

The Response of Eucalypt Populations to a Changing Environment

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Abstract

A large amount of genetic diversity in ecological traits exists both within and between the Tasmanian eucalypt species. This variation is generally associated with spatial variation in habitat. Major changes in the distribution of eucalypt species have no doubt occurred in response to past environmental change and even today, populations are continually reacting to short- or long-term changes in the environment. The processes by which populations respond to environmental change are addressed, with particular emphasis on gene flow and the role of hybridisation in the expansion and contraction of species ranges.

Introduction

The rugged Tasmanian topography results in a mosaic of environments to which eucalypts exhibit a close adaptive response (Pryor and Johnson 1971; Pryor 1976). While mixed, usually subgeneric, associations of eucalypt species can be observed (Noble 1989—cf. Parsons and Rowan 1968; Rogers and Westman 1979), varying degrees of spatial segregation of species are more common. This is due to marked differences between species in response to ecological factors such as drought (Kirkpatrick and Marks 1985; Davidson and Reid 1989), waterlogging (Davidson and Reid 1987) and frost (Davidson and Reid 1985; Hallam *et al.* 1989). Narrow ecotones often separate species, with intricate mosaics of species maintained in response to spatial changes in a complex of factors such as drainage, aspect, altitude, topographic position and soil characteristics

(Jackson 1965; Hogg and Kirkpatrick 1974; Kirkpatrick and Nunez 1980; Kirkpatrick 1981; Davidson and Reid 1985, 1987, 1989). Many species may thus occur in close geographic proximity and, in south-eastern Tasmania, up to 17 of the 29 Tasmanian species may be observed within a distance of 10–12 kilometres (see Jackson 1965).

Even within species, marked genetic differentiation is regularly encountered as species respond to spatial changes in environment. Significant genetic differences between populations have been detected in all of the Tasmanian species examined to date. Genetically based, often multicharacter, clines frequently occur, not only amongst disjunct populations (e.g. *E. cordata*, Potts 1989), but also within continuous stands in response to strong habitat gradients (e.g. Barber and Jackson 1957; Barber 1965; Potts and Reid 1985a,b; Potts and Jackson 1986). In some cases, marked genetic differentiation may occur over extremely short geographical distances. For example, in the continuous stand of *E. urnigera* on Mount Wellington, there is a stepped transition at approximately 860 m from the shiny green foliage at low altitudes to the highly glaucous morphs near the summit (Barber and Jackson 1957). Furthermore, many of the recognised taxa in Tasmania are, in fact, clinally linked and genetically intergrade along environmental and geographical gradients (*E. vernicosa* - *subcrenulata* - *johnstonii*, Jackson 1960; *E. viminalis* - *dalrympleana*, Phillips and Reid 1980; *E. gunnii* - *archeri*, Potts and Reid 1985a,b).

Strong environmental gradients thus maintain a complex spatial mosaic of variation in

eucalypts both at the species and population level. However, there is no doubt that major changes in the distribution of this variation has occurred in response to past climatic change (e.g. Pryor 1976; Pryor and Johnson 1981; Churchill 1968; Parsons 1969; Marginson and Ladiges 1982). Despite a relatively ancient, possibly pre-Tertiary, origin of *Eucalyptus* (Hill and Carpenter 1990), a rapid spatial, and possibly major evolutionary, radiation of the genus appears to have occurred in the last 200 000 years (Singh *et al.* 1981) as a response to increasing aridity and decline of fire-sensitive elements of the flora. At higher latitudes at least, this radiation occurred during an era of rapid climatic change. In particular, the succession of Quaternary glacials has had a marked effect on species distribution patterns in Tasmania. Many of the extant eucalypt forests occur in regions which would have been treeless at the height of the last glaciation, and corresponding variation and distribution patterns must be less than 11 000 years old (Macphail 1980).

This raises questions of the nature and rate of response of eucalypt populations to environmental change and the stability of reproductive barriers. In many cases, the redistribution of variation will occur along continuous migration routes (e.g. altitudinal shifts). However, the patchy distribution of habitat coupled with the close ecological specificity of eucalypts will often result in suitable habitats being separated by large expanses of unsuitable habitat which prevent migration as a front. Of particular interest are the modes of invasion of habitat islands, created, for example, by climatic change, which occur some distance from a pre-adapted source population. In the absence of competition, viable populations can probably still be maintained on such ecologically marginal sites, particularly when supplemented by dispersal from surrounding sites. However, an evolutionary response will depend on the relative probabilities of *in situ* differentiation from within the local population (or deme *sensu* Endler 1977) versus invasion by a pre-adapted morph

(intraspecific gene flow) or species (interspecific gene flow). This article addresses some of the processes involved in the response of eucalypt populations to a changing environment, with particular emphasis on gene flow and the role of hybridisation in the expansion and contraction of species ranges.

