seed. The extremely low moisture content of the pollen undoubtedly plays an important role in such a comparison. Although the limited data indicatec that nuclear lethality might be expected at approximately 20 kr, additional study is underway in our laboratory to evaluate a broader range of radiation exposures; the results of that investigation will be published in a later edition of this journal.

Summary

The radiosensitivity of pre-meiotic male buds from Pinus nigra was examined in the exposure range of 0 to 2 kr. Exposures above 0.5 kr caused severe cytological damage and it is suggested that treatment of male buds for mutation induction work be restricted to levels below this value. Analysis of irradiated pollen was made for several conifer species. In vitro germination was obtained up to 600 kr with an LD-50 at approximately 200 kr. These pollen germination values are assumed to represent cytoplasmic tolerances only. The pollen nucleus sensitivity was examined in a breeding study using Picea *glauca*. Exposures ranged from 0.5 to 4 kr, with a significant increase in empty seed at the higher level, although seed germination based on total filled seed did not show a treatment effect.

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Variation and Taxonomy in Eucalyptus camaldulensis

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(Received for publication November 24, 1967)

Introduction

Eucalyptus camaldulensis, widely called Red Gum is one of the best known of eucalypts both in the wild and as a cultivated plant (Figure 1). In natural occurrence it is confined to the Australian mainland and it does not appear in Tasmania nor is it found in New Guinea where half-a-dozen species of the genus grow naturally and are shared with Australia.

Within the main Australian landmass of some 3,000,000 square miles it is found in all States. In the ecological sense it has a striking feature. It is a species characteristic of watercourses — either along streams, on adjoining levee banks, or on nearby flood plains (Figure 2). In the case of watercourses in the more arid areas in which water flows spasmodically with long periods of no flow, it is often along the sandy bottoms and the margins too.

It is a distinctive and important tree of many rural Australian landscapes and it has some morphological peculiarities which are absent or infrequent in other species of the genus. In many areas it is often the largest tree by far in places where tree growth is difficult and where surrounding vegetation is at the best merely of tall shrubs. As a cultivated plant it is mainly a shelter or ornamental tree in southern Australia but in plantations outside Australia it is of particular importance as one of the most widely planted species, approached in frequency of use only by E. globulus, E. grandis, E. gomphocephala, E. tereticornis and E. viminalis.

Because of its sylvicultural prominence the need for closer examination of the variation patterns within the populations commonly assigned to this species for a century has often suggested itself. Such examination has become more readily possible in recent years with rapidly improving communications. In 1963 therefore, preliminary collections of seed and specimens were made from a range of sites and the study was supported by field examination in 1960 of the populations in Western Australia from Williams to the Murchison River and the peculiar and somewhat related situation in the vicinity of Wee Waa in New South Wales which had been examined first in 1956 by PRYOR and JOHNSON who will report the findings soon.

When provenance collections of seed of eucalypts were accelerated, in 1964 by the Australian Forest Research Institute it was obvious that E. *camaldulensis* should be one of the species first to receive attention. Substantial collections of seed were made from a wide range of localities in 1964 and these are at present the basis for tests in several extra-Australian localities. E. LARSON (pers. com.), J. F. LACAZE (pers. com.) and KARSCHON (1967). From these tests and complementary ones in Australia much more detailed information will become available in the future and a great deal more will be known about the species. Nevertheless, with such a wide ranging species more intensive sampling and collection still will be necessary to understand it in the thorough way that some European or North American species are known.

While this study is of limited extent so far as the whole is concerned it has revealed a number of points of interest and it is possible to suggest some further ideas about the

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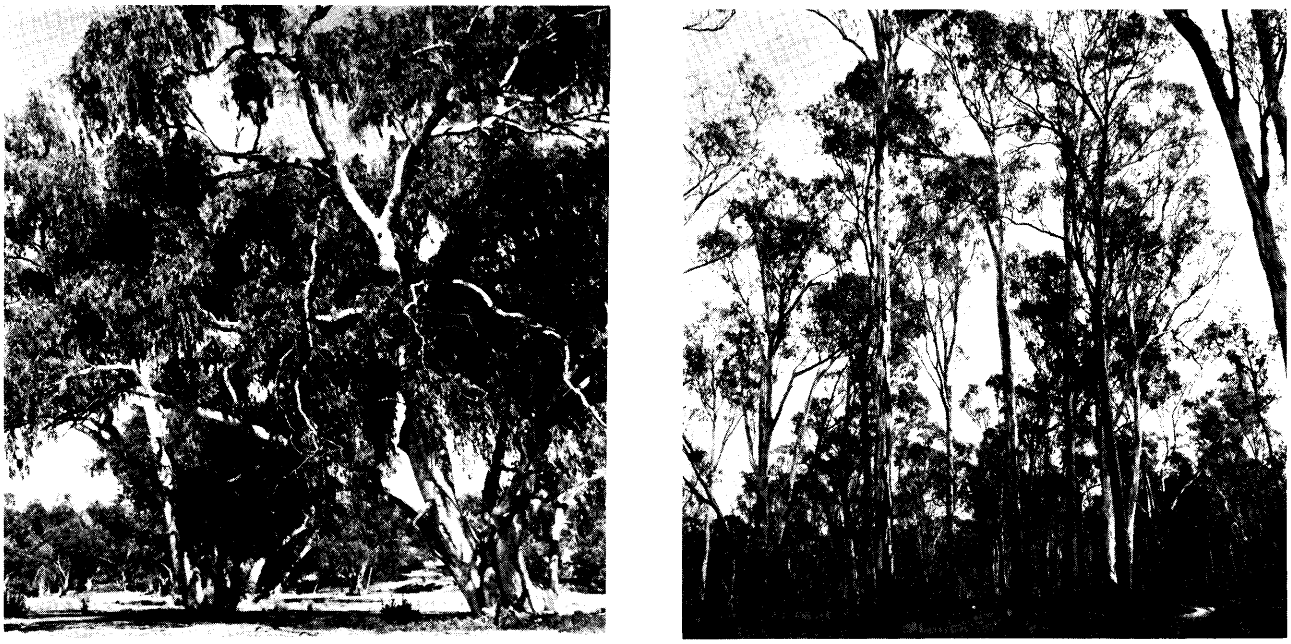

