

apparently not receptive to pollen at this stage. A characteristic exudation indicative of its receptivity appears only 1–4 days after the operculum has fallen. Thus cross-pollination is usually favoured. However, that chance self-pollination is a distinct possibility is indicated by the following circumstances: All the flowers on the same eucalypt tree and even within the same inflorescence do not mature together and therefore transference of pollen from an younger flower to an older flower (with its receptive stigma) of the same individual can induce self-pollination, and as we shall see later, many species of eucalypts have been shown to be self-fertile. Again, in some species the inner anthers retain a little pollen longer and as their filaments unfold they more or less brush against the stigma of the same flower thus inducing selfing if successful cross-pollination has not already occurred. Sometimes pollen is shed before the operculum falls and pollen grains may be seen adhering to the stigma while the operculum is still in place. In short, while the eucalypt flower is suited for cross-pollination, self-pollination, at least to some extent, is always possible.

3. Breeding system

The few eucalypt species that KRUG and ALVES (1949) examined in Brazil, were self-sterile. However, most of the species that PRYOR (1951 a) examined in Australia produced ample fertile seed after self-pollination by hand. Self-fertility therefore exists in many eucalypts and inbreeding is possible. However, as we have already seen in the preceding paragraphs, eucalypt flowers are well adapted for cross-pollination and some outcrossing does occur. In fact the general variability of eucalypt populations indicates that sufficient outcrossing takes place and maintains quite a high degree of diversity in the populations. However, to what extent outcrossing normally occurs in nature remains to be estimated.

4. Controlled pollination

The flowers of eucalypts are not difficult to handle for controlled pollination (Fig. 2) so necessary in a breeding programme. Emasculation is easy and is done just before

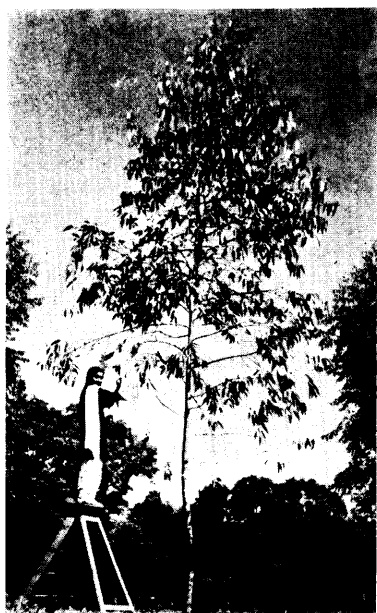


Fig. 2. — Controlled pollination on a 3-year old hybrid eucalypt. — Note the erect branch habit.

the operculum falls off from the flower bud. Using a safety-razor blade or a converted nail-clipper, a not-too-deep, circular incision is made into the receptacle just below the staminal ring. The cut top of the bud then neatly comes off as a lid carrying with it the operculum and the stamens, leaving behind intact the entire pistil. A few inner stamens that may still remain behind after such an incision can be picked away with forceps. In those few species where the stamens and operculum do not readily come off after the incision, a few longitudinal cuts may be given to release them from the stigma.

Muslin cloth or special terylene fabric was found suitable for bagging under the conditions prevailing at Dehra Dun. The bags, however, should not be kept too long after controlled pollination. At least in *E. tereticornis* and *E. kirtoniana* which have been investigated at present, all the flowers in a cluster do not mature at the same time. Therefore, to ensure that no selfing occurs, all the buds in a cluster may be emasculated at the same time and the stigma hand-pollinated repeatedly at intervals to get as many of them as possible in the receptive condition.

In all the controlled pollination trials done so far at Dehra Dun, fresh pollen was used from flowers opening at the time the emasculated flowers of the seed parents were receptive. However, successful storage of pollen has been shown to be feasible in eucalypts and this should be specially valuable where geographical separation and/or different flowering times prove to be a barrier to manipulated hybridization. Preliminary tests by PRYOR (1951 a) indicated that pollen can be stored in a refrigerator up to three months without serious loss of germinability. BODEN (1958) mentions of F_1 hybrids of *E. cinerea* F. MUELL. and *E. maculosa* R. T. BAKER having been successfully produced by using pollen stored for as long as 7 months in deep freeze at a temperature of -16° C.