Local adaptation

Most traits of ecological and taxonomic significance in plants appear to be under quantitative genetic control (Lawrence 1984; Lande and Barrowclough 1987), and *Eucalyptus* seems to be no exception (e.g. Tibbits *et al.* 1991). Such characters are usually controlled by many genes each having relatively small effects (cf. Mendelian traits) and the genetic basis of phenotypic differences among populations, races and species is usually of this type (Grant 1971; Lande and Barrowclough 1987). For such characters, the genetic and hence evolutionary response (R) of the local population to selection can be predicted from the equation,

$$R = h^2 * \sigma_p * I \quad (1)$$

where h^2 is the narrow-sense individual heritability, σ_p is the phenotypic standard deviation of the trait and I is the intensity of selection (Falconer 1986). In combination, the heritability and the phenotypic variance provide an estimate of the level of additive genetic variability (σ_a^2) in the population, which determines the response to selection. In the case of natural selection, the genetic response of a trait is dependent on the degree of association between the trait and individual fitness (Falconer 1986). At the more realistic, multitrait level, predicting the genetic response becomes much more difficult. The response of a single trait is, in fact, determined not only by the intensity of selection acting on the trait *per se*, but the genetic correlations which exist with other traits undergoing selection. Genetic correlations arise through numerous factors

Table 1. Some estimates of heritabilities (individual, narrow-sense - h^2) in eucalypt populations.

Species	Trait	h^2	Source
<i>E. globulus</i>	height (6 yr)	0.12	Volker <i>et al.</i> (1990)
	diameter	0.24	
	volume	0.19	
<i>E. grandis</i>	height (15 mth)	0.11	van Wyke (1976)
	diameter	0.08	
	volume	0.10	
	frost resilience	0.29	Reddy and Rockwood (1989)
<i>E. nitens</i>	freezing resistance	0.49-0.66	Tibbits <i>et al.</i> (1991)
<i>E. regnans</i>	height (5-6 yr)	0.21-0.60	Eldridge (1972)
	diameter	0.11-0.20	
	basal area	0.11-0.20	
	height (45 mth)	0.13-0.43	Griffin & Cotterill (1988)
	diameter	0.19-0.46	
	volume	0.16-0.45	
<i>E. tereticornis</i>	height (4 yr)	0.25	Kedharnath & Vakshasya (1978)
	diameter	0.17	

including pleiotropic gene action and linkage, and a genetic change may occur in selectively neutral traits simply because of this correlated response. Predictions of the genetic response at the multivariate level thus requires a knowledge of character heritabilities, phenotypic variances and the genetic correlations amongst the characters (see Mitchell-Olds and Rutledge 1986), as well as their covariance with estimates of fitness.

Pedigreed breeding programmes and progeny trials are required to estimate these quantitative genetic parameters (Lawrence 1984). However, due to the time and expense of undertaking these experiments, additive genetic variability is rarely monitored in population genetic and conservation studies (see Lande and Barrowclough 1987). Nevertheless, these parameters are regularly estimated in applied plant breeding and the recent interest in tree breeding has generated unique opportunities for their estimation for eucalypt populations. Several estimates of heritabilities and levels of additive genetic variation are already published for growth

traits (Table 1), and in most cases they do suggest that small, but significant, levels of additive genetic variance reside within local populations, which would be available for selection. Significant variation between families within populations in progeny trials is also indicative of additive genetic variation within populations, and significant effects have been noted for a range of ecologically important traits in species such as *E. obliqua* (e.g. Green 1971; Brown *et al.* 1976), *E. regnans* (e.g. Eldridge 1972; Griffin and Cotterill 1988), *E. nitens* (Tibbits and Reid 1987; Tibbits *et al.* 1991) and *E. gunnii* (Potts and Reid 1985b). However, the level of additive genetic variation within local populations is usually small when compared to the variation between populations or provenances within *Eucalyptus* species (e.g. Potts and Reid 1985b; Tibbits and Reid 1987; Potts 1989). Only in the absence of gene flow will these measures of additive genetic variance within local populations truly reflect that available for selection.

Gene flow

Intraspecific gene flow

Gene flow from surrounding, genetically different areas may significantly increase the levels of genetic variation within the local population, with both positive and negative effects. On the one hand, gene flow may oppose selection, and, if sufficiently high, prevent local genetic differentiation. On the other hand, immigrant genes, alone or following recombination, may provide a source of novel, fitter genotypes (Endler 1977). Gene flow is usually measured as the root mean square (i.e. standard deviation) of the dispersal distances, written as either σ (e.g. Crawford 1984) or l (e.g. Endler 1977). In plants, the distance of total gene flow is dependent on both pollen and seed dispersal, with the combined variance for total gene flow (σ^2) estimated from the equation,

$$\sigma^2 = \frac{1}{2} t \sigma_{\text{pollen}}^2 + \sigma_{\text{seed}}^2 \quad (2)$$

where t is the outcrossing rate, σ_{pollen}^2 is the variance of pollen dispersal distances and σ_{seed}^2 is the variance of seed dispersal distances (Crawford 1984). In eucalypts, the outcrossing rate is generally high, about 0.7 (Moran and Bell 1983; Potts and Savva 1989), suggesting a heavy weighting of the pollen component. However, despite the importance of these gene flow parameters, there are few quantitative estimates of either seed- or pollen-mediated dispersal in *Eucalyptus*.