Fig. 1. — *Eucalyptus camaldulensis.* — Left: Northern form, Todd River, Alice Springs. — Right: Southern form near Tocumwal, N. S. W.

nature of the species. These will require critical scrutiny when still more information comes to hand in subsequent years.

Systematic and Nomenclatural Position of E. camaldulensis

The name *Eucalyptus camaldulensis* Dehnhardt is attached to a specimen in the Herbarium of the National History Museum in Vienna. This is a small leafy shoot with buds but no fruits and was collected about 1832 from a tree grown in a nursery near Naples in Italy. The specimen was seen by Maiden who considered it conspecific with *E. rostrata* Schlechtendal, this latter name being attached to a specimen from South Australia published in 1847. Subsequently, several authors familiar with the tree in the field in Australia have seen the Vienna specimen and are in agreement with Maiden's opinion. Because of the priority rules, Blakely accepting Maiden's view as to conspecificity rightly adopted the name *E. camaldulensis* in place of *E. rostrata* in his "Key to the Eucalypt" in 1935.

Nothing is known of the precise Australian origin of the seed from which the plant was raised in Italy and little more can be inferred other than by transferring the records and descriptions of *E. rostrata* to *E. camaldulensis.*

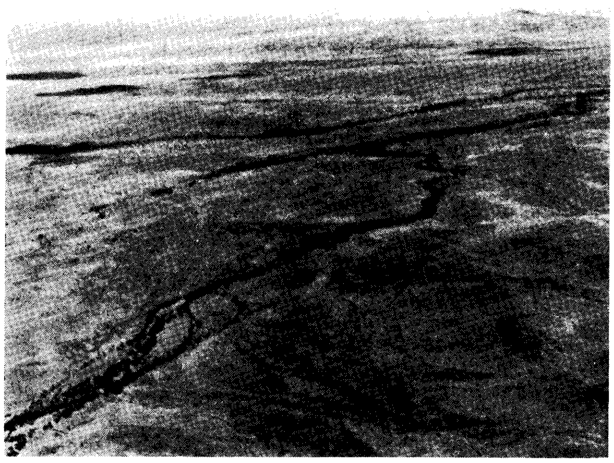

Fig. 2. — *E. camaldulensis* fringing an ephemeral watercourse in northern South Australia.

The type locality of *E. rostrata* in South Australia is probably in the vicinity of Adelaide or a little north of the city. As the name implies it has a distinctly rostrate operculum and so has the type specimen of *E. camaldulensis.*

Bentham and Mueller both applied the name *E. rostrata* to include forms, especially in the more northern parts of South Australia as for example near Oodnadatta, as part of the species even though the buds from these more northern situations were mostly ovoid and not often rostrate *(Figure 3).* This concept of the species was expanded by Maiden to cover the populations of Central Australia and north Queensland and north west Western Australia, and in doing so he accepted both the ovoid or rostrate bud as occurring in the species and regarded these alternatives and any intermediates merely as intraspecific variation.

Blakely (1955) in adopting the name *Eucalyptus camaldulensis* transferred this interpretation so that in his description he writes "Operculum ovoid to rostrate.......". Since the Type has rostrate buds this is an extension of the application of the name which the authorities felt justified in making regarding the whole of the populations thus encompassed as comprising a single species.

It happens that buds have been available in all the critical specimens and that these are of particular value in the taxonomy of the group. Other characters such as those of fruits or lignotubers may be of similar significance but they cannot be determined for the Type and have been treated in less detail historically. Indeed the study of lignotubers has been largely neglected.

