

GENE FLOW BETWEEN THREE EUCALYPT SPECIES AT SNUG PLAINS

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(with two tables and eight text-figures)

DAVIDSON N.J., REID, J.B. & POTTS B.M., 1987 (30:vi): Gene flow between three eucalypt species at Snug Plains. *Pap. Proc. R. Soc. Tasm.*, 121: 101-108. ISSN 0080-4703. Department of Botany, University of Tasmania, Hobart, Tasmania, Australia 7001.

The extent of hybridisation and gene flow between the three *Monocalyptus* species, *Eucalyptus pulchella*, *E. coccifera* (series *Piperitae*) and *E. delegatensis* (series *Obliquae*) at Snug Plains (600 m) in southeastern Tasmania was examined. The flowering time of *E. pulchella* was two months later than usual for this normally low-altitude species. It consequently overlapped the flowering period of both sub-alpine species *E. coccifera* and *E. delegatensis* and had its peak flowering period intermediate between the two. The movements of pollinators across the species boundaries indicated the potential for hybridisation between *E. pulchella* and the other two species.

Adult morphology suggested that the Snug Plains *E. pulchella* tended towards *E. coccifera* compared to typical, low-altitude *E. pulchella* and progeny tests reinforced this view. In addition, two out of twelve *E. pulchella* adults sampled appeared intermediate between this species and *E. coccifera* and produced progeny overlapping those from *E. coccifera*. These results suggest that introgression of *E. coccifera* genes may be occurring into *E. pulchella* at Snug Plains although adaptive convergence cannot be excluded. Quite a different picture is seen for the results of hybridisation between *E. pulchella* and *E. delegatensis*. Six putative F₁ hybrids between *E. pulchella* and *E. delegatensis* occurred in progeny from two *E. pulchella* mothers. However, this appears to have had little genetic impact on the species, since no evidence of introgression or convergence was apparent in adult populations of these species.

Key Words: gene flow, hybridisation, introgression, eucalypt species, Tasmania

INTRODUCTION

While genetic isolation appears to be maintained at the subgeneric level in the genus *Eucalyptus*, there are few absolute barriers to interbreeding between species within a subgenus although the extent of natural hybridisation varies considerably (Curtis & Morris 1975, Pryor 1976). In Tasmania hybridisation between closely related species from the informal series *Piperitae* (subgenus *Monocalyptus*, Pryor & Johnson 1971) is common (Potts & Reid 1983, 1985a) with many recognised taxa exhibiting complete intergradation (e.g. Shaw *et al.* 1984). In contrast, despite frequent geographical contact between species from the series *Piperitae* and the series *Obliquae* (also subgenus *Monocalyptus*), there are only a few records of inter-series hybrids (Pryor 1957a, Jackson 1958, Potts & Reid 1983). In the present study we compare the extent of inter-series and intra-series hybridisation and gene flow between two *Piperitae* species (*E. pulchella* Desf. and *E. coccifera* Hook. f.) and one *Obliquae* species (*E. delegatensis* R.T. Baker) at Snug Plains in southeastern Tasmania by examining the flowering phenology and adult and seedling morphology.

Snug Plains is one of the few areas where

these three species can be found in parapatry and is unique since an extensive plateau occurs at an intermediate altitude (approx. 600 m) near the upper and lower altitudinal limits respectively of the lowland (e.g. *E. pulchella*) and sub-alpine (e.g. *E. coccifera* and *E. delegatensis*) eucalypt floras. A complex mosaic of eucalypt species occurs on the plateau in response to microhabitat variations arising from the interaction of ecological factors such as frost, drought and water logging (Davidson & Reid 1985, 1987, Davidson 1986).

