

Geographical variation, subspecies discrimination and evolution in fruits, leaves and buds of *Eucalyptus caesia* (Myrtaceae)

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Abstract

Hopper, S. D., Campbell, N. A. and Caputi, N. Geographical variation, subspecies discrimination and evolution in fruits, leaves and buds of *Eucalyptus caesia* (Myrtaceae). Nuytsia 5(2): 179-194 (1984). Two races of *Eucalyptus caesia*, well known in the nursery trade as "Gungurru" and "Silver Princess" and recently given formal taxonomic status as subspecies *caesia* and subspecies *magna* were investigated to determine whether they are morphometrically distinguishable throughout their known ranges. Each of five fruit, three leaf and three bud measurements provides from 2-68% correct allocation to subspecies of the 138 plants measured, whereas multivariate analysis of three fruit and two leaf measurements achieves 98% successful allocation. Fruit, leaf and bud character subsets all make significant contributions to discrimination between the subspecies. Size differences in fruit and leaf characters account for 75% of the discrimination achieved. It is likely that subspecies *magna* was derived from an ancestral population (probably at Yanneymooning Hill) resembling subspecies *caesia*. A number of selective factors may have favoured the robustness of subspecies *magna* although adaptation to mobile bird pollinators is the only one for which some evidence is available at present.

Introduction

Eucalyptus caesia Benth. is a rare Western Australian mallee that is now well established as an ornamental garden plant. In the wild it occurs in small populations of 1-580 plants restricted to isolated granite outcrops in the central wheatbelt region inland from Perth (Figure 1, Chippendale 1973, Gardner 1979, Moran and Hopper 1983).

Two races of the species are known and are widely grown in cultivation under the names "Gungurru"* (which has relatively small fruits, flowers and leaves, and an upright habit), and "Silver Princess" (which has larger fruits, flowers and leaves, and a weeping habit). Brooker and Hopper (1982) have given these races formal taxonomic status as subspecies *caesia* (= Gungurru) and subspecies *magna* (= Silver Princess).

In 1978 a proposal was put to the Western Australian Wildlife Authority's Flora Committee that subsp. *magna* should be gazetted as rare under the Wildlife Conservation Act 1950-79 in order to curtail harvesting of seed from the small known wild populations by commercial seed collectors. If such a proposal was to be adopted, it could only be policed effectively by officers of the Department of Fisheries and Wildlife if specimens from subsp. *magna* populations could be distinguished consistently from those of subsp. *caesia* populations. To establish whether this is possible, a multivariate morphometric study of geographical variation in the species was carried out.

Apart from the solution of this applied problem it was anticipated that the study would be of general interest in elucidating the pattern of variation in a species of the informal subseries "Orbifolinae" (Pryor and Johnson 1971). Members of this subseries are remarkable

*"Gungurru" is now known to be a misapplied common name. It was actually used for *E. woodwardii* Maiden rather than for *E. caesia* by Aborigines of the Fraser Range district (Rye and Hopper 1981).