E. camaldulensis belongs to a natural set of species grouped together by Blakely in his "Key to the Eucalypts" to form the series, Exsertae. Blakely divides this series into four sub-series; the Phaeoxyla containing *E. exserta* and *E. morrisii;* the Erythroxyla containing *E. tereticornis, E. amplifolia, E. blakelyi, E. dealbata, E. dwyeri;* the Liberivalvae containing *E. parramattensis, E. seeana* and *E. bancroftii;* and the Rostratae containing *E. camaldulensis* and *E. rudis.* He includes some species additionally in these series but their status as a species is questionable and discussion may be limited usefully to those listed above. As a whole they are known colloquially as the "Red Gums"

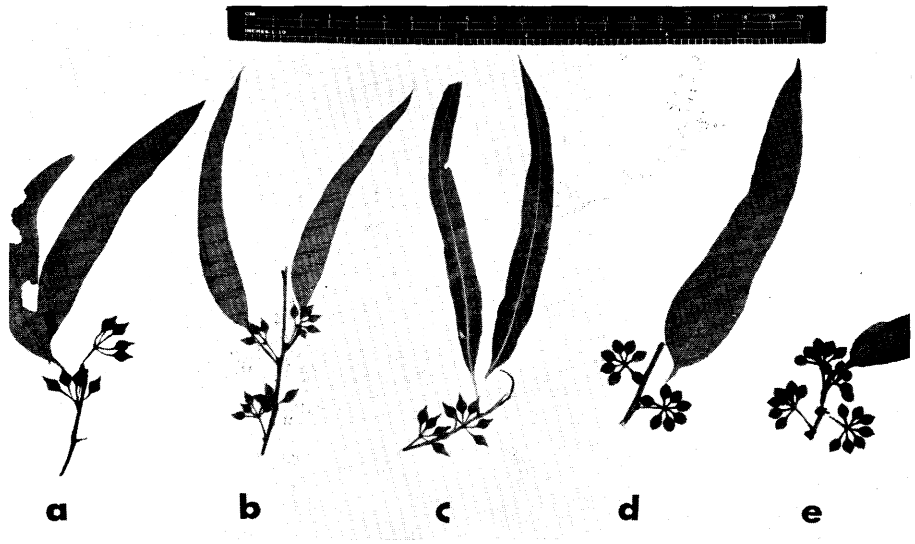

Fig. 3. — Bud variation in *E. camaldulensis.* — a. Port Lincoln. — b. Quorn. — c. Walgett. — d. Todd River. — e. Tennant Creek.

and they are regarded by most as a "natural" grouping distinctly "cut off" from other *Eucalyptus* species in their affinities and possessing a number of characteristics in common which justify their being unified in a single Series within the Genus as BLAKELY has placed them.

E. camaldulensis as described and as the name is applied to southern populations, stands somewhat apart from all of the other Red Gums in having a few features not found in the remainder of the group although it does of course display the common features. The special feature by which the Type is distinguished from others in the Series is the acuminate and rostrate operculum in the bud. Nevertheless this character is not consistent throughout the populations considered by BLAKELY to belong to the species and departure from recognising this character as an invariable feature of *E. camaldulensis* is recognized by his inclusion of at least two varieties, var. *brevirostris* and var. *obtusa* both of which have either non-rostrate buds and rounded opercula or at the most slightly acuminate opercula. Varietal categories of this kind are limited in value because they do not take into account the variation pattern in the population as a whole and represent a partial treatment based on the rather limited material available at the time.

Although under *E. camaldulensis,* BLAKELY lists several varieties, viz. *acuminata, brevirostris, obtusa, pendula* and *subcinerea,* these could be added to by many others of equivalent status if one so chose to select and erect them as varieties. The classical taxonomic approach has limited treatment of groups such as this and innovations to the treatment by MAIDEN and BLAKELY are necessary if more meaningful taxonomic results are sought. In spite of substantial population variation the fact remains that taken together the whole population which it must be inferred was regarded by BLAKELY and before him MAIDEN as *E. camaldulensis,* is essentially distinct from the remainder of the species which together comprise the Series Exsertae.

The most important taxonomic questions which arise are whether this total population should be regarded as a single species or whether it should be split into two or more subspecies or perhaps species. The question also arises as to how variation within the group which appears to be clinal should be treated, although the problem is of course not peculiar to this material.

Experimental Study of Variation

Methods

The pattern of geographic variation disclosed here is based on a study of selected characters among herbarium specimens and seedling progeny derived from twenty-two trees. These trees were distributed over nine sites which range from the Fergusson River in the Northern Territory to Port Lincoln in South Australia, that is from about latitude 14° S to 35° S. The localities for the most part lay between the meridians 130° E and 140° E except that both Walgett and Coonamble are further to the east, in New South Wales. The different localities are given in *Figure 4.*

The seed obtained from each tree was kept separate. It resulted from natural pollination for the particular tree. Whether these seed were in fact produced by self-pollination, cross-pollination or perhaps some intermediate degree of inbreeding cannot be said.

Seedlings were raised in Canberra under nursery conditions in lacquered metal tubes and grown out of doors, each progeny consisting of 50 seedlings. The data obtained represent growth responses during one season from October, 1963, to October, 1964. Measurements were made on seedling height at six months (coincident with cessation of growth during winter), frost damage and recovery from frost damage in injured plants, leaf length and breadth.