Seed dispersal Seed dispersal in most eucalypt species is mainly by wind and gravity (Cremer 1966, 1977). With the exception of the subgenus *Corymbia*, neither the seed nor fruits exhibit special adaptations to this mode of dispersal (Carr 1972; Cremer 1977). Studies of seedfall from commercial species indicate that virtually all seed is deposited within a radius of twice the tree or canopy height (e.g. Gilbert 1958; Cunningham 1960; Floyd 1962; Cremer 1966). The distance of seedfall is essentially

proportional to canopy height, seed weight (i.e. terminal velocity) and wind speed (Cremer 1977). The movement of seed, once deposited on the ground, is probably fairly limited in most species (e.g. Floyd 1962), although extensive seed harvesting by ants no doubt results in some effective dispersal.

Rare long-distance dispersal events necessary for colonisation and invasion may occur by several means. Under abnormal circumstances, seed or capsules may be dispersed by birds, floods, storms, or in fire updrafts (e.g. Jacobs 1955; Carr 1972; Kirkpatrick 1977). Indeed, with most eucalypt species being dependent on fire for regeneration, seed dispersal during non-fire periods will not lead to effective gene flow and may differ markedly from dispersal which is coincident with regeneration events. It is thus important that dispersal be monitored following regeneration events such as fire which may facilitate the dispersal of seeds to greater distances than normal (Carr 1972). Kirkpatrick (1977) suggests that small branches with capsules attached may be carried in fierce convectional updrafts during crown fires and deposited some distance from parent trees. This is more likely to be significant in the wetter forests, although in the drier, more open forests, high winds frequently blow capsules attached to small branches and twigs considerable distance along the forest floor. While strong-beaked birds may break open woody capsules to eat seed (Jacobs 1955; Long 1984), their significance as a mode of dispersal has not, as yet, been demonstrated. Water transport may also be significant, particularly for species growing on river margins or floodplains (e.g. *E. camaldulensis*).

Estimates of the standard deviation of seed dispersal distances (σ_{seed}) for the tall forest species, *E. regnans*, range from only 18 to 48 m (Table 2). The distance of seedfall decreases with canopy density (Table 2) and, under normal circumstances, it is unlikely that even these distances would be achieved with a closed canopy (Levin and Kerster 1974). Furthermore, most of these measurements

Table 2. Estimates of seed dispersal in eucalypts.

Species	Seed Dispersal σ_{seed} (m)	Canopy Height (m)	Source
<i>E. risdonii</i> ¹	4.6	2.5	Potts and Reid (1988) (from boundary)
<i>E. regnans</i> ²	17.5	55.0	Cunningham (1957 Table 2) (SE of 2 trees)
	41.2	76.2	Gilbert (1958 Table 5.3) (SE of 2 trees)
	30.3	61.0	Gilbert (1958 Table 2.10) (SSE of dense forest edge)
	31.6	61.0	Cremer (1966 Fig. 1A) (SSE of dense forest edge)
	45.1	61.0	Cremer (1966 Fig. 1B) (SE of sparse forest edge)
	48.4	61.0	Cremer (1966 Fig. 1C) (SE of isolated tree, adjusted canopy height)

¹ Distribution of seedlings established after wildfire

² Seed traps

were taken downwind of a seed source whereas recent studies indicate a marked asymmetry in seed dispersal with a nearly 15-fold increase in the number of seed dispersed downwind of a source (B. Potts, unpublished data). Nevertheless, few species achieve the height of *E. regnans*, and seed dispersal in the majority of eucalypt species is likely to be considerably less. For example, the distance of seed-mediated gene flow of the mallee *E. risdonii* measured after wildfire ($\sigma_{\text{seed}} = 4.6$ m) was nearly one tenth that of *E. regnans* and no seedlings were found more than 20 m from a source. Comparable levels of seed dispersal are probably common in eucalypts as similar canopy heights are frequently encountered in species growing at the extremes of altitude, fire or drought and are typical of the mallee communities in the drier regions of Australia (Onans and Parsons 1980).

Pollen dispersal In contrast to seed dispersal, the breeding system of *Eucalyptus* appears to be well adapted for pollen-mediated gene flow (Barber 1965; Pryor 1976). Flowers are generally protandrous, outcrossing rates are high and pollination is usually effected by active, generally non-

specific pollinating vectors such as birds and insects (Barber and Jackson 1957; Ashton 1975; Barber 1965; Hopper and Moran 1981; Ireland and Griffin 1984; Savva *et al.* 1988). While there is very little quantitative information on pollen-mediated dispersal in *Eucalyptus* (Table 3), as with seed, most pollen is probably deposited in relatively close proximity to a source. Birds tend to follow a close to nearest-neighbour foraging pattern (e.g. Hopper and Moran 1981; Savva *et al.* 1988) although pollen may be carried over for several trees (Savva *et al.* 1988). Nevertheless, as noted by Barber (1965), gene flow in *Eucalyptus* is probably more a function of pollen than seed, and it is particularly in the frequency of rarer long-distance dispersal events, *viz.* the tail of the dispersal curve, that pollen probably surpasses seed.