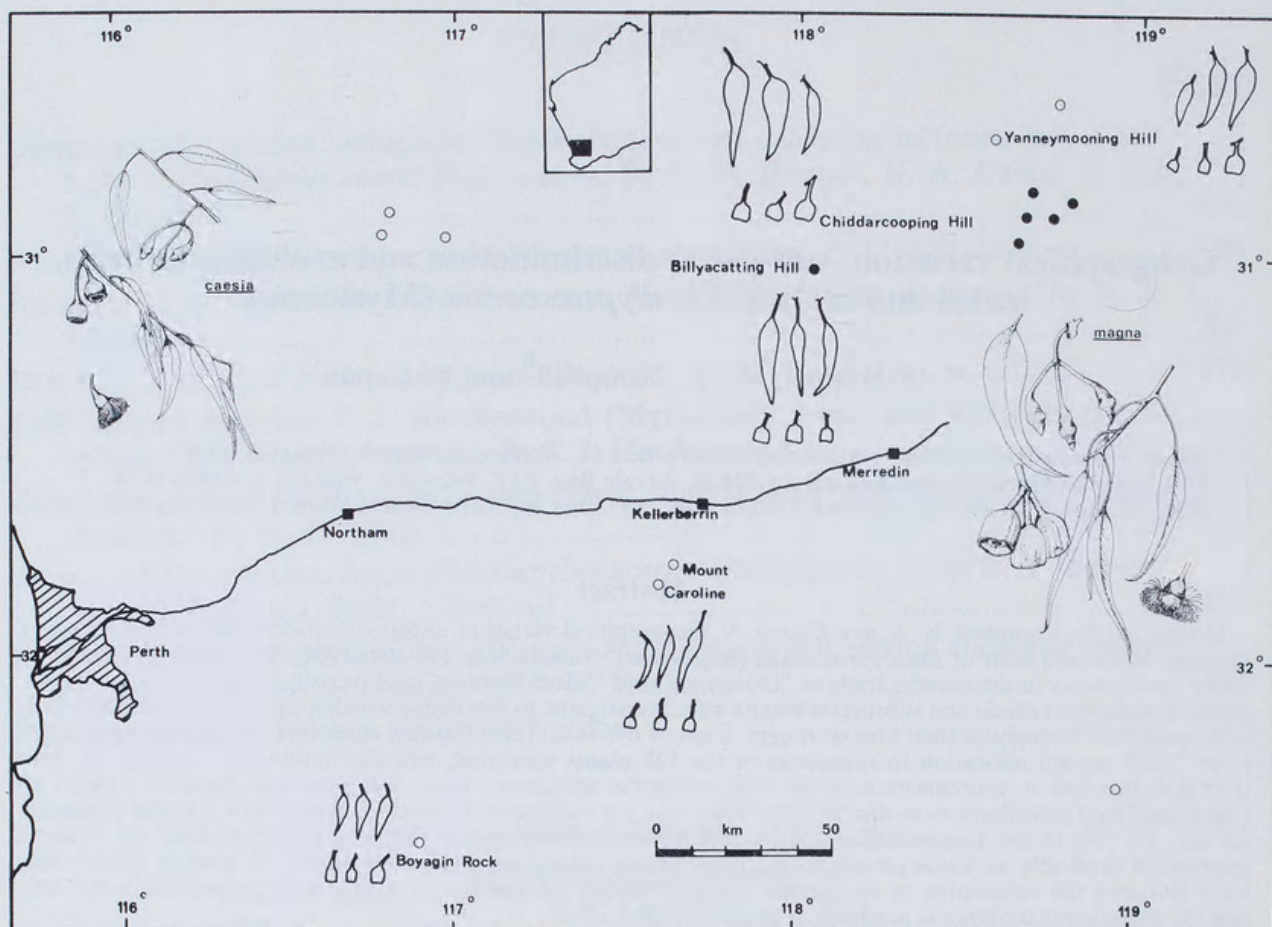


Figure 1. Geographical distributions of subsp. *caesia* (o) and subsp. *magna* (●) in south-western Australia. Tracings from a leaf and fruit from three plants from a sample of populations are given. Note the variability of plants from Yanneymooring Hill (see text). Drawings (by S. J. Patrick) illustrate typical fruits, buds, flowers and leaves of the two subspecies.

among eucalypts in the insularity and geographical separation of their populations, and therefore might be expected to show unusual patterns of evolution.

This morphometric study complements other work on *Eucalyptus caesia*, including a survey of allozyme variation (Moran and Hopper 1983), cladistic and phenetic analyses of phylogeny (Hopper and Burgman 1983), an investigation of nectar flow and pollinators (Hopper 1981, Wyatt and Hopper unpubl.), the formal description of the two races as subspecies (Brooker and Hopper 1982), notes on the species' distribution and use of the name "Gungurru" (Rye and Hopper 1982), and an assessment of *E. caesia*'s conservation status (Hopper et al. 1982).

Materials and methods

Field sampling and measurements taken. Known locations of *Eucalyptus caesia* were established through a literature search (e.g. Blakely 1965, Chippendale 1973, Gardner 1979), from specimen labels at the Western Australian Herbarium, and from information supplied by professional and amateur botanists in Western Australia. Each location was then surveyed in 1978 or 1979. Suitable granite rocks near to the known locations were also surveyed exhaustively for new populations of the species.

The species was found at 15 major locations (Hopper et al. 1982) and material was sampled from 11 of these. Two populations separated by a few hundred metres were sampled at two locations (Chutawalakin Hill and Chiddarcooping Hill), while only a single sample