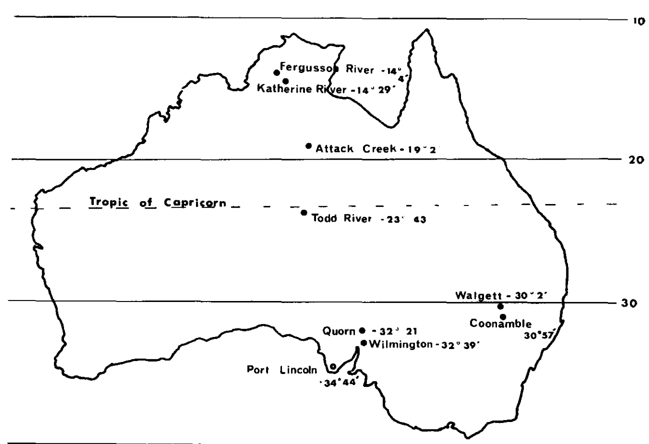

Fig. 4. — Map of localities at which collections were made.

The presence of lignotubers was scored at two years. Although all these characters obviously have survival value for the plant they probably vary in importance as far as the effect of natural selection on the overall variation pattern is concerned.

Results and Discussion

Progeny means and coefficients of variation for the different characters are given in *Table 1*. These data are summarised in *Table 2* in which statistics for each of the nine geographic localities are given. Particular points of note follow in relation to various measured features.

a) *Seedling Height.* — Analysis of variance indicated significant differences not only among different progeny but also among the different populations. There is some tendency for height to increase with decrease in latitude suggesting a faster growth rate in the seedling stage for the northern populations. An exception to this trend was the southernmost population at Port Lincoln which was represented only by a single progeny. This population is perhaps somewhat unique compared with the inland populations. It comprised few trees and grows on a limestone outcrop which is an unusual edaphic site for the species. In spite of the trend no significant regression was obtained for seedling height on latitude. Perhaps the most striking feature of the data is the difference among the coefficients of variation. Coefficients for Todd River and more northerly populations are fairly uniform and considerably less than those calculated for the southern populations. One may suggest that such a marked difference in variation reflects an underlying difference in genetic structure between these two groups of populations. Perhaps the northern group has a higher inbreeding coefficient than the southern one, or alternatively perhaps there is a marked difference in selection pressure operating on each.

b) *Frost Damage and Recovery.* — These features were measured quantitatively on the basis of a score given to each plant to assess the extent of frost damage and another to record the capacity of affected plants to recover. Recovery was always by the production of a lateral shoot from the uppermost bud which survived frost. Frost recovery was scored in terms of the number of nodes produced. It may be argued that such a score is entirely a measure of growth rate and this is probably the case. However, in terms of survival from such an adverse environmental episode, this is probably a reasonable estimate. Account is taken also of damaged plants which did not recover.

Analysis of variance indicated highly significant differences for frost damage both between progenies and between populations with by far the greatest contribution being due to population differences. From *Table 1* it can be seen that northern populations are more susceptible than southern populations. However, the two progenies from Walgett, N. S. W. showed considerable damage, in fact for one, all individuals received the maximum score.

As reported for seedling height, the coefficients of variation for the northern populations were considerably less

Table 1. — Means of seedling characters for progeny obtained from twenty-two trees growing in nine different localities. — Coefficients of variation are given in parentheses ( ) for seedling height, frost damage and frost recovery.

Tree No.	Locality	Seedling Height, cm.	Leaf Length, cm.	Leaf, Breadth, cm.	Frost Damage	Frost Recovery	Lignotuber %
1.	Port Lincoln, S.A.	18.3 (33.7)	6.42	1.53	1.44 (85.4)	5.11 (49.6)	0.0
2.	Quorn, S.A	16.7 (25.0)	5.52	1.76	0.90 (79.4)	4.00 (65.5)	0.0
3.	Wilmington, S.A.	16.2 (34.0)	5.92	2.12	2.00 (79.5)	5.22 (62.8)	0.0
4.	Coonamble, N.S.W.	20.4 (32.0)	7.07	1.67	1.13 (110.6)	6.63 (54.4)	0.0
5.	Coonamble, N.S.W.	16.5 (38.0)	6.79	1.51	1.31 (90.8)	4.71 (88.7)	8.3
6.	Walgett, N.S.W.	18.1 (32.4)	5.92	1.66	3.60 (35.7)	6.98 (63.7)	0.0
7.	Walgett, N.S.W.	22.3 (42.7)	5.81	1.59	5.00 (0.0)	1.69 (140.9)	0.0
8.	Todd River, N.T.	22.0 (24.3)	7.86	2.13	3.39 (18.1)	5.65 (67.4)	43.7
9.	Todd River, N.T.	22.5 (26.1)	7.23	2.08	2.41 (40.6)	3.62 (102.5)	53.1
10.	Todd River, N.T.	20.5 (17.1)	6.75	1.94	2.18 (35.8)	8.16 (60.2)	82.9
11.	Todd River, N.T.	17.2 (19.9)	6.76	1.96	2.77 (29.1)	8.37 (56.8)	4.2
12.	Todd River, N.T.	18.1 (20.6)	6.87	2.26	2.92 (30.7)	6.04 (74.0)	6.2
13.	Todd River, N.T.	22.7 (17.4)	6.26	1.79	2.58 (20.9)	7.29 (59.5)	20.8
14.	Todd River, N.T.	16.6 (25.6)	6.35	1.93	2.69 (30.8)	9.87 (39.5)	10.4
15.	Katherine River, N.T.	20.6 (29.1)	6.68	1.71	4.14 (17.1)	5.06 (90.6)	65.9
16.	Katherine River, N.T.	21.0 (26.2)	7.99	1.77	3.74 (20.48)	6.34 (63.6)	43.4
17.	Attack Creek, N.T.	17.2 (22.7)	6.89	1.62	3.04 (23.2)	3.73 (153.5)	86.3
18.	Attack Creek, N.T.	16.8 (30.1)	7.04	1.58	3.62 (23.8)	8.12 (55.3)	68.7
19.	Attack Creek, N.T.	19.5 (22.0)	7.46	1.71	3.33 (28.6)	7.54 (69.5)	57.7
20.	Attack Creek, N.T.	20.8 (25.2)	6.78	1.58	3.35 (20.9)	8.42 (59.2)	68.7
21.	Attack Creek, N.T.	17.6 (26.6)	6.31	1.81	3.60 (17.0)	5.92 (83.5)	73.3
22.	Fergusson River, N.T.	21.7 (22.5)	7.35	1.43	4.78 (8.7)	3.56 (89.5)	60.4