Over five per cent of all inter-tree foraging movements by birds involve long-distance (out-of-sight) escape or exploratory flights (Hopper and Moran 1981; Savva *et al.* 1988). It is difficult to assess exactly how far the tail of the pollen dispersal curve extends. Progeny analysis, using interspecific hybrids as genetic markers, is one of the most practical ways of assessing pollen dispersal (Pryor 1976; Potts and Reid 1988). Rare hybrids with lowland

species are regularly found in eucalypt populations on mountain summits and our best example, verified to the second generation, is an *E. urnigera* x *E. ovata* hybrid found in an open pollinated family grown from seed collected for *E. urnigera* nearly 5 km from the nearest source of *E. ovata* pollen (B. Potts and M. Savva, unpublished data). Long-distance dispersal of *E. risdonii* pollen into the range of *E. amygdalina* is rare, yet even at half a kilometre, F1 hybrids were located at a frequency of about 1 in a 1000 in open-pollinated progenies of *E. amygdalina* (Potts and Reid 1988). The tail of the pollen dispersal curve is probably extremely long, particularly where bird pollination is involved, and information from the distance and frequency of interspecific hybrids is likely to underestimate the frequency of long-distance pollen dispersal within species.

Barriers to gene flow

Post-mating barriers within species

Flowering time is a major post-mating barrier to pollen-mediated gene flow in *Eucalyptus* (Pryor 1976) and marked differences in flowering time may occur within species. There are often waves of flowering along altitudinal gradients (e.g. *E. coccifera*, Shaw *et al.* 1984; *E. urnigera*, Barber and Jackson 1957, Savva *et al.* 1988) as well as variation with aspect (e.g. *E. amygdalina*, Potts and Reid 1985c). The variation in flowering time within species may be large, even between contiguous populations in close geographical proximity. On the Central Plateau, for example, there is virtually no overlap in the flowering of populations of *E. gunnii* which are separated by 200 m of altitude and 4 km apart (Potts and Reid 1985a). The outcrossing rate may not only change with distance from a source, but may also be markedly asymmetrical. The protandrous development of the eucalypt flower (Pryor 1976) results in pollen release commencing from several days (Pryor 1976) to nearly two weeks (Savva *et al.* 1988) before stigma receptivity, favouring pollen flow from late to early flowering trees. For gene flow outside of a local population, the outcrossing rate, t , will thus be a variable

Table 3. Estimates of pollen dispersal parameters in eucalypts.

Species	Pollen Dispersal σ_{pollen} (m)	Source
<i>E. urnigera</i> ¹	13.0	Savva <i>et al.</i> (1988)
<i>E. stoatei</i> ¹	5.6	Hopper and Moran (1981 Fig. 3)
<i>E. fastigata</i> ²	21.0	Pryor (1976)
<i>E. risdonii</i> ²	82.0	Potts and Reid (1988)

¹ Pollinator foraging movements, axial estimates

² F1 hybrids in open pollinated progenies of contiguous species

parameter acting in most cases to reduce the significance of the pollen dispersal component in Equation 2. Indeed, at the population and species level, the parameter t will be a measure of reproductive isolation and a continuum of values within the genus ranging from the individual outcrossing rates ($t = 0.4$ – 1.0 ; Moran and Bell 1983) to complete reproductive isolation ($t = 0$, as in the case of species from different subgenera) is envisaged.

Geographical barriers Barton and Hewitt (1985) consider a distance of 100σ would constitute a moderately strong barrier to gene flow. Assuming $\sigma_{\text{pollen}} = 80$ m (probably an overestimate) and $t = 0.7$, then for the seed dispersal estimates for *E. risdonii* and *E. regnans* in Table 2, a major barrier to total gene flow within a species would be of the order of 5 to 7 km respectively. Many species of *Eucalyptus* are distributed as small, disjunct populations which are no doubt completely isolated from gene flow with other populations of the species. The gene pool of the endemic *E. cordata*, for example, appears to be geographically subdivided into about 15 genetically isolated lineages ranging in size from 6 to over 5000 individuals, with the average distance between individual populations being 45 km (Potts 1989). Several recent studies have used indirect methods based on isozyme data to estimate the rate of immigration amongst isolated eucalypt populations. Prober *et al.* (1990) estimated

a



b



Figure 1. The distribution of (a) dolerite over 600 m altitude and (b) *E. coccifera* (modified from Jackson 1965) in Tasmania.

that the rate of migration (proportion of the average effective population size migrating per generation) amongst populations of *E. paliformis* separated by an average of 1.5 km (range 0.3-2.5 km) was 0.0004. Their estimates of the rate of migration amongst populations of *E. parvifolia* separated by 1-2 km ranged from 0.017 (approximately 1 km) to 0.066 (1-2 km). Govindaraju (1989) only presents data for the estimated average number of migrants exchanged per generation amongst populations of *E. pauciflora* (6.5) and the two subspecies of *E. caesia* (ssp. *magna*, 1.1, and ssp. *caesia*, 0.76). However, integrating the latter results with size of the isolated *E. caesia* populations given by Moran and Hopper (1983) yields an estimate of a migration rate of 0.005 and 0.007 for ssp. *caesia* and ssp. *magna* respectively. The latter rates appear relatively high considering that the average distance between populations of this species is 90 km (Moran and Hopper 1983).