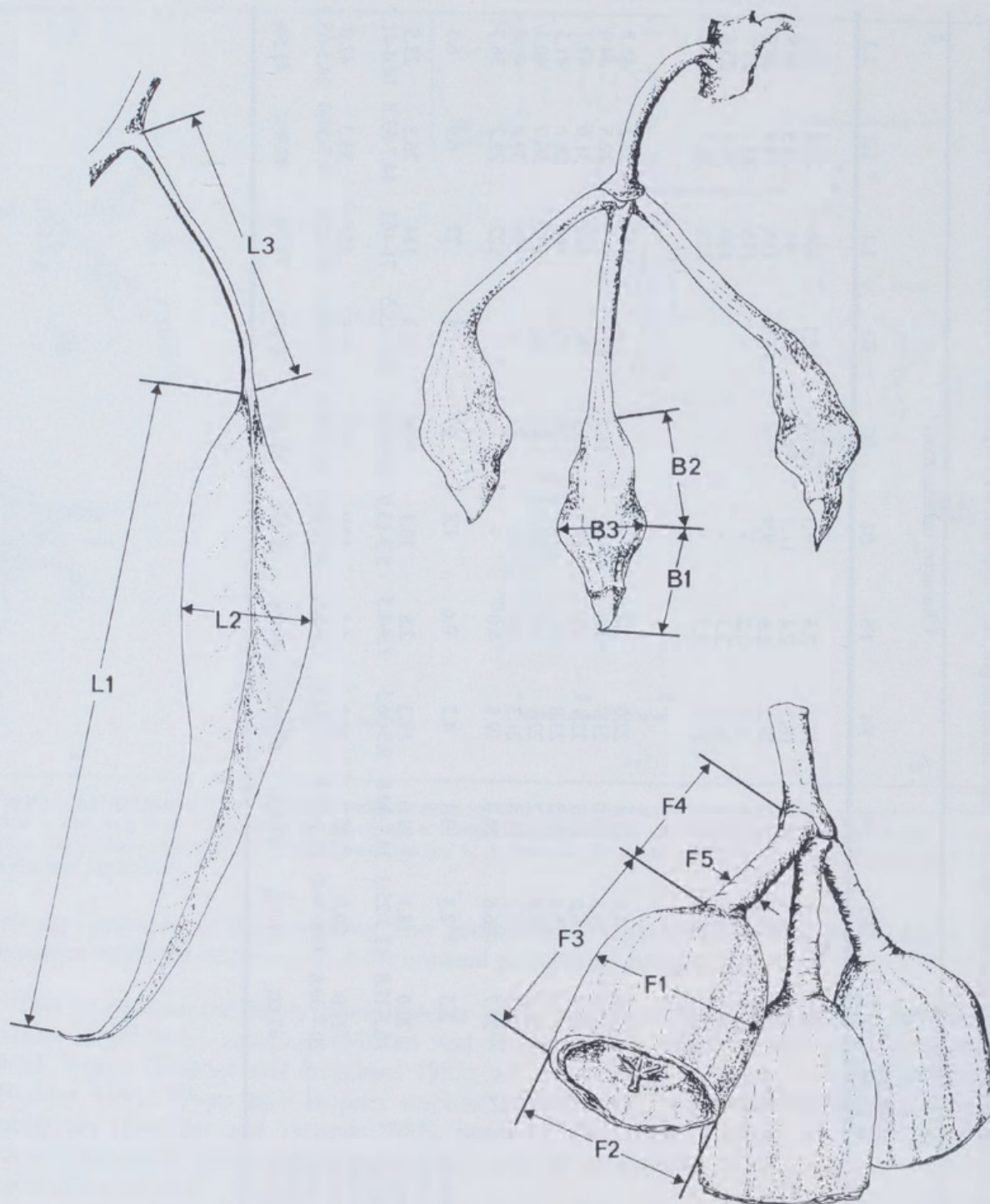


Figure 2. Fruit, leaf and bud measurements taken in the study. Fruit: F₁, mid-fruit diameter; F₂, fruit top diameter; F₃, fruit length; F₄, pedicel length; F₅, pedicel thickness. Leaf: L₁, leaf length; L₂, leaf width; L₃, petiole length; Bud: B₁, operculum length; B₂, hypanthium length; B₃, bud diameter. Drawing by S. J. Patrick.

was taken elsewhere, giving a total of 13 populations sampled (Table 1). A sprig with leaves and fruits was selected from each of up to 15 plants on line transects in each population. Seven of the populations were visited sufficiently early (May-July) in the flowering season to include mature buds as well as leaves and fruits on the sample sprigs.

The longest leaf, fruit and bud on each sprig were selected for measurement of the eleven characters illustrated in Figure 2. Only a single organ per plant was measured since preliminary studies indicated that variation within plants was minimal compared with that between plants and between populations.

Material from each population was pressed and dried prior to measurement, since a preliminary examination showed significant differences in all measurements taken on the same specimens when fresh and dried. There was no significant measurement error when the same dried specimens were remeasured. Voucher specimens from each population have been lodged with the Western Australian Herbarium.

Statistical techniques. Multivariate differences between and within populations were investigated primarily through canonical variate analysis (Bartlett 1947, Rao 1952, Phillips et al. 1973). This technique is used to define linear combinations of the original measurements that maximize variation between populations relative to the variation within populations. The first linear combination (canonical variate) maximizes the ratio of the between- to within-populations sums of squares of the resulting canonical variate scores. This ratio is usually referred to as the canonical root.

The basic aim of canonical variate analysis is one of separation or description of population differences. In many cases, a scatter diagram of the scores for the first two (or few) canonical variates conveys much of the information about the population separation achievable for the characters measured.

The overall separation between the populations can be partitioned into components reflecting variation in size and shape. The approach adopted in this paper is to define a suitable size variable, and then use regression-based techniques to define shape variables. The size variable is defined as the sum of the original characters on the logarithmic scale.

Shape is commonly defined in terms of proportions or ratios (Mosimann 1970, 1975, Mosimann and James 1979, Mosimann and Malley 1979). When the original data are expressed on a logarithmic scale, proportions become differences and the usual linear techniques of multivariate analysis are applicable.

Shape variables are defined here by projecting the data orthogonally to the vector associated with the size variable, or by taking the residuals from the within-groups regressions of the original characters on the size variable. The analysis of the projected data removes that component of size which is independent of shape — the *isometric* component. Size-related shape changes — the *allometric* effects — may still be present. The analysis of the residuals removes both the isometric and the allometric effects, at least to the degree that the linear regressions summarize this latter effect. [Williams et al. (1981) discuss the use of polynomial regressions to describe allometry]. Comparison of the ordinations and canonical vectors from these two analyses will give some insight into the contribution of allometric effects to the overall population separation.

Allocation of plants not included in the reference populations is here based on the total Mahalanobis distances. Leave-one-out calculations are used for the reference populations. The calculations for the probabilities of membership of each population are based on multivariate Student densities (see equations (2.7) and (2.1) of Aitchison et al. 1977). Typicality probabilities are first calculated (see equation (2.12) of Aitchison et al. 1977) by referring the Mahalanobis distances to the F-distribution.

These allocation procedures assume underlying multivariate Gaussian distributions. Probability plots of the Mahalanobis distances are used to examine this assumption (see, e.g. Gnanadesikan 1977 p. 172, Campbell 1980).

Three sets of analyses are reported here. One details the analyses for those populations for which all fruit, leaf and bud characters are available (Table 1). Another details the analyses for leaf and fruit characters for all populations (except those with few individuals).