Table 2. — Showing weighted estimates of means of the different characters for each population

Population	Latitude	Seedling (Height cm.)	Leaf Length (cm.)	Leaf Breadth (cm.)	Frost Damage	Frost Recovery	Lignotubers %
Port Lincoln	34°44'	18.3	6.42	1.53	1.44	5.11	0.0
Wilmington	32°39'	16.2	5.92	2.12	2.00	5.22	0.0
Quorn	32°21'	16.7	5.52	1.76	0.90	4.00	0.0
Coonamble	30°57'	18.3	6.93	1.59	1.22	5.67	4.0
Walgett	30° 2'	19.3	5.86	1.62	4.30	4.26	0.0
Todd River	23°43'	19.5	6.87	2.01	2.75	7.05	31.6
Attack Creek	19° 2'	18.2	6.91	1.66	3.39	6.75	71.0
Katherine	14°29'	20.8	7.39	1.69	3.96	5.70	54.5
Fergusson River	14° 4'	21.7	7.35	1.43	4.78	3.56	60.0

than for the southern ones. The southern populations normally experience colder winters and more severe frosts than the northern populations with the possible exception of Todd River where the mean minimum temperature for the coldest month is 38.9° F. More intensive selection for frost resistance would be expected in southern populations than northern ones and this is suggested by the change in score with latitude, although this regression was not significant. The southern populations were approximately three times as variable in their response to frost as were the northern ones. Even Todd River, where these selective forces may be of the same order as further south, the coefficient of variation was only 28.7%. This marked reduction in variation within the northern group tends to support the earlier suggestion that there may be considerable inbreeding in these populations.

The mean performance of progenies with respect to frost recovery varies from 1.69 nodes for tree 7 from Walgett to 9.87 nodes for one of the Todd River trees. There was no correlation between frost damage and recovery from frost damage but within those progenies moderately susceptible to frost there was a tendency for the mean recovery to be low. In No. 7 only 20 out of the 49 damaged plants showed any recovery at all. Generally most seedlings were able to recover from the effect of slight frost damage — there being considerable variation both between and within progenies for this ability. Analyses of variance showed highly significant differences between populations and also between progenies in spite of the rather high within-progeny variance. However, the population differences were not related to changes in latitude. Coefficients of variability varied from about 40% to over 150% suggesting that in all progenies there was much greater variation for this character than any others measured. Presumably a large portion of this variation in phenotype is genetic and probably has not been changed much by natural selection. It is likely that under field conditions, where a multitude of factors operate in determining fitness, only those individuals not affected by frost appreciably in a given locality stand much chance of survival. In any tree improvement programme where seedling establishment is normally under nursery conditions there would be considerable scope for selection within progenies for this character.

Significance of Lignotubers in Eucalyptus Systematics

Lignotubers in eucalpts were described many years ago and various accounts are given by Kerr (1925), Jacobs (1955) and Chattaway (1958).

The general condition in *Eucalyptus* is that lignotubers are present — their absence has been recorded in only about 30 of the total 600 species. Through the different sections of the genus there are some variations in lignotuber form especially as the plants age but all originate in the same way as a pair of woody protuberances which develop in the axils of the cotyledons early in the life of the seedling *(Figure 5)*. These woody organs contain a mass of buds and much starch. If the seedling is decapitated shortly above them they sprout vigorously from the numerous buds they possess. In many species additional pairs of these structures appear in the first, second and even third pair of leaf nodes above the cotyledonary node and these often coalesce as growth proceeds. In most species, as the seedling becomes a sapling the lignotuber is covered differentially with less wood than the adjoining stem and hypocotyl