In most species that PRYOR examined, the fruit took from 10–12 months to mature after pollination. The fruit is better harvested when it is fully ripe. Otherwise the seeds may not be plump.

5. Taxonomy

A taxonomic survey provides basic information of value to the breeder. *Eucalyptus* is a large genus and more than 500 taxonomic species have been named. But several of the eucalypts originally named as species have, on subsequent study, turned out to be merely segregating genotypes of interbreeding species. As we shall see later, natural interspecific hybridization is of rather frequent occurrence in eucalypts. Taxonomic botanists relying only on single herbarium specimens without accompanying field study of populations have often described hybrids as species. *E. kirtoniana* F. MUELL., a natural hybrid between *E. robusta* and *E. tereticornis* is just one case in point. Such examples can be multiplied. PRYOR has adduced evidence to show that many species which have been accorded species rank by BLAKELY in his key, are only hybrids. Thus there seems little doubt that as our knowledge increases of the crossability and range of variation within this genus, many of the taxonomic species may eventually come to be reduced to mere varieties or even genotypes of polymorphic species.

Ever since the treatment of this genus by BENTHAM, the structure of the anther, specially its shape, has been the primary feature on the basis of which this large genus is unequally divided into 5 major sections namely *Macrantherae*, *Renantherae* (including *Renantheroideae*), *Poran-*

theroideae, *Terminales* and *Platyantherae*. Of these, *Macrantherae* is the largest with more than 200 species and *Terminales* is the smallest with hardly 25 species. *Porantheroideae* and *Terminales* can and do naturally interbreed with one another whereas *Macrantherae* and *Renantherae* do not do so. On the basis of known interbreeding affinities of the foregoing groups, PRYOR (1959) feels that the genus consists of at least four subgenera which are almost entirely reproductively isolated from one another.

6. Chromosome constitution

Not much data is available on the chromosome number within this large genus. Most of the nearly 62 species of eucalypts investigated cytologically have a chromosome number of $2n = 22$ (RUGGERI, 1960). Only in a few species, a number of $2n = 20$ and $2n = 24$ have been reported (DARLINGTON and WYLIE, 1955; RUGGERI, 1960). At least as far as our existing knowledge goes, polyploidy seems to have played but an insignificant role in speciation within the genus. However, on account of the comparatively small chromosome numbers known, induced polyploidy through colchicine treatment and production of tetraploids and triploids, may be one line of improvement of desirable species of *Eucalyptus*.

Heritability of characters: —

Not much information is available about the genetics of eucalypts. Whatever knowledge of heritability of various characters we have, has been derived mostly from progeny trials of naturally occurring hybrids. However, inheritance of juvenile leaf characters have been studied in F_1 hybrids following controlled pollination also. In general, the characters are determined by multiple factors and consequently progeny derived from hybrids show a graded series of characters, intermediate in varying degrees between the two parents, rather than definite, clear-cut differences. The characters whose heritability PRYOR (1951 b, 1953 b) and others have studied pertain to anther shape, inflorescence, resistance to leaf cutting insects, juvenile leaf shape, juvenile leaf anatomy, bud and fruit shape, vigour of growth, presence or absence of ligno-tubers, bark and wood characters. In controlled *E. maideni* and *E. macarthuri* DEANE and MAIDEN hybrids, PRYOR (1951 a) noticed transmission of the highly distinctive geranium oil by the pollen of *E. macarthuri*. WILLIS (1951) studied the inheritance of oil yield and constitution.

PRYOR found that many juvenile leaf characters offer good markers for genetic studies in Eucalypts. In crosses between species with isobilateral juvenile leaves and those with dorsiventral juvenile leaves, the hybrids were intermediate between the two parents. This was also true of the distribution of the stomata. In crosses involving parents with no stomata on the upper leaf surface and those with more or less equal number of stomata on both leaf surfaces, the hybrids have some stomata on the upper surface of the leaf. Leaf anatomical characters such as number of layers of palisade cells, the proportion of stomata on the upper surface to the lower surface of the leaves, the number of epidermal cells surrounding the stomata, the size and nature of the stomatal chamber all showed the same type of inheritance pattern.