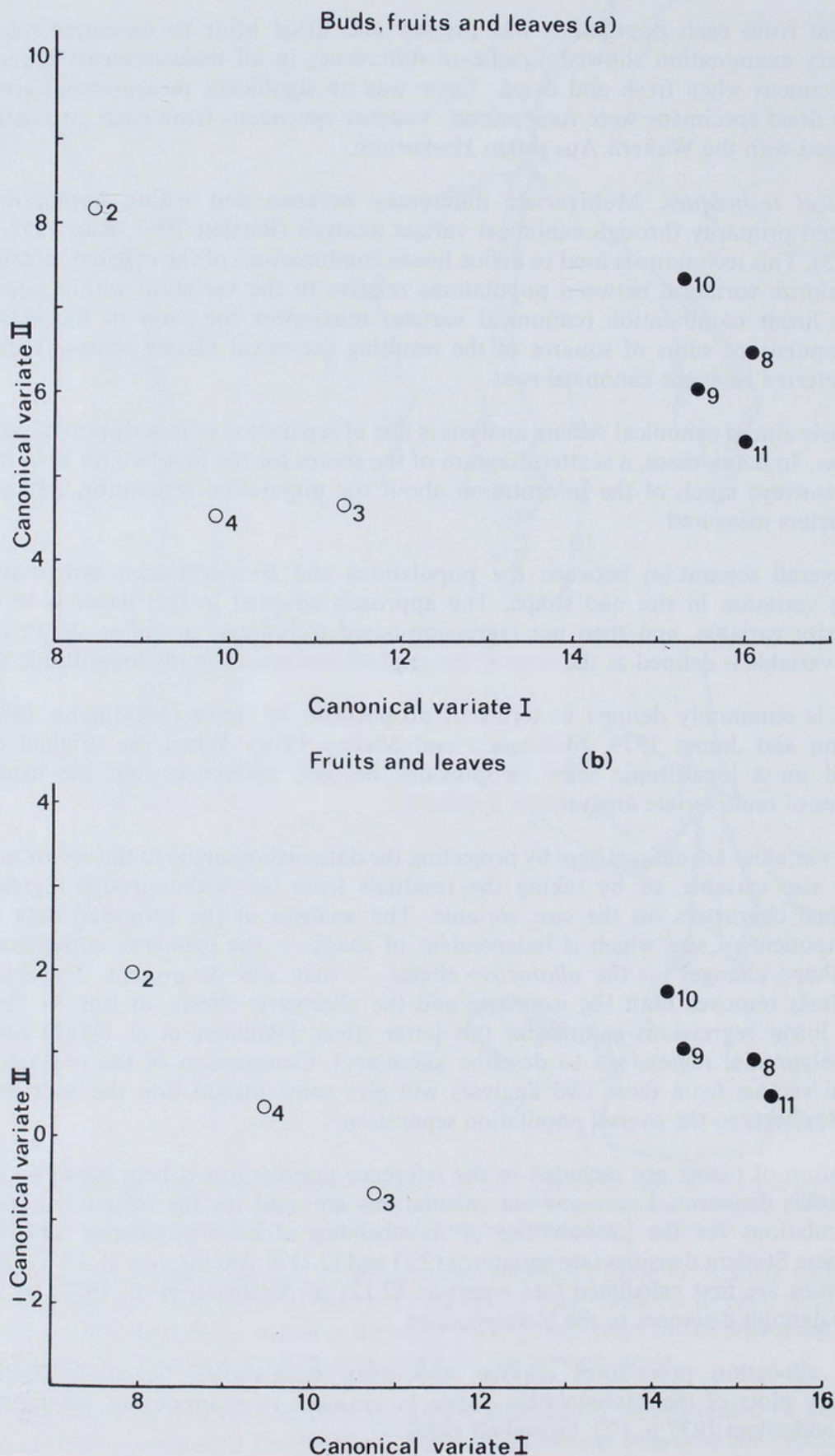


Figure 3. Canonical variate means for the analyses based on 7 populations of *Eucalyptus caesia* for (a) bud, fruit and leaf characters, and (b) fruit and leaf characters. The canonical vectors are standardized so that scores have unit variance within populations. Population identification is given in Table 1. o - subsp. *caesia*, • - subsp. *magna*.

In the third set of analyses, populations are bulked into those of subsp. *caesia* and those of subsp. *magna* to examine subspecific relationships. The bulking is on the basis of *a priori* taxonomic judgements, complemented by the results from the first two sets of analyses.

Results

Univariate allocation of plants to subspecies. Means, pooled standard deviations and minimum/maximum values for all characters measured are given in Table 1. The best univariate discrimination between subspecies occurs for mid-fruit diameter, fruit top diameter, pedicel thickness, bud diameter and petiole length. The ranges of all characters overlap between the two subspecies (from 32% to 98%). Hence allocation of plants to subspecies on single measurements (using resubstitution calculations) is, at best, only 68% successful.

Multivariate analyses of fruit, leaf and bud characters. A preliminary canonical variate analysis was undertaken on those seven populations (Table 1) for which bud measurements, as well as fruit and leaf measurements, were available. The first canonical variate of this analysis accounts for 74.6% of the total population separation. It effectively separates populations of subsp. *caesia* from populations of subsp. *magna* (Figure 3a). Characters important in achieving this separation include fruit length, mid-fruit diameter, bud diameter and operculum length. Leaf length, petiole length and fruit top diameter are also important. Leaf width and hypanthium length make the least contribution to separation along this canonical variate.

A second analysis omitting bud characters results in a similar ordination of the seven populations (compare Figure 3b with Figure 3a). Total separation along the first canonical variate is reduced by only 13.1% of that achieved when bud measurements are included (canonical roots of 8.66 and 9.97 respectively for the two analyses). Consequently, no further analyses involving bud measurements are undertaken. This allows an additional six populations (for which no bud measurements were taken) to be included in the ensuing analyses.

Multivariate analyses of population divergence in fruit and leaf characters. An analysis of fruit and leaf characters for 13 populations again separates populations of subsp. *caesia* from populations of subsp. *magna* along the first canonical variate (76.6% of the total variation; Figure 4a). Characters important for separation of populations along this variate are mid-fruit diameter, fruit top diameter, fruit length, leaf length and petiole length. Deletion of the remaining three characters (pedicel length, pedicel thickness and leaf width) from a subsequent analysis reduces population separation along the first canonical variate by only 3.5% (canonical root of 6.12 compared with 6.34 when all eight characters are analysed). All of the five important discriminating characters except for fruit length have positive coefficients for the first canonical variate, indicating that size is important in discriminating between the subspecies. This is analysed further below.