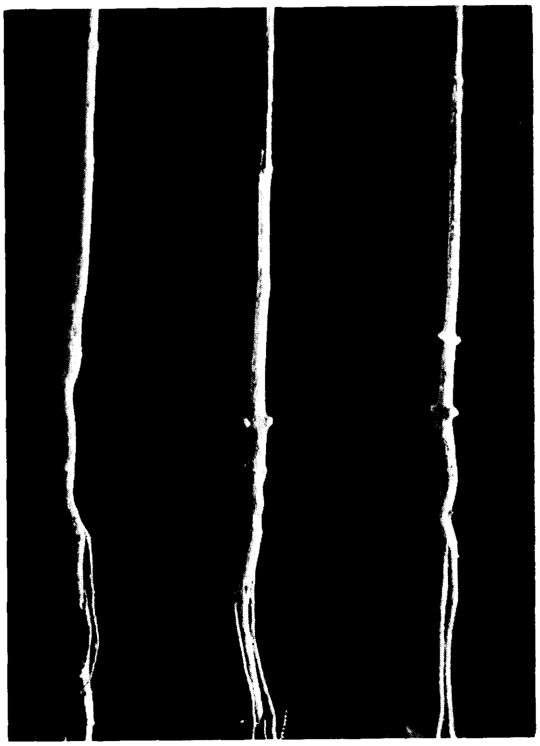

Fig. 5. — *E. camaldulensis* at two years of age. — Left: without lignotubers. — Centre: with a single pair of tubers. — Right: with a supplementary pair of tubers.

so that after a few years generally it can no longer be seen as a distinct organ. The age at which the first cotyledonary tubers are clearly discernable is not the same in all species. In some they may be seen when the plant is a few months old and merely 8 inches tall whereas in others they may not appear until after the end of the first year. At times they are exceedingly prominent whereas in other individuals or species they may be present but insignificant in appearance. In cases where lignotubers are absent there exists often a swelling in the hypocotyl region which may perhaps be mistaken for the organ itself.

The absence of lignotubers is ordinarily absolute for a particular species and is correlated with sylvicultural behaviour (Jacobs, 1955). For example, *E. regnans, E. delegatensis, E. pilularis, E. diversicolor, E. grandis* and *E. fastigata* produce seed heavily and regularly, are relatively fire sensitive and regenerate vigourously giving often dense regrowth crops. All of these species are known well throughout their range and lignotubers have never been found. Occasionally individuals with lignotubers are found but these have been shown on closer examination and progeny testing to be interspecific hybrids, the second parent being one of those species which regularly has lignotubers.

Something is known of the inheritance of the organ. In a series of manipulated F_1 interspecific hybrids the lignotuber develops as in the parent which ordinarily possesses it. In an F_2 population between *E. pulverulenta* (with lignotubers) and *E. grandis* (without lignotubers) segregation and recombination for this and a set of other morphological characters is in accord with the idea that the feature is expressed by what is a strongly inherited, largely dominant trait. The limited evidence from manipulated interspecific crosses is matched with what is found commonly in the field. The absence of lignotubers is complete for a species which has not them ordinarily except in marginal situations where interspecific hybridization can be inferred as likely.

While it is known that several species without lignotubers have never been found to develop them except in the above circumstances of interspecific hybridization, study of the reverse situation is more difficult and less satisfactory. KARSCHON (1967) has pointed out that the appearance of the tuber in *E. camaldulensis* is transient and this is generally true of all tuber bearing species.

It may well be that some species display the feature in a variable way so that its presence is to be seen as a percentage less than 100% in the total seedling population.

In many species there is polymorphism of this kind — a very common example being the glaucous and non-glaucous leaved individuals in species such as *E. melliodora, E. sideroxylon* and *E. blakelyi.* These are generally accepted as merely an expression of a variation pattern within the species.

In examining the position with *E. camaldulensis* care must be taken to weigh such points. There are many populations from the northern areas of *E. camaldulensis* which display a high percentage of lignotubers but none in which at 2 years (the age at which it is usually most prominent), tubers are present on every plant, 87% being the highest recorded in this survey. From the Todd River at Alice Springs only about 50% developed tubers and there is a wide variation between separate single tree progenies at this site from 4% to 83%. As one proceeds north over very considerable distances the number of lignotubers seen in progeny of different provenances increases but in none does it reach 100%. It is clear also that on the basis of the way in which different provenances display the character, that the development of pairs of lignotubers in the first or second primary leaf pair nodes is also an inherited trait in this species as indicated in *Figure 5.*

It may be that the absence of the lignotuber in *Eucalyptus* is a derived character, the general condition for the genus being the presence of lignotubers which is expressed in the large majority of species.

We may perhaps see the effect in *E. camaldulensis* of the operation of a lignotuber suppressing mechanism which becomes complete at times in southern populations and is weak or largely absent from northern ones. Further examination will be necessary to determine the likely nature of the control of this character and also to assess its significance, but it seems improbable that interspecific hybridizing with distinctly different species in peripheral situations, though present in some segments of the population is the cause of the high incidence of tubers in the northern populations.

The pattern of tuber occurrence seen in this study suggests the need for a critical re-examination of the situation in species ordinarily considered to possess tubers and a re-evaluation of their taxonomic significance.