MATERIALS AND METHODS

The study site was a shallow rocky ridge on the eastern side of Snug Plains at an altitude of 600 m (see Davidson & Reid 1985 for details) where a small population of *E. pulchella* (200-500 mature trees) approximately 50 m wide followed the ridge crest for 0.5 km flanked by populations of *E. coccifera* to the west and *E. delegatensis* to the east. At this site herbarium samples of adult foliage (fig. 1) and fruit were collected from six trees of *E. delegatensis* and *E. coccifera* and two samples of six trees of *E. pulchella*. The first *E. pulchella*

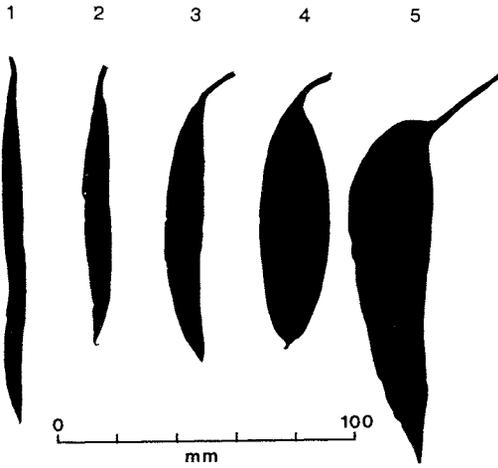


FIG.1 — Typical adult leaves for lowland *E. pulchella* (1), Snug Plains *E. pulchella* from the ridge top (2) and a shallow depression (associated with *E. coccifera*) (3), Snug Plains *E. coccifera* (4), and Snug Plains *E. delegatensis* (5).

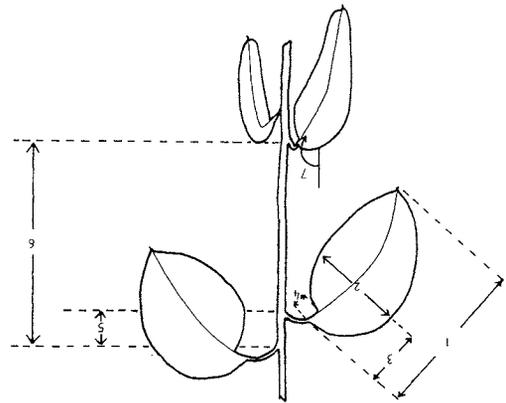


FIG.2 — Seven of the morphological characters measured from seedling leaves: 1 = lamina length, 2 = lamina width, 3 = length to widest point of the lamina, 4 = basal asymmetry of the leaf, 5 = intranode length, 6 = internode length, and 7 = leaf rotation (from the vertical).

population came from a ridge top site where shallow soil occurred over dolerite bedrock, while the second came from a slight depression in the ridge crest with deeper soil in which adults of both *E. pulchella* and *E. coccifera* occurred (near stand D, fig. 2 in Davidson & Reid 1985). A separate collection of herbarium specimens and fruit was also made for six trees from a lowland population of *E. pulchella* at a site 5 km east of the study area, at an altitude of approximately 100 m. Six representative leaves and 20 capsules were selected from the material collected from each tree. A limited set of morphological characters was measured for the adult leaves and air-dry weights were obtained for the capsules. The leaf characters measured were a subset of those used by Potts & Reid (1983) and were previously shown to be sufficient to discriminate between *Monocalyptus* species (Potts & Reid 1983, 1985a). They included petiole length, leaf lamina length, leaf lamina width, length to widest point of the leaf, and basal asymmetry of the leaf (fig. 2). Statistical analysis of the adult leaf and fruit data set included analysis of variance and canonical variates analysis. Canonical variates analysis (Seal 1966) has been widely used in the study of hybridisation in *Eucalyptus* (e.g. Hopper *et al.* 1978, Potts & Reid 1983).

Replication trials were conducted for the five

populations sampled in the field [lowland *E. pulchella*, Snug Plains *E. pulchella* (two populations), Snug Plains *E. coccifera*, and Snug Plains *E. delegatensis*]. The seed, which was collected concurrently with the herbarium samples from six adult trees, was stratified for four weeks at 4°C in a cold room, then germinated on moist vermiculite and pricked out, at the cotyledonary stage, into plywood veneer tubes filled with potting soil. Ten replicate seedlings were planted for each tree (a total of 300 seedlings). The seedlings were arranged in a randomised block design, with an edge row in a glasshouse. The seedlings were watered three times weekly and nutrient was supplied via slow release fertilisers (Osmocote, blood and bone) present in the potting mix.