Separate analyses of fruit characters and of leaf characters for the 13 populations (Figures 4b and 4c) result in similar ordinations of populations into the two subspecies along the first canonical variate. However, separation of populations in the fruit analysis along the first canonical variate is 57% of that achieved when fruit and leaf characters are analysed together. For leaf characters the separation achieved is 42%. Hence both the fruit and the leaf character subsets each make a significant contribution to the discrimination between the subspecies.

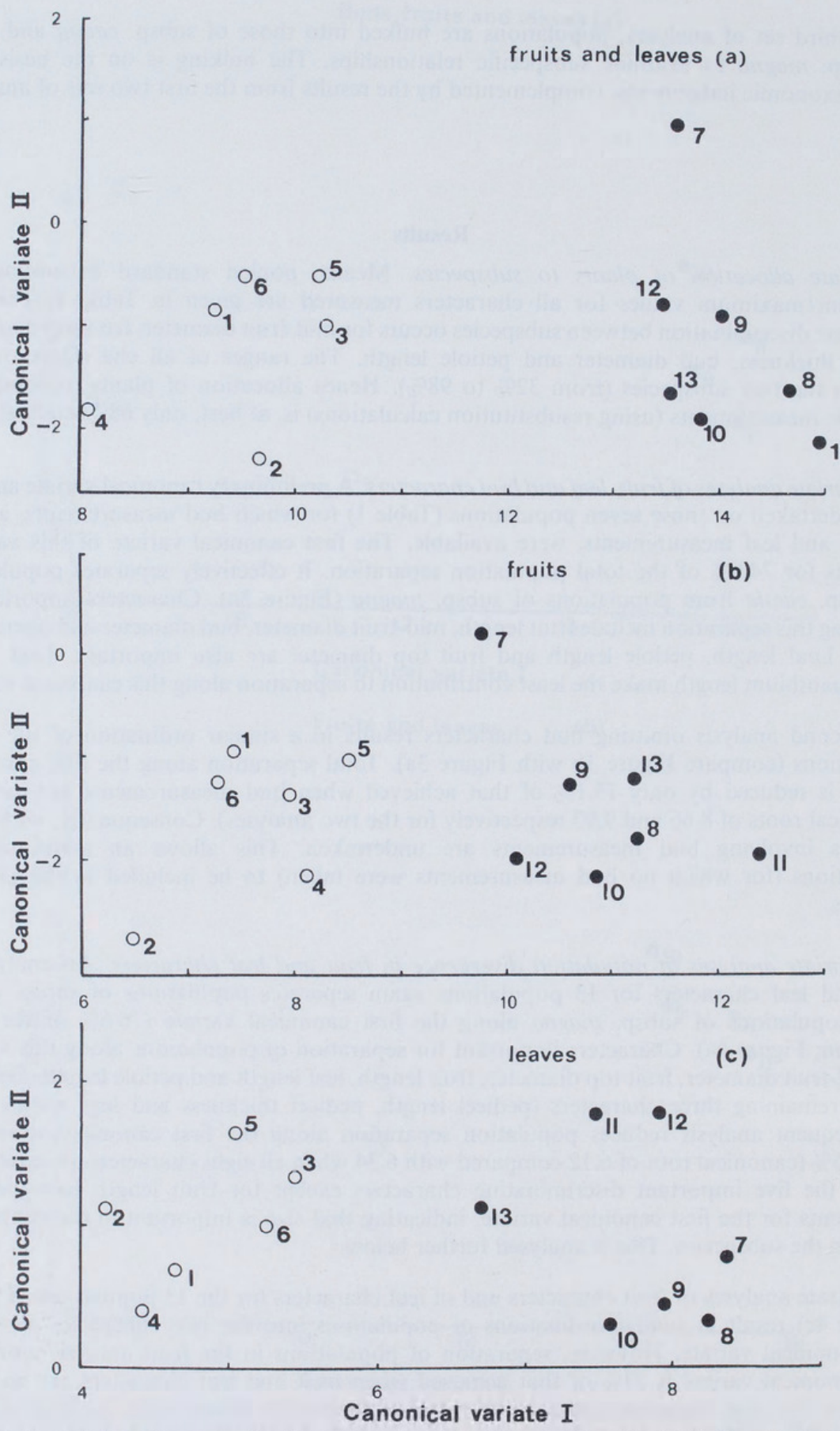


Figure 4. Canonical variate means for the analyses based on 13 populations for (a) fruit and leaf characters, (b) fruit characters and (c) leaf characters. The canonical vectors are standardized so that scores have unit variance within populations. Population identification is given in Table I. o - subsp. *caesia*, • - subsp. *magna*.