Broad Variation Patterns in E. camaldulensis

On a total population basis knowledge of the variation patterns in the species rests largely on field and herbarium assessment. This of course is enough merely to give a hint as to what exists and to suggest where additional sampling and measurement might be particularly rewarding. It is clear that in more than one zone of contact there is morphological integration between it and other species. The most extensive example is that in Western Australia from some little distance south of Perth beyond Geraldton to-

Fig. 6. — Leaves and capsules of *Eucalyptus rudis, E. camaldulensis* and a natural hybrid.

wards the Murchison River, a distance of some 300 miles, in which one passes from "pure" *E. rudis* to "pure" *E. camaldulensis* through a graded intermediate zone. This pattern fits closely that which is described as a zone of introgression and if regarded as such must be one of the most extensive existing (see *Figure 6).* In passing, it might be mentioned that it is likely that *E. algeriensis* came from somewhere near the centre of this zone as an introduction to the Mediterranean and probably did not originate in that region as has been otherwise supposed.

The same kind of pattern exists although in a more restricted way between it and an undescribed species of Red Gum in the vicinity of Wee Waa, N. S. W., where integrating zones extend for 30 or 40 miles as for example, along the Coonabarrabran and Wee Waa roads from Narrabri. Both these situations are readily comprehended in the field since the second putative parent in the combination is a rough barked species possessing this and other characters which are clearly evident on inspection and which contrast strongly with those of *E. camaldulensis.*

There are hints of similar situations between *E. camaldulensis* and *E. tereticornis* over substantial areas in Queensland but further analysis of this is not feasible in the absence of more precise study. Limited examples have also been seen as between *E. camaldulensis* and *E. bigalerita* on Bedford Downs in the Kimberley Area, Western Australia.

On the other hand in many parts of southern Australia the species shows no sign of gene flow to others except for sporadic and even rare instances of what appear to be F_1 interspecific hybrids such as with *E. ovata* near Melbourne which has been described as *E. studleyensis,* with *E. viminalis* in the south east of South Australia which has been described as *E. kalangadooensis* and the *E. cladocalyx* at Port Lincoln which has not been formally described.

Although *E. camaldulensis* is in contact with the closely related *E. blakelyi* in the upper reaches of the Murrumbidgee River and other streams in N. S. W. no hybrids have as yet been found, there evidently being some effective isolating meachnism which permits the two species to grow frequently side by side without any obvious hybridization.

Through many areas of its occurrence in South Australia, north west Victoria, western New South Wales and south west Queensland and Central Australia there is no other species of the genus found in contact with *E. camaldulensis* with which it is capable of interbreeding assuming the intrageneric barriers to hybridization reported for many species (PRYOR, 1959) operate in this case. The interspecific combinations mentioned above give fertile hybrids although the vigour of the progeny has not been ascertained and may be less than that of the parents.

In addition the hybrid *E. largiflorens* × *E. camaldulensis* has been located near Deniliquin and described as *E. oxypoma*. It is likely that occasionally single trees of *E. melliodora* × *E. camaldulensis* occur since two or three individuals resembling phenotypically this hybrid have been seen in localities where both putative parents occur. Both of these combinations are probably totally sterile. Future search may reveal others but such, if they occur, must indeed be rare.

In conditions remote from the natural stands where species are brought together in arboreta, though they are well separated geographically in their natural occurrence, additional hybrids are known to have resulted. Perhaps the best example of this is that described as *E. trabuti* which arose as an F_1 in Sardinia and was planted subsequently at Tre Fontana near Rome probably as an F_2. This is from the combination of *E. camaldulensis* × *E. botryoides*.

Apart from these presumed interspecific sources of variation there is extensive variation which may be considered intraspecific if considered throughout the population customarily regarded as *E. camaldulensis*.

In this there is evidence of some latitudinal trend although gradients are certainly not smooth. It is not yet possible to say certainly whether these are more or less evenly graded or whether there are distinct discontinuities. A break appears possible at about latitude 27° S although there is still lack of adequate sampling to confirm or refute the suggestion without doubt.

The southern forms have rostrate opercula, small fruit, no (or few) lignotubers, short non-glaucous juvenile leaves, leaden coloured bark and upright habit. There are no doubt other characters — perhaps many of them — which will be found to follow a similar pattern and some have been reported by KARSCHON (1967) already on seedlings from a wide set of provenances raised in Israel.

Of course such descriptive statements as the above are inadequate to describe the situation. For example, glaucousness is found at times in southern populations which are otherwise similar to the southern type as also is the blunt operculum. Such descriptive approximations do not take account adequately of the magnitude of such exceptions.

Differences too are found which may be more in the nature of aberrations, some of which are general, though infrequent, in other species of *Eucalyptus*. The complex inflorescence described in a specimen of *E. camaldulensis* by CARR and CARR (1959) is probably of this kind. There are others too which are often enough seen but seldom recorded. One such is the occurrence of "box-like" bark for example, referred to by MUELLER and reported by BENTHAM, 111, 240 (1863), examples of which are seen from time to time scattered very thinly in the populations in various localities.

All of these factors must be evaluated before a definitive treatment of the group can be attempted and it is likely that methods now being developed will have particular application to the study of this variable population.