After four months growth a single leaf was removed from nodes 5, 7 and 10 of each seedling and a set of morphological characters measured for each leaf. The set of measurements made for the seedling leaves were the same as those measured for adult leaves apart from addition of measures of leaf glaucousness (scored on a 1 to 5 scale), lamina thickness and rotation of the leaf to the vertical [scored on a 1 (horizontal) to 4 (vertical) scale, fig. 2]. Where seedling leaves were sessile (e.g. *E. coccifera*) basal leaf width at the point of junction with the stem was measured. This measure was

combined in one variable with petiole length by recording it as a negative distance, mutually exclusive to a positive petiole length (see Potts & Reid 1985a). Internode length and intranode length were also measured at nodes 5, 7 and 10. Internode length was measured between the node at which the leaf characters were measured and the immediately preceding node. Analysis of variance and canonical variates analysis was performed on the above set of seedling morphological characters. The data for node 10 only are presented since essentially similar results were obtained from the analysis of data from each node.

The field populations of *E. pulchella* (ridge top population), *E. coccifera* and *E. delegatensis* at Snug Plains and the lowland population of *E. pulchella* were also assessed for time and intensity of flowering. The same random sample of thirty trees were visually assessed on each visit to each population. The sites were visited fortnightly between October 1981 and April 1982 and the intensity of flowering was scored on a 1 to 10 scale (0 = no open flowers) for each tree and a population mean determined.

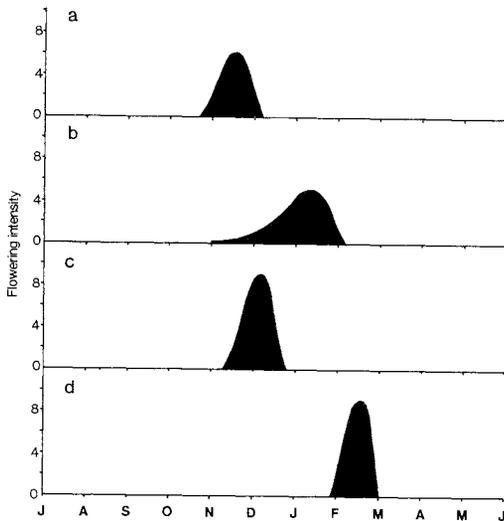


FIG.3 — Flowering time (month) versus intensity (on a 0 to 10 scale) during 1981-82 for: (a) lowland *E. pulchella*, (b) the ridge top population of *E. pulchella* at Snug Plains, (c) Snug Plains *E. coccifera*, and (d) Snug Plains *E. delegatensis*.

RESULTS

Flowering Time

The flowering time of the three *Monocalyptus* species present on Snug Plains (600 m), *E. pulchella*, *E. coccifera* and *E. delegatensis*, overlapped (fig. 3). The peak flowering time for typical Snug Plains *E. pulchella* from a ridge site was midway between the peaks for *E. coccifera* and *E. delegatensis* and showed a skewed distribution, starting at a low intensity before, and continuing throughout, the flowering period of *E. coccifera*. This indicated the potential for hybridisation exists between these three largely parapatric eucalypt species, although the probability of *E. pulchella* hybridising with *E. coccifera* or *E. delegatensis* would be much greater than hybridisation between *E. coccifera* and *E. delegatensis*. The peak flowering time for the Snug Plains *E. pulchella* was two months later than for *E. pulchella* from a nearby low altitude site (100 m) and the Snug Plains *E. coccifera* was more than a month earlier than normal for this species (Potts & Reid 1983). Observations of the movements of New Holland honeyeaters (*Phylidonyris novaehollandiae*), yellow wattle birds (*Anthochaera paradoxa*) and a variety of pollinating insects which fed from flowers in the crown of each of the species at Snug Plains indicated that these pollinators move indiscriminantly across species boundaries during occasions when the flowering periods of the eucalypt species overlapped.

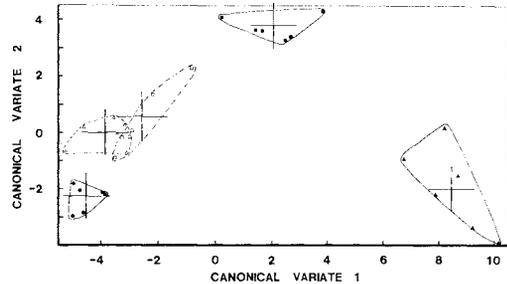


FIG.4 — Canonical variate 1 versus canonical variate 2 derived from an analysis of six morphometric characters measured on adult foliar and capsule material collected in the field for: lowland *E. pulchella* (●), Snug Plains *E. pulchella* from the ridge top (△), and shallow depression (□), Snug Plains *E. coccifera* (■), and Snug Plains *E. delegatensis* (▲). Means are shown for each population.