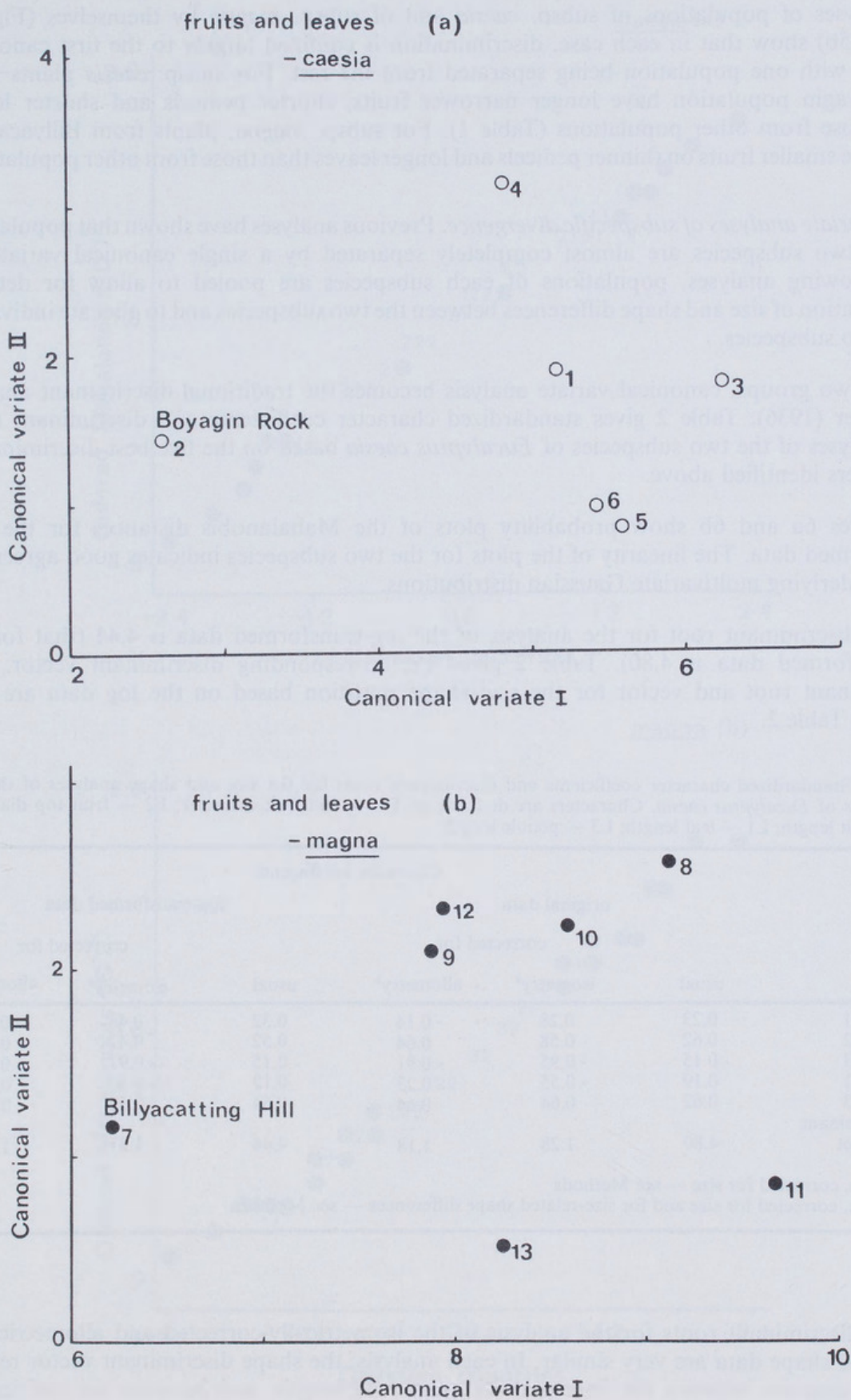


Figure 5. Canonical variate means for the analyses based on fruit and leaf characters for (a) subsp. *caesia* and (b) subsp. *magna*. The canonical vectors are standardized so that scores have unit variance within groups. Population identification is given in Table 1.

Analyses of populations of subsp. *caesia* and of subsp. *magna* by themselves (Figures 5a and 5b) show that in each case, discrimination is confined largely to the first canonical variate, with one population being separated from the rest. For subsp. *caesia* plants from the Boyagin population have longer narrower fruits, shorter pedicels and shorter leaves than those from other populations (Table 1). For subsp. *magna*, plants from Billyacatting Hill have smaller fruits on thinner pedicels and longer leaves than those from other populations.

Multivariate analyses of subspecific divergence. Previous analyses have shown that populations of the two subspecies are almost completely separated by a single canonical variate. In the following analyses, populations of each subspecies are pooled to allow for detailed investigation of size and shape differences between the two subspecies and to allocate individual plants to subspecies.

For two groups, canonical variate analysis becomes the traditional discriminant analysis of Fisher (1936). Table 2 gives standardized character coefficients and discriminant roots for analyses of the two subspecies of *Eucalyptus caesia* based on the five best discriminating characters identified above.

Figures 6a and 6b show probability plots of the Mahalanobis distances for the log-transformed data. The linearity of the plots for the two subspecies indicates good agreement with underlying multivariate Gaussian distributions.

The discriminant root for the analysis of the log-transformed data is 4.44 (that for the untransformed data is 4.80). Table 2 gives the corresponding discriminant vector. The discriminant root and vector for the size/shape partition based on the log data are also given in Table 2.

Table 2. Standardized character coefficients and discriminant roots for the size and shape analyses of the two subspecies of *Eucalyptus caesia*. Characters are denoted as: F1 — mid-fruit diameter; F2 — fruit top diameter; F3 — fruit length; L1 — leaf length; L3 — petiole length.

	Character coefficients					
	original data			log-transformed data		
	corrected for			corrected for		
	usual	isometry ^a	allometry ^b	usual	isometry ^a	allometry ^b
F1	0.23	0.28	- 0.14	0.32	0.48	0.06
F2	0.62	0.58	0.64	0.52	0.42	0.48
F3	- 0.15	- 0.95	- 0.91	- 0.15	- 0.97	- 0.92
L1	0.19	- 0.55	- 0.23	0.12	- 0.60	- 0.36
L3	0.62	0.64	0.64	0.64	0.68	0.74
discriminant root	4.80	1.28	1.18	4.44	1.27	1.01

^a i.e. corrected for size — see Methods
^b i.e. corrected for size and for size-related shape differences — see Methods.