Major barriers to dispersal in Tasmania: the case of *E. coccifera* The Pleistocene glacial cycles would have resulted in a complex pattern of barrier formation and removal in Tasmania (Kirkpatrick and Brown 1984; Potts and Jackson 1986). Little is known of the sequence of *Eucalyptus* evolution in Tasmania, although Jackson (1965) notes that the wholly endemic groups and relic distributions of species with mainland affinities indicates periods of isolation and reciprocal invasion. Apart from the severing of the northern land bridge, there is evidence for a major glacial barrier within Tasmania between northern and southern high altitude eucalypt floras which would have acted as a barrier to invasion of mainland species and radiation from a south-eastern glacial refugium (Potts and Jackson 1986). The latter area appears to have been a major area of eucalypt speciation in Tasmania (e.g. Ladiges *et al.* 1983). The existence of this historically persistent barrier is supported by the absence of several



Photo 1. Twenty-year-old planted *E. coccifera* growing at 1445 m on Ben Lomond.

endemics such as the *E. vernicosa* cline forms, and *E. urnigera* and *E. coccifera* from apparently suitable habitats on the north-eastern mountains.

The absence of *E. coccifera*, in particular, provides strong evidence that limited dispersal coupled with problems of invading a pre-established community is one of the main reasons these species do not occur on the mountains of the north-east. *E. coccifera* is the normal treeline species on other dolerite-capped mountains in Tasmania (Fig. 1). Its closest occurrence to the north-eastern mountains is on the Central Plateau and the Eastern Tiers (Snow Hill) which are separated from the north-eastern mountains by the extensive Midlands Graben and the South Esk River Valley respectively. The suitability of habitat on these north-eastern mountains for *E. coccifera* is strongly suggested by the 20-year-old plantings of this species on Ben Lomond (Davies and Davies 1989; Photo 1), which are relatively vigorous and have set

viable seed. In fact, the plantings are growing in shrubbery 200 m above the present *E. archeri* treeline. Where *E. coccifera* and *E. archeri* co-occur on the Western Tiers, *E. coccifera* grows to a much higher elevation than *E. archeri* (see Jackson 1973). This suggests that if *E. coccifera* had invaded Ben Lomond, the treeline could be several hundred metres higher than at present without invoking climatic change. Kirkpatrick and Brown (1984) similarly suggest that the absence of particular endemic plants toward the north may be a result of remoteness from glacial refugia rather than unsuitability of habitat, and cite *E. tenuiramis* and *E. pulchella* as examples.

Interspecific gene flow

Geographical barriers to dispersal appear to have been a major determinant of the extant distribution patterns. For species dispersal, it is only the seed dispersal component of Equation 2 which is usually relevant. Thus,

for seed dispersal, disjunctions of the order of 0.5 and 5 km would constitute major barriers to the seed-mediated invasion by *E. risdonii* and *E. regnans* respectively. Most other species probably lie somewhere between these two extremes clearly indicating that habitat disjunctions, as noted for *E. coccifera*, would constitute extremely strong barriers to species invasion.

However, hybridisation within subgenera is common amongst eucalypts (Griffin *et al.* 1988; Duncan 1989), and it has been argued (Potts and Reid 1988) that even where the rate of natural hybridisation is low, seed dispersal may be so limited compared to pollen dispersal that hybridisation may significantly increase the flow of genes into the range of a potentially interbreeding species. Long-distance pollen dispersal and hybridisation followed by resurrection of the phenotype of the pollen parent from a segregating hybrid swarm may be one possible mechanism of long-distance habitat invasion in *Eucalyptus* (Fig. 2). This mechanism has been detailed in a localised area for the Tasmanian endemics, *E. risdonii* and *E. amygdalina*, by Potts and Reid (1988). Ashton and Williams (1973) had independently envisaged this scenario in relation to sporadic occurrences of *E. obliqua* x *E. regnans* in the Trentham Forest of Victoria. There are many other examples of hybrid, or at least intermediate, types occurring some distance from a source of the pollen species in *Eucalyptus* (Kirkpatrick *et al.* 1973; Parsons and Kirkpatrick 1972 cf. Watson *et al.* 1987; Pryor and Johnson 1981; Potts and Reid 1983; Ashton and Sandiford 1988). However, unless founder events can actually be observed, it is extremely difficult to differentiate between hypotheses of long-distance seed dispersal, long-distance pollen dispersal, phantom hybrids arising from range restriction or simply convergent evolution. Nevertheless, major advances in the resolution of these hypotheses should be possible with organelle and nuclear DNA fingerprinting techniques which are currently being developed for eucalypts.

