A Probable Hybrid Swarm in Eucalyptus

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Eucalyptus globulus and E. bicostata (nomenclature follows BLAKELY, 1955) are two discrete, although closely related taxa commonly recognized as distinct species and known to be relatively constant throughout their ranges. Both have been recorded from the Otway Ranges in south east Australia (HALL, JOHNSTON and MARRYAT, 1963).

E. globulus and E. bicostata are part of a species complex including all the naturally occurring species in the subseries Euglobulares and Pluriflorae (BLAKELY, 1955; nos. 248—261 a). E. globulus has single-flowered inflorescences, although with occasional terminal twos and threes, a larger four-ribbed fruit and smaller, slightly more falcate leaves than E. bicostata. The occasional terminal twos and threes found in E. globulus populations are in most cases unassociated with any other intermediacy in adult or juvenile characters which might have suggested introgression with another eucalypt such as E. viminalis (unpublished data). Thus they are probably mostly an expression of the inherent variability within the species.

E. bicostata has triple-flowered inflorescences, usually smaller two-ribbed fruits and long usually lanceolote leaves. Although there is some overlap in fruit size between the two species it is small in comparison with the complete size range, and is exceptional in its occurrence. It is held by some taxonomists that E. stjohnii is merely a small-fruited form of E. bicostata (pers. comm. L. D. PRYOR). If so, the former name must take precedence over the latter, E. stjohnii having been described at an earlier date. This view, if accepted, would extend the lower size range of the now E. bicostata, but would in no way affect the use of fruit size as a distinguishing character between E. globulus and E. bicostata.

This article aims to describe a probable hybrid swarm which appears to encompass almost all the Otway population of Blue Gum (a common name used in southern Victoria which covers both species and their mutual intermediates — E. bicostata is known as Eurabbie in the northern part of its range and E. globulus is known most commonly as Blue Gum) and to analyze some of the environmental and morphological relationships of the population. Although wide zones of interspecific intermediates in *Eucalyptus* have been recorded (e.g. BARBER, 1965; LARSEN, 1963; PRYOR, 1956, 1957, 1959 and 1959 a) very little detailed work has been published on them.

The Otway Ranges occurrence is disjunct from other populations of both suggested parent taxa, and is situated predominantly near the coast between the 30— and 60—inch mean annual isohyets, mainly on soils formed on Jurassic sandstones and mudstones, as a dominant or co-dominant with other Eucalyptus spp. (Figures 1 *and* 2).

Both species occur in environments of broadly similar edaphic and moisture status. However E. bicostata occurrences are more continentally located than those of E. globulus (Figure 1). Consequently, the ranges in the differences between the mean temperatures of the warmest and coldest months are mutually exclusive in the two occurrences. The means are not similarly discrete although most E. bicostata occurrences have lower winter temperatures than most E. *globulus* occurrences. The differences between the means range from 21.9° F. to 28° F. for weather stations on known E. bicostata occurrences, from 13.9° F. to 17.6° F. for occurrences where putative hybrids are found and from 10.8° F. to 15.9" F. for E. globulus localities.

Methods

Bud and fruit samples were collected from 17 sites within the Otway Ranges and two sites elsewhere for the suggested parent species. The main criteria were accessibility and the achievement of a representative coverage. Samp-

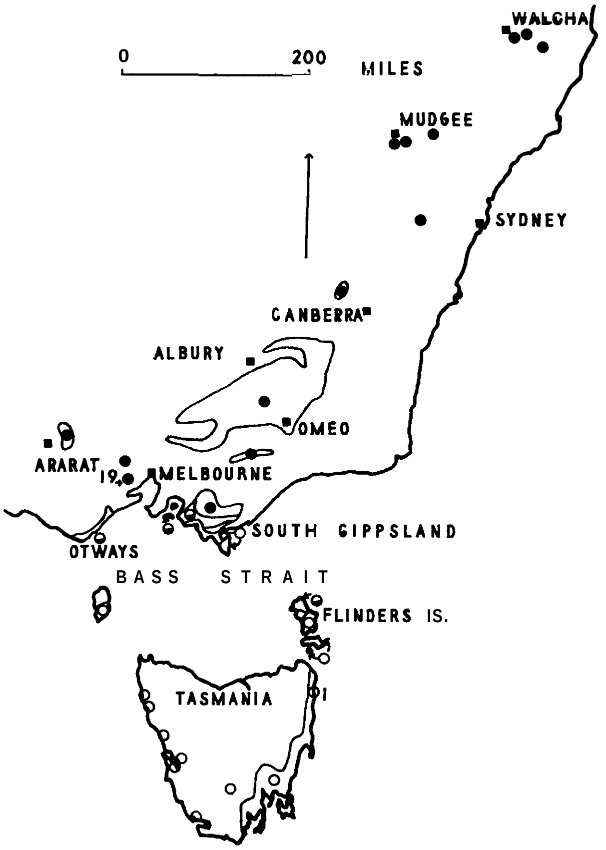

Figure 1. — The distribution of Blue Gum showing the location of sample sites 1 and 19.