Possible Genetic Explanations and Taxonomic Implications

From the evidence so far available it might be suggested that the populations which have been known collectively throughout Australia as *E. camaldulensis*, in spite of a blurring of the boundaries in some places as has been described in Western Australia and in north western New South Wales, is well cut off from other species but may itself be made up of at least two distinct taxa. The northern populations have a number of characteristics in common and these depart from those displayed by the type which is representative of populations confined largely to the Murray/Darling River system of South Australia, Victoria, New South Wales and perhaps south west Queensland. If one regards these populations as falling into two discrete units, a northern and a southern one, the main problem is to understand the nature of the variation at the boundaries between them and whether there is substantial integration which would make it difficult to define the separate taxa (either subspecies or species) or whether in fact there is something of a discontinuity in the variation pattern across a general geographical zone. The zone in which such could occur is somewhat difficult of access and the distances are such that the examination is still inadequate to resolve this point.

If however, one considers as a hypothesis that there are two species which at some stage previously have been distinctly separated from each other but which by later migration following climatic shifts and perhaps topographic change, have been brought into contact, many situations in which there is a mingling of characters in particular stands would occur. Also the extensive introgression zone with *E. rudis* might represent a later coming together of previously separate populations after a separation in time still more remote, and the mixing might have been between a population on the part of *E. camaldulensis* which already was the product of genetic blending of two separate preexisting taxa.

The weight of evidence at present is that the total population hitherto referred to as *E. camaldulensis* in Australia consists of two main taxa, one occupying a northern zone and the other a southern region.

Their characters in contrast are set out below:

	South	North
Operculum	Rostrate	Rounded, minutely umbonate
Juvenile Leaves	Narrow, green	Broad, glaucous
Bark colour	Patches leaden gray	Mostly "whitewashed"
Lignotubers	Mainly absent	Present in high proportion
Branching habit	Somewhat upright	Spreading

While a closer study of populations between 23° and 30° S latitude is necessary to determine the abruptness of the change, the transition from one to the other on present evidence is rather abrupt. It is evident also that there is the possibility of further separation within the groups as KARSCHON (1967) points out for the northern section.

It is striking that the coefficient of variation is so sharply separated in the north and south populations in the material studied and also that there are no closely correlated clinal patterns associated with latitudinal provenances.

Such conditions are in accord with the idea that two distinct taxa occupying different zones of the total area should be recognized.

It is considered therefore, that the northern and southern populations would best be regarded as separate taxa but it is of course premature to designate them precisely.

Implications in Future Tree Improvement Work

From evidence based upon the study of open-pollinated progeny it was seen that the variance within sites is in a number of cases greater than that between sites. Nothing is known, as a result of experimental work, of the breeding system of *E. camaldulensis*, but the fact that the northern populations have in the main a coefficient of variation which is about half that of the southern populations, suggests either that there is some effective difference in the breeding system of the northern group, or that there is a marked difference in selection pressures between the two regions. From the evidence of variation between trees from any given provenance (with the exception of the Walgett sample, where all individuals were damaged at the temperature level to which they were subjected out of doors in Canberra) it is clear that whereas all populations can withstand quite a degree of frost, this feature has not been subject to rigid selection beyond moderate frost intensity levels, and that many individuals, scattered more or less at random through the total population examined, produce offspring which are considerably more frost resistant than others and also which recover from frost damage more readily than others. The high level of variation in this character which is paralleled by that in other features, together with the likely rather high correlation in parent offspring relationships as has already been established in a few cases studied suggest that there is a particularly good opportunity for effective selection, both by choosing individual trees from populations of a given provenance and by further selecting within the nursery where a suitable screening stress can be applied. The fact that it might be supposed that there are two distinct taxa involved, even though they would still be regarded as closely related units, further aids the planning of experiments in seeking to improve material for particular uses. Up to the present, almost all plantations of *E. camaldulensis* planted as an exotic on a world basis are of types characteristic of the southern population, and it is only in plants raised here and there in the last ten years that plots of trees are seen which are undoubtedly from the northern population. Recognition of this situation will have a marked bearing on the speed at which further improvement can take place in what is probably the most widely planted *Eucalyptus* species at the moment, and in what appears to be one of the most plastic, as a plantation tree, of all the species of the genus.

Acknowledgements

Technical assistance given by the following members of the Botany Department is gratefully acknowledged — viz. Mr. R. WILLING and Mrs. H. KNIGHT for care in raising plants and collection of data; and Mrs. J. MACDONALD and Mrs. P. HOLDEN for some illustrations.

Summary

Study of a set of trees of *E. camaldulensis* distributed through the latitudinal range 14° S to 35° S, approximately on meridian 135° E, discloses that there are distinct differences between the northern and the southern populations. Some of these differences are morphological, others are expressed in their physiology. The coefficient of variation for various phenotypic characters in the northern population is only about half of that in the southern populations. In various characters studied the lack of clear clinal gradation with latitude, together with an apparent discontinuity about latitude 27° S suggests that the total population, considered in the past as one taxon would be better regarded as forming two rather closely related taxa — perhaps most appropriately treated as subspecies. The two taxa thus constituted have in common a strong ecological preference for sites along or near stream banks.

Study of the zone of discontinuity has so far been inadequate to resolve this supposition and additional examination is desirable.

High levels of variation between trees and sites, but strong parent/offspring correlations, suggest that very effective improvement could be made by simple selection in these stands of *E. camaldulensis* which at present is one of the most widely planted of all species of *Eucalyptus*.

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