TABLE 1
Adult Foliar and Capsule Parameters

Mean (\pm S.E.) leaf lamina length (LL), leaf lamina width (LW), length to the widest point of the leaf (LWP), petiole length (PL), basal asymmetry of the leaf (Basym), and capsule weight (Cap.wt.), measured for adult foliar and capsule material collection from lowland *E. pulchella*, Snug Plains *E. pulchella* from the ridge top and the shallow depression, *E. coccifera* and *E. delegatensis*. n = 6.

Species	LL (mm)	LW (mm)	LWP (mm)	PL (mm)	Basym (mm)	Cap.wt (g)
<i>E. pulchella</i> (low)	105.4 \pm 2.5	6.36 \pm 0.09	54.6 \pm 1.6	6.59 \pm 0.18	0.156 \pm 0.005	0.053 \pm 0.002
<i>E. pulchella</i> (ridge top)	79.4 \pm 1.3	7.68 \pm 0.13	42.4 \pm 0.5	7.54 \pm 0.20	0.144 \pm 0.010	0.135 \pm 0.006
<i>E. pulchella</i> (depression)	79.6 \pm 0.7	9.15 \pm 0.44	39.7 \pm 0.4	10.17 \pm 0.54	0.213 \pm 0.009	0.170 \pm 0.014
<i>E. coccifera</i>	84.1 \pm 1.5	19.44 \pm 0.96	35.3 \pm 0.9	16.21 \pm 0.62	0.383 \pm 0.097	0.346 \pm 0.004
<i>E. delegatensis</i>	111.9 \pm 2.0	26.27 \pm 0.27	29.8 \pm 0.8	21.59 \pm 0.61	6.839 \pm 0.379	0.266 \pm 0.009

Adult Morphology

The five populations differed significantly ($P < 0.001$) for each of the six adult characters scored (table 1). The two populations of *E. pulchella* from Snug Plains were intermediate between the low altitude *E. pulchella* and the *E. coccifera* populations for all characters except lamina length and basal asymmetry of the leaf.

Canonical variates analysis of the adult characters clearly separated the *E. coccifera*, *E. delegatensis* and low altitude *E. pulchella* populations (fig. 4). Canonical variate 1 (CV1) contained 81% of the variation and mainly separated *E. delegatensis* from the two *Piperitae* species and was dominated by a comparison between lamina length and length to the widest point of the leaf. Canonical variate 2 (CV2, 17% of variation) mainly discriminated between *E. coccifera* and *E. pulchella* populations based primarily on a comparison of capsule weight and lamina length. The high altitude

E. pulchella populations from Snug Plains were distinct from the low altitude *E. pulchella* population and tended in the direction of *E. coccifera*.

Seedling Morphology

Analysis of variance indicated significant differences ($P < 0.001$) between the five populations for all ten characters scored (e.g. table 2). Canonical variates analysis using the ten seedling characters clearly separated the progeny from the *E. coccifera*, *E. delegatensis* and low altitude *E. pulchella* populations (fig. 5). Canonical variate 1 contained 76% of the variation and discriminated *E. delegatensis* from the other populations based on petiole length and lamina length while canonical variate 2 (22% of variation) discriminated *E. coccifera* from the other populations and contrasted lamina width with lamina length and petiole length. The progeny from the two Snug Plains populations of *E. pulchella* were intermediate (figs 5 and 6) and

TABLE 2
Juvenile Foliar Parameters

Mean (\pm S.E.) for log (lamina length/lamina width) (log LL/LW), petiole measure (PM) and basal asymmetry (Basym) for juvenile leaves of progeny from lowland *E. pulchella* (n = 52), Snug Plains *E. pulchella* from the ridge top (n = 57) and the shallow depression (n = 55), *E. coccifera* (n = 53) and *E. delegatensis* (n = 51).