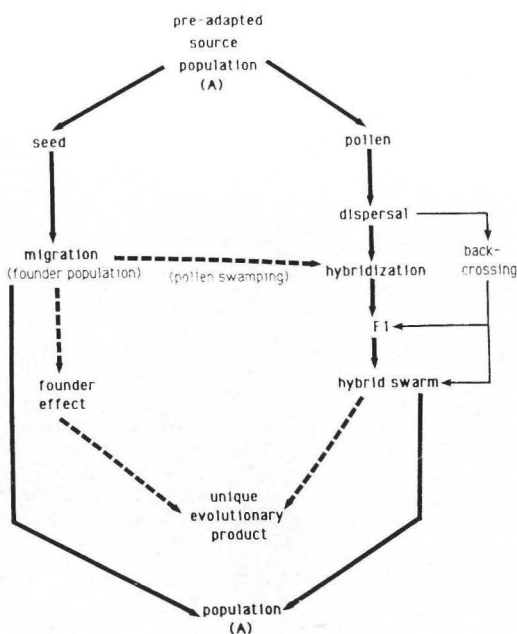


Figure 2. Modes of invasion of habitat islands within the range of a potentially interbreeding species (from Potts and Jackson 1986).

Pollen-mediated invasion: the case of *E. risdonii* Classically, it has been argued that hybridisation is of little evolutionary significance, and that while sporadic hybrids occur at species boundaries, their distribution is limited and that, in each generation, intense selective forces would eliminate these hybrids from the population (Wagner 1970). Species integrity and boundaries would then be re-established in later stages of the life cycle. However, this scenario assumes environments and species boundaries are stable, which is clearly questionable (see Ashton 1981) and does not appear to be the case of one boundary studied between *E. risdonii* and *E. amygdalina*.

E. risdonii is confined to the mudstone hills on the eastern shore of the Derwent River where it has a patchy distribution within forests of *E. amygdalina*. These two species are closely related but morphologically distinct. Natural hybridisation occurs and the phenotype of the F1 hybrid is known from artificial crosses and can be identified (Potts and Reid 1985b). In most parts of its range, *E. risdonii* is a fire-



Photo 2. *Eucalyptus risdonii*/*amygdalina* boundary in the Government Hills after wildfire in 1980.

induced mallee about 2-3 m high although it can occur as a small tree. As with most eucalypts, it is dependent on fire for effective seedling regeneration when mass seed release occurs. The population dynamics and regeneration following wildfire has been studied for a normal boundary and hybrid zone between these two species in the Government Hills, near Hobart (Potts 1986; Photo 2). There was a marked fitness differential between these two species at their common boundary, and in the specific areas studied, *E. risdonii* was invading the range of *E. amygdalina* by both pollen and seed dispersal (Potts and Reid 1985c; Potts 1986). This invasion appears to have persisted for several regeneration cycles and may have resulted from a combination of factors favouring *E. risdonii* (e.g. drought, insect predation and increased fire frequency). However, there appeared to be a marked inertia in the species boundary because of extremely slow population turnover (due to extensive

vegetative regeneration from lignotubers) and limited seed dispersal.

The F1-type hybrids were more competitive with *E. amygdalina* than *E. risdonii*. There was an asymmetric distribution of F1-type hybrids across the boundary, and it was suggested that, in such cases where seed dispersal was limited, a moving front may be heralded by a wave of hybridisation (Potts 1986). F1-type hybrids are established at low frequency well beyond the range of normal seed dispersal, and hybrid swarms occur, not only along the boundary, but occasionally well out in the *E. amygdalina* forest. There is little doubt that the majority of long-distance dispersal events end in extinction. Nevertheless, small, isolated patches of abnormal phenotypes can be found within the *E. amygdalina* forest ranging from those dominated by intermediates to those dominated by *E. risdonii* types. Many of these patches occur well outside the range of normal dispersal of *E. risdonii* seed, and the large lignotuber

diameters would suggest that at least some of these patches have been founded by F1-type hybrids (Potts and Reid 1988). Of particular significance is that in some cases young seedlings or saplings superficially resembling *E. risdonii* can be found associated with the old hybrids in areas well outside the range of normal dispersal of *E. risdonii* seed. This suggests the possibility that long-distance invasion could occur completely independent of seed dispersal. Progeny trials have demonstrated that the genetic potential exists for directional selection to shift the composition of these isolated hybrid swarms toward the *E. risdonii* phenotype on suitable sites (Potts and Reid 1988). The intermediate inheritance of traits such as flowering time (Potts and Reid 1985c) would result in these hybrid patches becoming a focal point for future long-distance pollen dispersal and subsequent backcrossing would then be expected to speed the resurrection process.