7. Interspecific hybridization

Occurrence of natural interspecific hybridization in eucalypts has been suspected since as far back as the years

1800–1810 when GEORGE CALEY correctly described some specimens he collected as those of a hybrid between *E. hemiphloia* BENTH. and *E. siderophloia* BENTH. (PENFOLD and WILLIS, 1961). BRETT (1937), both by study in the field and by progeny testing showed that natural hybridization had occurred between many eucalypts of Tasmania resulting in hybrid swarms. By progeny testing and by using as genetic markers, the distinctive morphological characters of juvenile leaves of many species, and in some cases by experimental synthesis of hybrids by controlled pollination, PRYOR (1951 a,b) has provided conclusive evidence for interspecific hybridization in eucalypts. He further deduced (1953 a) that in their native habitats in Australia, potentially interbreeding eucalypt species are ecologically isolated and those that occur sympatrically, are reproductively isolated. BODEN (1964) states that each eucalypt community in Australia contains 2 or 3 codominant species which do not interbreed. Thus for example, in the Southern Highlands of Australia, species of the three non-interbreeding subgenera *Macrantherae*, *Renantherae* and *Terminales* occur side by side in the field without crossing with each other. But when natural communities containing species of the same subgenera come into mutual contact at ecological population boundaries, natural interspecific hybrid swarms are formed even in undisturbed natural communities. Where disturbance has occurred through man's activities such as clearing, grazing and fire, such natural hybrids occur in even greater numbers (e.g. *E. robusta* SM. and *E. grandis* MAIDEN; *E. tereticornis* SM. and *E. robusta* SM.). From all the foregoing facts, it would appear that interspecific hybridization and introgression have played a significant role in speciation within the genus and to this, disturbance of the primeval habitats of eucalypts and creation of intermediate habitats by man's activities must have contributed its part.

From what has been said in the foregoing paragraphs it follows that if natural geographical barriers are eliminated, certain eucalypts can be expected to hybridise with each other. Such is the situation in an arboretum or a plantation containing closely placed individuals of potentially intercrossable species provided, of course, they flower at the same time. Alternatively, artificial hybrids can also be produced by manipulated pollination.

There is evidence of heterosis effect in species crosses of eucalypts. Hybrids produced between *E. robusta* and *E. pulverulenta* SIMS, and between *E. maideni* and *E. bicostata* MAID., BLAK. et SIMS. have grown vigorously. SHELBORNE (1962, 1963) reports that in Rhodesia naturally occurring hybrids of *E. saligna* and *E. grandis* HILL. with *E. camaldulensis* and *E. tereticornis* have shown definite hybrid vigour. They continue fast growth even after they reach 12.20 m. — 15.25 m. (40–50 feet) while height growth of either *E. saligna* and *E. grandis* normally slows down considerably after this stage. Hybrids of *E. grandis* and *E. tereticornis* produce a durable heavy pole combining the excellent form of the former with timber properties of the latter. BODEN (1964) has suggested production of F_1 hybrid combinations between the following species for trials in particular habitats of India: *E. grandis* and *E. robusta* for areas with poor drainage and also a certain degree of salinity; *E. gomphocephala* DC. and *E. cornuta* LABILL. for calcareous soils; *E. botryoides* and *E. camaldulensis* (the hybrid found in Algeria and named *E. trabuti* VILMORIN) as well as *E. tereticornis* and *E. rudis* for wet sites and *E. globulus* and *E. maideni* F. v. M. to extend the range of *E. globulus* on to poorer soil types.



Fig. 3. — A 3-year old flowering tree of *E. tereticornis* in the foreground. — Note the drooping branch habit.

At Dehra Dun attempts are being made to produce hybrids of *E. tereticornis* (Fig. 3), *E. robusta*, *E. rudis* and *E. camaldulensis* by controlled pollination. It has been found that these species do not all flower at the same time. However this difficulty of differing flowering times may be overcome by resorting to pollen storage under below freezing temperatures as already indicated. Work is in progress in this direction.