The discriminant roots for the analysis of the isometrically-corrected and allometrically-corrected shape data are very similar. In each analysis, the shape discriminant vector results from a contrast between the fruit diameter and fruit length, and between the leaf length and petiole length. The fruits of subsp. *caesia* are narrower, relative to their length, than those of subsp. *magna*. The petioles of subsp. *caesia* are also shorter relative to leaf length than those of subsp. *magna*.

Size differences account for about 75% of the overall divergence between subspecies, with marked separation of populations of subsp. *caesia* from populations of subsp. *magna*. This marked separation is not evident for the shape vector, though the population means for subsp. *caesia* are smaller than those for subsp. *magna*. The nature of the shape vector contrasts with that of the overall vector; the latter has positive components for all but fruit length. Shape differences account for only about 25% of the overall divergence.

Multivariate allocation of plants to subspecies and their populations. Allocation of plants using Mahalanobis distances for the five best discriminating characters shows that only three individuals (2%) out of 138 are allocated to the wrong subspecies. All three occur in populations of subsp. *caesia* one from Yanneymooning Hill and the other two from Mount Stirling. The correct allocation of a further two plants (one each from the Billyacatting Hill and SW Chiddarcooping Hill populations of subsp. *magna*) is doubtful. Eleven plants are atypical for all populations but each is closer to its correct subspecies. Some plants are nominally allocated to other populations of their subspecies, but all are also typical of their own population.

The wrongly allocated plants are in this case also clearly identified by a visual appraisal of histograms of first canonical variate scores for each of the 13 populations included in the analysis of fruit and leaf measurements (Figure 7). The Yanneymooning Hill population differs from others of subsp. *caesia* in having several plants with fruits and leaves bordering on the size seen in subsp. *magna*. It also has plants typical of subsp. *caesia*. This range of variation is evident in the histogram of canonical variate scores in Figure 7.

Discussion

Success of the multivariate approach. This study demonstrates that two morphometrically distinguishable races exist in *Eucalyptus caesia*. A multivariate analysis of five characters (mid-fruit diameter, fruit top diameter, fruit length, leaf length and petiole length) results in only three (2%) of the 138 plants measured being allocated to the wrong subspecies. Such a low rate of misallocation justifies the formal recognition of the races as subspecies (Brooker and Hopper 1981).

The multivariate analyses have shown that most (c. 75%) of the differences between subsp. *caesia* and subsp. *magna* are related to size, with subsp. *magna* being larger in all measured dimensions. It also has been demonstrated that measurements taken on both fruits and leaves all make a significant contribution to the discrimination between the subspecies.

Measurements of individual characters show relatively poor discrimination between the two subspecies with, at best, only 68% of plants falling outside the subspecific range overlap for any single measurement. A multivariate approach to discriminate between subspecies is clearly necessary to improve on this situation.

We conclude that it is possible to distinguish reliably between subsp. *magna* and subsp. *caesia*, and that the gazettal of subsp. *magna* as rare under the Wildlife Conservation Act 1950-79 would not create an unworkable identification problem for officers of the Department of Fisheries and Wildlife who police the activities of commercial seed collectors. However, it is now clear that both subspecies require special legislative protection because of their rarity in the wild. This would alleviate any difficulties arising in those very few instances where the allocation of plants to subspecies by morphometric procedures is doubtful. The Western Australian Wildlife Authority has already accepted the latter proposal, and *Eucalyptus caesia* (together with 99 other taxa) was gazetted as rare on November 14, 1980 (Rye and Hopper 1981).