Seed-mediated founder events Even where the initial founder event occurs through long-distance seed dispersal, hybridisation with surrounding species may still have a significant genetic impact (Potts and Jackson 1986). The level of F1 hybridisation increases markedly with decreasing patch size. For example, at the boundaries of large stands of *E. risdonii*, the average level of hybridisation is around 3 per cent, but in small patches this increases to more than 14 per cent, with some individuals exceeding 75 per cent (B. Potts, unpublished data). The only other alternative for a founder is self-fertilisation and inbreeding, not an attractive proposition for a eucalypt (Potts *et al.* 1987). In contrast to the classic ideas of a reduction in genetic variability in founder populations (Provine 1989), it has been argued that hybridisation with potentially interbreeding species may result in an increase in genetic variability and allow ample opportunity for adaptive or non-adaptive gene exchange to occur (Potts and Jackson 1986). Where hybrid products are less fit than either parent, there will be intense selection pressure on the smaller

population to evolve reproductive isolating mechanisms and hence reduce the loss of gametes through hybridisation with the surrounding more abundant species. Indeed, reproductive barriers are most likely to evolve in small populations (Barber 1965; Gore *et al.* 1990); the selection pressure will be clearly asymmetrical and may lead to the evolution of unilateral cross-incompatibility (Gore *et al.* 1990). The evolution of such reproductive barriers may not only isolate the small population from the surrounding species, but may indirectly result in the reproductive isolation of the founder population from conspecific populations.

Population extinction The former argument is equally valid for the case of range contraction, where hybridisation may also be intimately involved in the process of population extinction. While many small relic populations show very little effect of hybridisation (e.g. Wiltshire and Reid 1987), in some cases, high levels of hybridisation occur (e.g. Pryor 1951; Potts and Reid 1985b; Potts 1989). Specific integrity may only be broken down in the last stages of extinction when pollen swamping is at a maximum. This is seen in many of the small relic populations of higher altitude species which were isolated on hill tops in eastern Tasmania after the last glacial (Potts and Reid 1985b; Potts 1989). In cases where reproductive barriers are poorly established, hybridisation may be widespread. For example, altitudinal clines linking small populations of the tree-line species *E. coccifera* with the surrounding low altitude populations of *E. nitida* seen on Tim Shea are believed to be partly a result of introgression and to reflect a genetic trail of the post-glacial, upslope migration of *E. coccifera* (Shaw *et al.* 1984). Genetic invasion of small relic populations may result in phantom hybrid populations (Parsons and Kirkpatrick 1972) and even the assimilation of the genetic remnants into the gene pool of surrounding species. In contrast, slow gene exchange with contiguous species may be one means by which small relic populations

may retain genetic variability and evolutionary flexibility (see Potts and Jackson 1986).

Conclusion

A large amount of genetic diversity in ecological traits exists both within and between the Tasmanian eucalypt species. However, major changes in the distribution of eucalypt species have no doubt occurred in response to past environmental change and even today, populations are continually reacting to short or long-term changes in the

environment. There may be a marked lag in the response of eucalypt populations to environmental change due to slow population turnover and limited seed dispersal. Geographical barriers to seed dispersal have probably been a major determinant of the extant distribution and evolutionary patterns within the genus. Environmental change may result in a breakdown of delicate barriers to gene flow, and the role of hybridisation in the dynamics of range expansion and contraction is emphasised, both as a source of novel genetic variation and a means of gene dispersal.