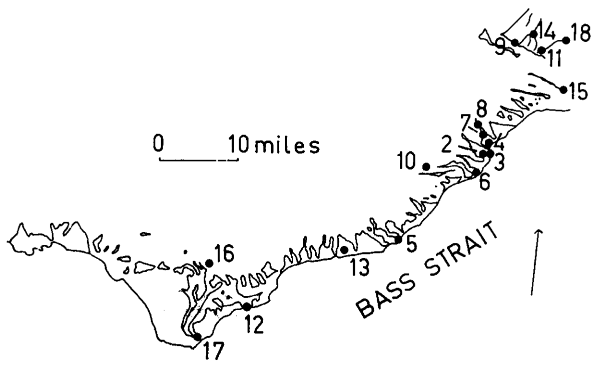

Figure 2. — The distribution of Blue Gum in the Otways showing the location of sampling sites 2 to 18.

ling, which required at least 10 trees per site, was limited both by past clearing and recent fires. The fact that Blue Gum does not flower until several years after severe fire damage prevented sampling over one sixth of the occurrence.

Buds and fruits were collected from living trees where possible. It was also found necessary to sample from logged and fire felled trees and to collect fallen branches and individual fruits and buds where there was reasonable certainty that they were from the same tree. Thus it was found impossible to achieve a fully random sample and there may be some bias in the data. However, there was no pre-knowledge of the composition of the stands and the characters measured were too subtle for ready visual assessment.

A number of inflorescences varying from 20 to 60 were collected from each tree, and the number of single-flowered inflorescences was expressed as a percentage of the total number of inflorescences. Attachment scars were present where flowers had been lost since flower initiation. These were used to assess the original number. From 10 to 40 fruits were collected and measured. They were measured only if their valves were open. As fruit size appears to vary with both seasonal conditions and position on stem it is not as reliable a character as the number of flowers per inflorescence.

The narrowest diameter was measured when the fruits were not perfectly round in cross-section; *E. globulus* having rounder fruits than *E. bicostata*. As *E. globulus* fruits are usually larger than those of *E. bicostata* differences are thus maximized.

Using the average data for each tree, product-moment correlation co-efficients were calculated, relating the morphological variables to each other and to distance from the sea and altitude, for the 17 sites in the Otway Ranges.

To assess within-stand variation the standard deviations of the morphological data were calculated for every site.

Results

Table 1 shows almost complete intermediacy in the averages of the Otway sites between the putative parent species. Some Otway sites have lower standard deviations in fruit diameter than the putative parents sampled. This may be partially due to the weight the high mean of the *E. globulus* stand gives to its standard deviation.

On a tree basis the range and limits of fruit diameter do not vary significantly with the percentage of single-flowered inflorescences, almost all combinations of the two characters being found.

Correlation analysis indicated no significant (10% level) correlations between fruit diameter, percentage of single-flowered inflorescences, distance from sea, or elevation for the 17 Otway-Range stands which were sampled.

Discussion

It is considered that the data present evidence for hybridization between *E. globulus* and *E. bicostata* in the Otway Ranges (*Table 1*). This is supported by the fact that (1) taxonomists have suggested that both putative parents occur in the Otways (Hall, Johnston and Marryat, 1963). — (2) the occurrence is in an intermediate environment. — (3) casual observation suggests that marked intermediacy also exists in leaf size and shape and rib number on fruit.

With the exception of site 12, all the sample sites within one-third of a mile from the sea had average numbers of single-flowered inflorescences of 80 percent or more of the total numbers, a level reached in no other sample site in the Otways. Site 2 was, in fact, very close to the *E. globulus* stand (site 1) in this character and in the standard deviation from its mean. However the fruits of the large number of trees with single-flowered inflorescences in these stands and elsewhere in the Otways were only rarely as large as the smallest *E. globulus* fruits from site 1 and seen on extensive collecting trips throughout the range of the species. This narrow coastal strip of trees with close affinities to *E. globulus* could be due to gene segregation towards the environment most suited for this taxon in the Otways. There is no comparable segregation towards *E. bicostata*, probably indicating that its environmental requirements are not met as well as those of *E. globulus* in this region. Apart from the coastal stands there is a complete range of intermediates in each stand, the within-stand variation encompassing most of the range of the between-stand variation.

A considerable gap exists between the Otways occurrence and the nearest occurrences of the putative parents; approximately 30 and 80 miles for *E. globulus* and *E. bicostata* respectively (*Figure 1*). The Otways occurrence has been isolated from the nearest Tasmanian *E. globulus* populations for at least 14,000 years by Bass Strait (Little-

Table 1. — The data by sample sites (cross-referenced to *Figure 2*).