8. The "Mysore hybrid" and its further improvement

From available literature on the subject, the history of the "Mysore hybrid" seems to be as follows: According to NANJUNDAPPA (1957) and KAIKINI (1961) some old *Eucalyptus* trees exist in the Nandi hills in the Mysore state some of which are up to 6 feet in girth. The exact time of the introduction of these plants from Australia is not known but since the year 1937, bulked seeds from these mother trees have formed the initial source wherewith all the earlier plantations of eucalypts in the state were raised. These latter plantations in turn are now the main source of the so called "Mysore hybrid" *Eucalyptus* seed which is now being utilized to raise newer plantations on a large scale in several states of India. However, not till the years 1954–55 was an attempt made to identify the species of these several old mother trees on Nandi hills. Herbarium sheets of these trees were sent to Australia during these years and the identification revealed that not only did these trees represent 10 different species but that along with them there were also some trees which were natural hybrids. From herbarium specimens, the hybrids were identified as possible combinations between *E. robusta* and *E. tereticornis*; *E. botryoides* and *E. tereticornis*, and *E. tereticornis* and *E. camaldulensis*. Presumably it was from this time onward that the term "Mysore hybrid" *Eucalyptus* or *Eucalyptus* "hybrid"—Chickballapur variety gained currency among foresters of this country, although it is quite clear from what has been said above that this entity is a mixture of pure species as well as of some genetic segregates of interspecific hybrids. Interspecific hybridization between some species of eucalypts is fairly frequent as we

have already seen. In fact, according to BODEN (1964), progeny trials conducted in Australia reveal that the species named as *E. kirtoniana* F. v. M. is a natural hybrid between *E. robusta* and *E. tereticornis*. All of the four pairs of species involved in the "Mysore hybrid" belong to the same section *Macrantherae*. Within this large section free hybridization is known to occur within some of the subgroups. Under plantation conditions geographical barriers are eliminated and therefore if the flowering times synchronise intercrossing can be expected. Besides the above four species, others like *E. saligna*, *E. grandis*, *E. longifolia*, *E. propinqua*, *E. punctata* and *E. rudis* come under the same interbreeding group so that any of them are likely to hybridise between themselves provided they flower at the same time. We have, however, no available data on the flowering norms of these species wherever they are under cultivation in India and therefore we cannot say if natural hybridization between these species is occurring in this country also. Many of the flowering and fruiting specimens examined during a recent visit to plantations of the "Mysore hybrid" in Mysore and Madras states were such as to be readily classified as *E. tereticornis*. But there were others which appeared to be segregates of one of the interspecific hybrids. Identification of the remaining trees in such plantations will have to await their coming to flower and fruit which are essential for identifying closely related eucalypts. However, at least at present, since seed for further planting work is being collected only from these fruiting trees, such selective harvesting may eventually result in almost pure stands of *E. tereticornis*. This species in its native Australia occurs over a wide latitudinal range of 2,000 miles and under cool temperate to tropical conditions. It also occurs in New Guinea. Hence for any future comparisons between this species and the *tereticornis*-like isolates from the "Mysore hybrid" complex, it is advisable to obtain specific provenances from different parts in the natural range of *E. tereticornis*. Provenance trials of other widespread species like *E. camaldulensis* and *E. grandis* are also desirable.

To what extent existing populations of eucalypts derived originally from the "Mysore hybrid" seed source are really of hybrid parentage and to what extent they are mere mechanical mixtures of discrete species can be known only when a detailed genetic analysis is conducted. However, in either case the population derived from this seed source is expected to show a wide range of variability, the result of seed mixture of pure species as well as of genetic segregation of hybrids originally formed. It would be interesting to find out and identify the individual trees that do best and dominate in plantations raised originally from seeds of the "Mysore hybrid" and located in different environmental conditions. Whatever these may turn out to be, such dominant and best individual trees would be those that have been naturally selected and have survived best under the particular environments they have been growing in. Such trees are worthy of preservation as seed trees (Fig. 4). If a sizable number of such trees exist in a particular plantation, at least part of that plantation should be converted into an *Eucalyptus* seed production area to ensure future seed supply of the desired species or hybrid segregates best suited for the site in question and thereby avoid perpetuation of the variability of the same entity "Mysore hybrid" over and over again. Needless to say that such seed production areas besides helping evolve by selection types specially adapted to particular localities will also make the different states and areas more and more