Species	log LL/LW	PM (mm)	Basym (mm)
<i>E. pulchella</i> (low)	0.99 \pm 0.019	-2.8 \pm 0.34	0.00 \pm 0.000
<i>E. pulchella</i> (ridge top)	0.73 \pm 0.022	-5.1 \pm 0.63	0.10 \pm 0.046
<i>E. pulchella</i> (depression)	0.63 \pm 0.027	-11.7 \pm 0.87	0.03 \pm 0.021
<i>E. coccifera</i>	0.12 \pm 0.010	-28.1 \pm 0.53	0.00 \pm 0.000
<i>E. delegatensis</i>	0.22 \pm 0.008	8.5 \pm 0.40	4.02 \pm 0.245

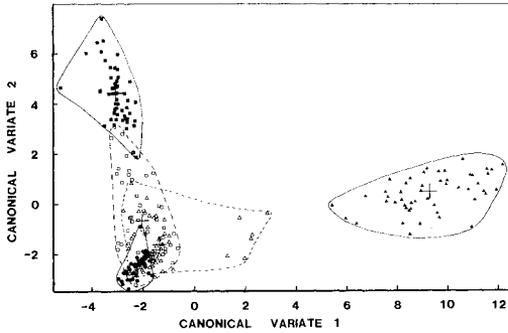


FIG. 5 — Canonical variate 1 versus canonical variate 2 derived from an analysis of ten morphometric characters measured at the tenth node from glasshouse grown progeny of: lowland *E. pulchella* (●), Snug Plains *E. pulchella* from the ridge top (△) and a shallow depression (associated with *E. coccifera*) (□), Snug Plains *E. coccifera* (■), and Snug Plains *E. delegatensis* (▲). Means are shown for each population.

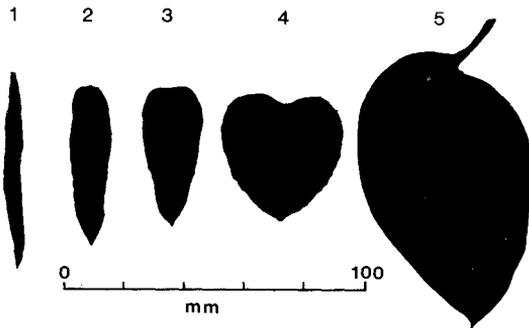


FIG. 6 — Typical seedling leaves from progeny of lowland *E. pulchella* (1), Snug Plains *E. pulchella* from the ridge top (2) and a shallow depression (associated with *E. coccifera*) (3), Snug Plains *E. coccifera* (4), and Snug Plains *E. delegatensis* (5).

showed greater variability than the low altitude, allopatric *E. pulchella* population. However, in all but the progeny from one tree this increased variability seemed to be a result of interdependence of the variance and the mean on CV2 (fig. 7).

The two Snug Plains *E. pulchella* populations were significantly different (table 2). Both produced individuals overlapping the low altitude *E. pulchella* population and also individuals tending towards

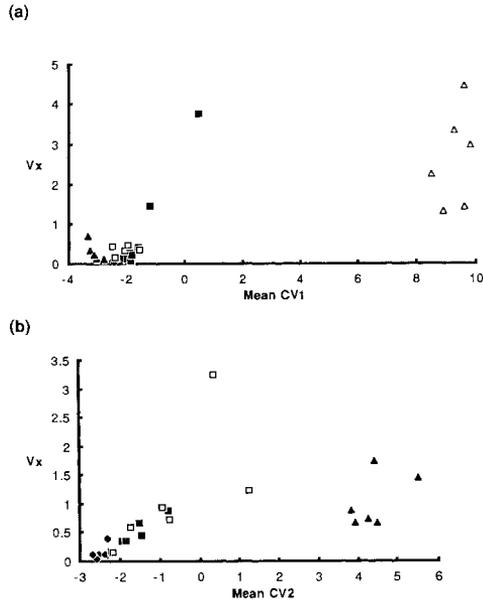


FIG. 7 — The variance of CV1 (a) and CV2 (b) scores (see fig. 5) plotted against the mean value for open pollinated progenies of lowland *E. pulchella* (◆), samples of *E. pulchella* from the ridge top (■) and shallow depression (□) on Snug Plains, *E. coccifera* (▲) and *E. delegatensis* (△) from Snug Plains.