Site No.	Fruit Diam. mm.	S. D. Fruit Diam.	% of single Inflorescences	S. D. % of single Inflorescences	Distance from Sea, miles	Altitude, ft.
1.	25.4	1.6	99.0	2.0	.02	20
2.	17.1	1.4	97.9	4.2	.33	425
3.	18.7	1.3	89.9	26.5	.02	35
4.	18.3	1.0	80.6	27.1	.33	200
5.	18.9	0.8	88.3	16.2	.25	250
6.	18.8	1.2	83.5	26.2	.33	300
7.	17.5	1.6	72.9	35.1	1.00	650
8.	16.0	2.3	70.5	32.7	2.00	950
9.	17.1	1.5	45.8	25.1	5.25	1200
10.	17.8	1.6	68.5	28.9	2.25	1100
11.	18.1	1.6	63.8	36.5	5.75	650
12.	18.2	1.8	61.9	36.0	.33	230
13.	18.3	0.9	67.3	35.5	.50	525
14.	15.8	1.2	55.9	40.7	6.50	725
15.	17.1	1.7	44.8	37.5	1.50	100
16.	18.1	1.4	56.8	30.9	4.25	900
17.	18.9	1.8	78.4	21.8	.50	150
18.	19.0	1.2	41.3	37.2	7.00	350
19.	15.1	0.9	0.0	0.0	11.00	800

john and Martin, 1965). No gross divergence seems to have taken place, as is the case with most species having trans-Bass Strait distributions (Pryor, 1959), typical *E. globulus* being found both in South Gippsland and Tasmania *(Figure 1)*. In fact, intermediates similar to those found in the Otways have been seen by the author in South Gippsland and on Flinders Island *(Figure 1)*, suggesting that the rise of sea level since the Last Glacial has swamped a pre-existent pattern of distribution of both putative parent taxa and their mutual intermediates.

The pattern of variation between *E. globulus* and *E. bicostata* is probably the result of the sequence of isolation, divergence and recontact that Pryor (1959) has postulated for other *Eucalyptus* species, rather than divergence due to selection within a continuous population. The high variability of the Otway stands supports this view.

Most work on intraspecific and interspecific variation in *Eucalyptus* concerns clines that appear to display, compared to this study, a high degree of within site uniformity in the character or complex of characters being studied (e. g. Green, 1969; Barber, 1965).

Although much disturbance has taken place in the Otways, the trees in samples 10 and 16 were individuals who obviously predated European settlement in country untouched by logging to the date of sampling. These are among the more variable and intermediate stands. Thus it seems that the considerable areal extent of the intermediate stands does not fit easily into the hybridization of the habitat hypothesis of Anderson (1948) which has been supported for *Eucalyptus* in many cases by Pryor (1953).

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Summary

A disjunct occurrence of intermediates between *Eucalyptus globulus* and *E. bicostata* was sampled. With the partial exception of a very narrow coastal strip the populations were found to be highly variable, displaying a complete range of intermediates in two key characters, fruit size and flower number per inflorescence. This probable hybrid swarm cannot wholly be attributed to disturbance.

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Geographic Variation in Pinus flexilis and Pinus strobiformis and its Bearing on their Taxonomic Status[1]

By R. J. Steinhoff and J. W. Andresen[2]

In the mountainous areas of western North America and extending into Central America there exists a series of three, apparently closely related, taxa of soft pines. These are: (1) *Pinus flexilis* James, which grows from southern British Columbia and Alberta in Canada south to northern New Mexico and Arizona in the U.S.A. *(Figure 1)*; (2) *P. strobiformis* Engelmann, which ranges from southern Colorado to San Luis Potosi in Mexico; (3) *P. ayacahuite* Ehrenberg, which extends from Jalisco and Hidalgo in Central Mexico southeastward to El Salvador and Honduras (Critchfield and Little, 1966; Map 9).

Although these taxa are now accepted as separate species (Mirov, 1967; Critchfield and Little, 1966), the autonomy and taxonomic position of the central population has long been a source of confusion and controversy. It all began when Engelmann (1848) named and described *P. strobiformis* from specimens collected in northern Mexico. Thirty years later he (Engelmann, 1878) also proposed that specimens collected in Arizona represented several varieties of *P. flexilis* even though they collectively approximated his earlier description of *P. strobiformis* in leaf serration, cone size, and cone scale reflexing. He soon (Engelmann, 1882) proposed that one of these varieties be elevated to specific rank as *P. reflexa*. Following that, Sargent (1889) concluded that the Arizonan and Mexican specimens were drawn from the same population. He (Sargent, 1889) first said they probably should be associated with *P. ayacahuite*, but then later (Sargent, 1897) thought that the population deserved specific rank as *P. strobiformis* Engelm. Shaw (1909, 1914) again subdivided the population and assigned members of the Mexican subpopulation to *P. ayacahuite* as variety *brachyptera* Shaw and those from Arizona, New Mexico, and Texas to *P. flexilis*. More recently, Martínez (1948), in discussing the pines of Mexico, recognized both *P. ayacahuite* var. *brachyptera* and *P. reflexa*. A detailed review of the nomenclature and taxonomy of the complex has been presented by Andresen and Steinhoff (1971).

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