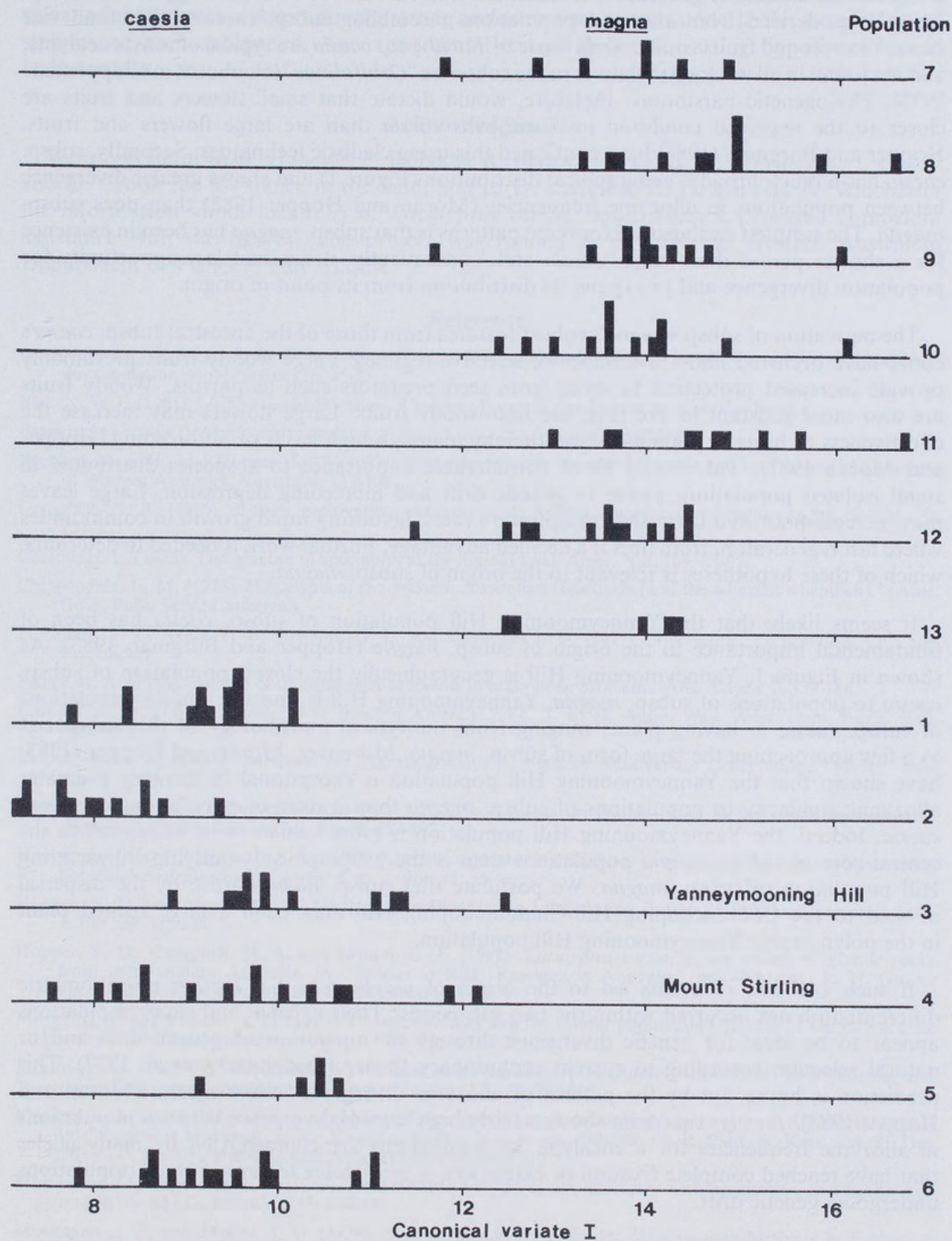


Figure 7. Histogram of scores for the first canonical variate for fruit and leaf measurements for all 13 populations. The canonical vectors are standardized so that scores have unit variance within groups. Population identification is given in Table 1.

Evolutionary aspects of geographical variation. Several lines of evidence suggest that subsp. *magna* was derived from ancestral populations resembling subsp. *caesia* rather than vice versa. Flowers and fruits smaller than those of *Eucalyptus caesia* are typical of most eucalypts, and are found in all its closest relatives in the subseries "*Orbifolinae*" (cf. photos in Chippendale 1973). Phylogenetic parsimony, therefore, would dictate that small flowers and fruits are closer to the ancestral condition in *Eucalyptus caesia* than are large flowers and fruits. Hopper and Burgman (1983) have confirmed this using cladistic techniques. Secondly, subsp. *caesia* has a much broader geographical distribution (Figure 1) and shows greater divergence between populations in allozyme frequencies (Moran and Hopper 1983) than does subsp. *magna*. The simplest explanation for these patterns is that subsp. *magna* has been in existence for a shorter period than subsp. *caesia* and, consequently, it has had less opportunity for population divergence and to expand its distribution from its point of origin.

The derivation of subsp. *magna*'s robust features from those of the ancestral subsp. *caesia*'s could have occurred under a number of selective regimes. Large woody fruits presumably provide increased protection to seeds from seed predators such as parrots. Woody fruits are also more resistant to fire than are non-woody fruits. Large flowers may increase the effectiveness of birds as pollinators and thereby maintain high levels of outbreeding (Hopper and Moran 1981). This would be of considerable importance to a species distributed in small isolated populations prone to genetic drift and inbreeding depression. Large leaves may increase photosynthetic and transpiration rates, favouring rapid growth in communities where fast regeneration from fires is a decided advantage. Further work is needed to determine which of these hypotheses is relevant to the origin of subsp. *magna*.

It seems likely that the Yanneymooning Hill population of subsp. *caesia* has been of fundamental importance in the origin of subsp. *magna* (Hopper and Burgman 1983). As shown in Figure 1, Yanneymooning Hill is geographically the closest population of subsp. *caesia* to populations of subsp. *magna*. Yanneymooning Hill is unusual among populations of subsp. *caesia* in having plants ranging from the typical morphology of this subspecies to a few approaching the large form of subsp. *magna*. Moreover, Moran and Hopper (1983) have shown that the Yanneymooning Hill population is exceptional in showing a greater allozymic similarity to populations of subsp. *magna* than it does to populations of subsp. *caesia*. Indeed, the Yanneymooning Hill population is more similar in its allozymes to the central core of subsp. *magna* populations than is the geographically-outlying Billyacatting Hill population of subsp. *magna*. We postulate that subsp. *magna* arose by the dispersal of seed to the Coorancooping Hill-Chiddarcooping Hill area from a large fruited plant in the polymorphic Yanneymooning Hill population.

If such a course of events led to the origin of *magna* why has further morphometric differentiation not occurred within the two subspecies? Their isolated and small populations appear to be ideal for genetic divergence through the operation of genetic drift and/or natural selection according to current evolutionary theory (Dobzhansky et al. 1977). This prediction is borne out by the pattern of allozyme divergence in the species (Moran and Hopper 1983). *Eucalyptus caesia* shows a fairly high level of divergence between populations in allozyme frequencies for a eucalypt. Its populations are characterised by many alleles that have reached complete fixation or extinction, a predictable feature of small populations undergoing genetic drift.

In contrast to this differentiated mosaic of allozyme variation, populations of *Eucalyptus caesia* are morphometrically stabilised as either subsp. *caesia* or subsp. *magna* (except for the Yanneymooning Hill stand). This morphometric stability must have a genetic base that is not influenced by genetic drift due to small population size. Carson's (1975) concept of a section of the genome closed to recombination and other factors generating genetic

divergence may well explain this striking difference between morphometric and allozymic variation in the species. Alternatively, strong uniform selection may underlie the morphological stability of each subspecies. An experimental test of these contrasting hypotheses would be instructive.

Acknowledgements

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