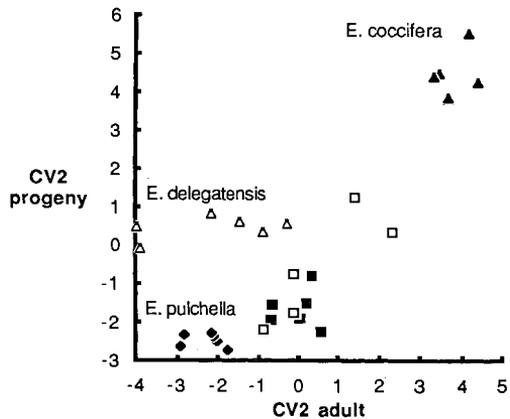


FIG. 8 — The progeny mean score on CV2 (fig. 5) plotted against the score of the maternal phenotype on CV2 from the analysis of adult morphology (fig. 4). Population symbols follow figure 7.

the *E. coccifera* population (fig. 5). However, in the ridge top population two trees phenotypically identical in adult morphology to normal Snug Plains *E. pulchella*, produced six individuals (11%) clearly separate from all other *E. pulchella* progeny and intermediate between typical progenies of *E. pulchella* and *E. delegatensis* as opposed to *E. coccifera* progeny (figs 5 and 6). Five of these intermediate types arose in progeny from a single *E. pulchella* tree and there can be little doubt these outliers are a result of F_1 hybridisation between *E. pulchella* and *E. delegatensis*. The presence of these outliers had a marked effect on the variability of these two *E. pulchella* progenies which were clearly more variable for canonical variate 1 than were the progeny from the other four trees from the ridge top site (fig. 7). The Snug Plains *E. pulchella* population sampled from the shallow depression produced individuals showing continuous variation up to and overlapping the distribution of *E. coccifera* progeny (fig. 5). There was a high percentage (c. 22%) of individuals in this population which, in this direction, lay beyond the range of *E. pulchella* progeny from the other Snug Plains population. The progeny overlapping the range of *E. coccifera* were mainly descended from the two parents in this population which were intermediate in adult morphology between *E. pulchella* and *E. coccifera* (fig. 8). However, the variability in open pollinated progeny from only one of these intermediates was greater than in other parental progenies (fig. 7b).

DISCUSSION

The ecological preferences of *E. pulchella*, *E. coccifera* and *E. delegatensis* tend to result in spatial separation of these species. Direct genetic interaction is frequently restricted to boundary zones (e.g. *E. coccifera* and *E. delegatensis*) and only rarely do stands of *E. pulchella* occur with the two sub-alpine species (e.g. *E. pulchella* and *E. coccifera* on Middle Peak, Shaw *et al.* 1984). Prezygotic reproductive isolation is further accentuated by differences in flowering time. The flowering times are usually distinct with *E. pulchella* flowering before either of the other two species. In its "normal" ecological position *E. pulchella* has almost completed flowering before *E. coccifera* commences, while *E. delegatensis* flowers after *E. coccifera* (Potts & Reid 1983). However, at Snug Plains all three species are parapatric and intermingle in boundary regions. *E. pulchella* flowers between the other two species and overlaps both. Together with the observed indiscriminate move-

ment of pollinators these conditions clearly suggest the potential for pollen transfer between *E. pulchella* and the other two species at this site. The reversed flowering of *E. coccifera* and *E. pulchella* may be partly a consequence of populations of both species occurring at the upper and lower altitudinal extremes of their species range as flowering time has been reported to be delayed with increasing altitude in several eucalypt species (e.g. Barber & Jackson 1957, Griffin 1980, Shaw *et al.* 1984).