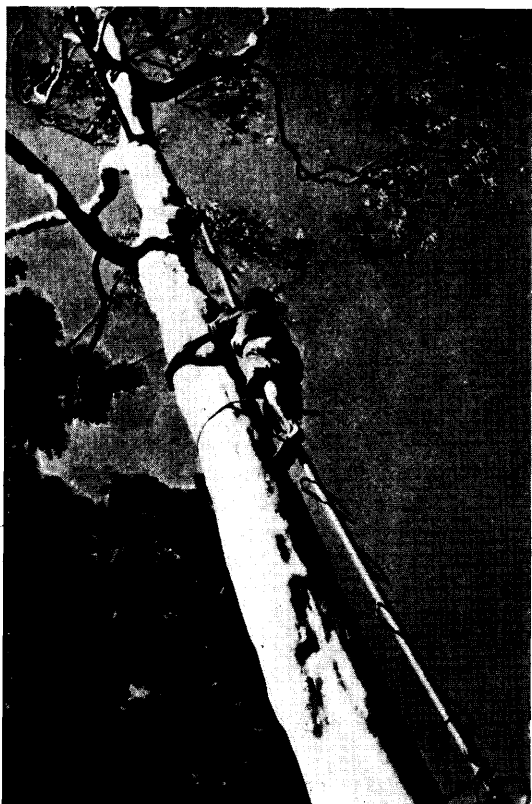


Fig. 4. — A seed collector climbing up a selected eucalypt tree for seed collection.

self-sufficient in regard to seed supply of *Eucalyptus* best suited to their own environments. Large quantities of bulked seed need not have to be imported from other areas or states with differing environments.

By simple selection in planted populations of eucalypts, an almost two fold increase of wood production per acre has been achieved in Brazil, (KRUG and ALVES, 1949).

The field forester may foresee certain practical difficulties in the removal of undesirable trees from stands of the "Mysore hybrid" eucalypt to create seed production areas. For instance, by such an action, in some parts of a stand good trees may be left too close together whereas elsewhere there may result wide blank spaces after removal of the undesirable trees. Such a difficulty is likely to arise in the creation of any seed production area and does not really matter. It should be recalled here that seed production areas are not themselves exploited for timber. They merely serve to produce good quality seeds in sufficient quantities to raise other plantations for commercial exploitation. Therefore, in the seed production area itself, it is not essential to have uniformly spaced trees all of the same age and girth class. The blank spaces can always be filled in by replacements from progenies raised from seed of selected trees.

Summary

The importance of introductions of Australian eucalypts in Indian forestry is indicated. Existing knowledge on the

floral biology, cytology and genetics of this genus is briefly reviewed because of its bearing on future genetic improvement of species of eucalypts cultivated in India. Possibilities of exploiting hybrid vigour by controlled interspecific hybridization are indicated. The status of the entity commonly known as "Mysore hybrid" *Eucalyptus* is discussed in relation to its possible origin. Selective improvement is suggested of existing plantations of this entity.

Résumé

Titre de l'article: *Amélioration des Eucalyptus en Inde.*

On signale l'importance pour la foresterie indienne des introductions d'*Eucalyptus* d'Australie. Les connaissances actuelles sur la biologie florale, la cytologie et la génétique de ce genre sont brièvement passées en revue en raison de leur rapport avec l'amélioration génétique des espèces cultivées en Inde. Les possibilités d'exploiter l'hétérosis suivant des hybridations contrôlées interspécifiques sont signalées. La structure du complexe appelé communément «Mysore hybride» est discutée sous l'angle de ses origines possibles. On suggère de pratiquer des sélections dans les plantations existantes de ce type.

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