silvestris L.

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(Eingegangen am 24. 9. 1956)

A. Einleitung und Fragestellung

Vor fünf Jahren wurde in Schmalenbeck mit der Resistenzzüchtung gegen die Kiefernschütte (*Lophodermium pinastri* SCHRAD.) begonnen. Auf dem Wege der Individualselektion gelang es inzwischen, eine Anzahl von widerstandsfähigen Kiefern zu finden. Über deren Eignung für die weitere Züchtungsarbeit wird man jedoch erst nach mehreren künstlichen Infektionen Verbindliches aussagen können (LANGNER 1951a, SCHÜTT 1957).

Mit dem Beginn dieses Vorhabens leitete LANGNER im Frühjahr 1951 Untersuchungen über die grundsätzliche Frage ein, inwieweit individuelle Befallsunterschiede in einer Population endogen bedingt sein können. Da das interessierende Merkmal — Schütteanfälligkeit — verhältnismäßig rasch in den Nachkommenschaften zu erkennen ist, können bereits jetzt einige Ergebnisse darüber mitgeteilt werden.

B. Material und Methoden

Aus mehrfach stark von der Schütte befallenen 4- bis 6jährigen Kiefern-Flächen wurde etwa die gleiche Anzahl wenig befallener („positiver") und stark befallener („negativer") Kiefern herausgesucht (Tab. 1) (LANGNER 1951 b). Beide Gruppen stellten in diesen Populationen etwa die Befallsextreme dar. Von ihnen wurden Reiser geworben und im Gewächshaus Pfropflinge hergestellt. Dabei fiel auf, daß die Anwuchsprozente bei den stark befallenen („negativen") Kiefern — vermutlich wegen ihrer herabgesetzten Vitalität — wesentlich niedriger lagen als bei den nur leicht befallenen („positiven"). Damit ist auch erklärt, warum einige Klone nur mit einem einzigen Pfropfling vertreten sind.

Zwei Jahre nach der Pfropfung kamen die Pfropflinge in das Infektionsquartier, wo sie im Spätsommer des gleichen Jahres dem Sporenflug ausgesetzt wurden. Eine Infektion läßt sich in der Weise erreichen, daß der Boden des Infektionsgeländes alljährlich mit einer dünnen Schicht Apothecien enthaltender Kiefernnadelstreu bedeckt wird. Regelmäßiges Feuchthalten während des Spätsommers fördert die Inokulation.

Während der Sommermonate 1955 und 1956 wurde mehrfach der Befall bonitiert. Wir bedienten uns dabei eines auf das Krankheitsbild von *Lophodermium* abgestimmten, sechsstufigen Bonitierungsschemas, welches Nadelalter und Exposition zur Sporenquelle berücksichtigt (siehe unten). Der Befall war 1955 stärker als 1956, innerhalb jedes Jahres aber auf der Fläche gleichmäßig. Die Ergebnisse der Einzeljahre wurden getrennt ermittelt und ausgewertet und später miteinander verglichen.