Six progeny from two of the *E. pulchella* mothers from the ridge top population at Snug Plains (fig. 7a) were intermediate in phenotype between the *E. pulchella* and *E. delegatensis* seedlings (fig. 5) and are most likely F_1 hybrids between *E. pulchella* and *E. delegatensis*. They were intermediate not only in the characters scored but in all other observable characteristics. No such individuals were found in progeny from the *E. delegatensis* mothers sampled nor progeny from the other population of *E. pulchella* sampled on Snug Plains. This asymmetric hybridisation between *E. pulchella* and *E. delegatensis* could be due to several factors including the effect of flower size (Tibbits 1986) and the earlier flowering of the *E. pulchella*. The protandrous nature of eucalypt flowers (Pryor 1976, Griffin & Hand 1979) would favour pollen of the later flowering species pollinating the earlier flowering species. A similar asymmetry has been noted between *E. risdonii* and *E. amygdalina* (Potts & Reid 1985a, Potts 1986). The adult population samples from the study site at Snug Plains (fig. 4) showed no tendency for individuals intermediate between *E. pulchella* and *E. delegatensis* but in a widespread examination of the natural stands in the region a single localised hybrid swarm was discovered (saplings 4 to 6 m tall). This suggests that although hybridisation may occur between these species the F_1 individuals only occasionally survive to maturity and consequently there is probably little gene exchange between these species at Snug Plains.

A very different picture is found when examining the interaction between the two *Piperitae* species. In both adult (fig. 4) and progeny (fig. 5) morphology the Snug Plains *E. pulchella* trees tend towards *E. coccifera* in phenotype relative to the trees from the low altitude *E. pulchella* population. This occurs for reproductive as well as vegetative characters. Further, at least two adults from the Snug Plains *E. pulchella* population in the slight depression (associated with *E. coccifera*) are intermediate between the rest of this population and *E. coccifera* (fig. 8) and may well represent hybrids between these two species. Some of the offspring

from these two trees overlap the distribution of the *E. coccifera* progeny (fig. 5). The lack of increased variability amongst progeny from one of these two trees suggests advanced generation hybridisation (fig. 7b). Furthermore, with populations of *E. pulchella* at Snug Plains significantly different from lowland *E. pulchella* and tending in the direction of *E. coccifera*, there is the possibility that this divergence is a result of introgression of *E. coccifera* genes into the *E. pulchella* population and subsequent genetic stabilisation. Such introgression could be of adaptive significance since the reduced leaf lengths found in the Snug Plains *E. pulchella* populations may be less prone to wind and ice damage in the sub-alpine environment. *E. coccifera* genes may also confer increased frost resistance on the *E. pulchella* population (see Davidson & Reid 1985). However, similar convergence of *E. pulchella* toward the *E. coccifera* phenotype could result from adaptive differentiation within *E. pulchella* since the direction of divergence (in several characters) is similar to that noted to occur with altitude in other *Eucalyptus* species. For example, in many species leaf length is reduced (Pryor 1957b, Barber & Jackson 1957, Phillips & Reid 1980, Shaw *et al.* 1984, Potts & Reid 1985b) and capsule size is increased (e.g. Phillips & Reid 1980, Shaw *et al.* 1984) with increasing altitude. In either case, the presence of phenotypes similar to the low altitude *E. pulchella* in the seedling cohort (fig. 5), but the absence of overlap in the adult populations may reflect strong selection against low altitude *E. pulchella* types at Snug Plains although this remains to be verified.

The plateau at Snug Plains is environmentally heterogeneous, with slight topographic changes resulting in various areas exposed to severe frosts and waterlogging while other areas are subject to drought (Davidson & Reid 1985, 1987; Davidson 1986). This results in a unique and complex mosaic of "typically" lowland and sub-alpine eucalypt species. Furthermore, with the intermediate altitude of the plateau it is conceivable that slight climatic changes may have a pronounced effect on its suitability as a habitat for lowland and sub-alpine eucalypt species. The introgression of *E. coccifera* genes into the *E. pulchella* gene pool may have allowed the lowland species, *E. pulchella*, to maintain a foothold in this largely sub-alpine region and avoid extinction. Adaptive introgressive hybridisation may genetically buffer a species against environment change, increasing evolutionary flexibility and allowing population stability in an unstable environment. Nevertheless, the genetic and evolutionary consequences of hybridisation

may vary markedly and while the present study demonstrates active F₁ hybridisation between *E. pulchella* and *E. delegatensis*, this seems to have had little genetic impact.

ACKNOWLEDGEMENTS

We wish to thank Mr L. Johnson, Ms A. Kitchener, Ms G. Permyakoff and Mr C. Raine for technical assistance.

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(accepted 23 March 1987)