References

- Ashton, D.H. (1975) Studies of the flowering behaviour in *Eucalyptus regnans* F. Muell. *Aust. J. Bot.* 23: 399–411.
- Ashton, D.H. (1981) The ecology of a boundary between *Eucalyptus regnans* F. Muell. and *E. obliqua* L'Hérit. in Victoria. *Proc. Ecol. Soc. Aust.* 11: 75–94.
- Ashton, D.H. and Sandiford, L.M. (1988) Natural hybridisation between *Eucalyptus regnans* F. Muell. and *E. macrorhyncha* F. Muell. in the Cathedral Range, Victoria. *Aust. J. Bot.* 36: 1–22.
- Ashton, D.H. and Williams, G. (1973) The occurrence of gum-topped stringybarks in the Trentham Forest. *Victorian Naturalist* 90: 90–92.
- Barber, H.N. (1965) Selection in natural populations. *Heredity* 20: 552–572.
- Barber, H.N. and Jackson, W.D. (1957) Natural selection in action in *Eucalyptus*. *Nature* 179: 1267–1269.
- Barton, N.H. and Hewitt, G.M. (1985) Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* 16: 113–148.
- Brown, A.H.D., Eldridge, K.G., Green, J.W. and Matheson, A.C. (1976) Genetic variation in *Eucalyptus obliqua* in field trials. *New Phytologist* 77: 193–203.
- Carr, S.G.M. (1972) Problems of the geography of the tropical eucalypts. In: *Bridge and Barrier: The Natural and Cultural History of Torres Strait* (ed. D. Walker), pp. 153–182. Australian National University, Canberra.
- Churchill, D.M. (1968) The distribution and prehistory of *Eucalyptus diversicolor* F. Muell., *E. marginata* Donn ex Sm. and *E. calophylla* R. Br. in relation to rainfall. *Aust. J. Bot.* 16: 125–151.
- Crawford, T.J. (1984) The estimation of neighbourhood parameters for plant populations. *Heredity* 52: 273–283.
- Cremer, K.W. (1966) Dissemination of seed from *Eucalyptus regnans*. *Aust. For.* 29: 252–262.
- Cremer, K.W. (1977) Distance of seed dispersal in eucalypts estimated from seed weights. *Aust. For. Res.* 7: 225–228.
- Cunningham, T.M. (1957) Seed production and seed fall of *E. regnans* (F. Muell.) *Aust. For.* 21: 28–39.
- Cunningham, T.M. (1960) *The Natural Regeneration of Eucalyptus regnans*. Bulletin No. 1. School of Forestry, Melbourne University.
- Davidson, N.J. and Reid, J.B. (1985) Frost as a factor influencing the growth and distribution of subalpine eucalypts. *Aust. J. Bot.* 33: 657–667.
- Davidson, N.J. and Reid, J.B. (1987) The influence of hardening and waterlogging on the frost resistance of subalpine eucalypts. *Aust. J. Bot.* 35: 91–101.
- Davidson, N.J. and Reid, J.B. (1989) Response of eucalypt species to drought. *Aust. J. Ecol.* 14: 139–156.
- Davies, J.B. and Davies, M.J. (1989) *Plant Communities of the Ben Lomond Plateau*. Occasional Paper No. 1. Queen Victoria Museum and Art Gallery, Launceston, Tasmania.
- Duncan, F. (1989) Systematic affinities, hybridisation and clinal variation within Tasmanian eucalypts. *Tasforests* 1: 13–26.
- Eldridge, K.G. (1972) Genetic variation in growth of *Eucalyptus regnans*. *Aust. For. Timb. Bur. Bull.* No. 46.
- Endler, J.A. (1977) *Geographical Variation, Speciation and Clines*. Princeton University Press, Princeton.
- Falconer, D.S. (1986) *Introduction to Quantitative Genetics*. Longman Scientific and Technical, Essex.

- Floyd, A.G. (1962) Investigations into the natural regeneration of blackbutt—*E. pilularis*. Research Note No. 10. Forestry Commission, New South Wales.
- Gilbert, J.M. (1958) Eucalypt-rainforest relationships and the regeneration of the eucalypts. Ph.D. thesis, University of Tasmania.
- Gore, P.L., Potts, B.M., Volker, P.W. and Megalos, J. (1990) Unilateral cross-incompatibility in *Eucalyptus*: the case of hybridisation between *E. globulus* and *E. nitens*. *Aust. J. Bot.* 38: 383–394.
- Govindaraju, D.R. (1989) Estimates of gene flow in forest trees. *Biol. J. Linn. Soc.* 37: 345–357.
- Grant, V. (1971) *Plant Speciation*. Columbia University Press, New York.
- Green, J.W. (1971) Variation in *Eucalyptus obliqua* L'Hérit. *New Phytologist* 70: 879–909.
- Griffin, A.R., Burgess, I.P. and Wolf, L. (1988) Natural and manipulated hybridisation in the genus *Eucalyptus*—a review. *Aust. J. Bot.* 36: 41–66.
- Griffin, A.R. and Cotterill, P.P. (1988) Genetic variation in growth of outcrossed, selfed and open-pollinated progenies of *Eucalyptus regnans* and some implications for breeding strategy. *Silvae Genetica* 37: 124–131.
- Hallam, P.M., Reid, J.B. and Beadle, C.L. (1989) Frost hardiness of commercial *Eucalyptus* species at different elevations. *Can. J. For. Res.* 19: 1235–1239.
- Hill, R.S. and Carpenter, R.J. (1991) Extensive past distributions for major Gondwanic floral elements: macrofossil evidence. *Pap. Proc. R. Soc. Tasm.* (in press)
- Hogg, A. and Kirkpatrick, J.B. (1974) The phytosociology and synecology of some Tasmanian eucalypt forests and woodlands. *J. Biogeogr.* 1: 227–245.
- Hopper, S.D. and Moran, G.F. (1981) Bird pollination and the mating system of *Eucalyptus stoatei*. *Aust. J. Bot.* 29: 625–638.
- Ireland, J.C. and Griffin, A.R. (1984) Observations on the pollination ecology of *Eucalyptus muellerana* Howitt in East Gippsland. *Victorian Naturalist* 101: 207–211.
- Jackson, W.D. (1960) Clinal variation in *Eucalyptus vernicosa*. Part 1. Taxonomic treatment. Ph.D. thesis, University of Tasmania.
- Jackson, W.D. (1965) The Vegetation. In: *Atlas of Tasmania* (ed. J.L. Davies), pp. 30–35. Lands and Surveys Department, Hobart.
- Jackson, W.D. (1973) Vegetation of the Central Plateau. In: *The Lake Country* (ed. M.R. Banks), pp. 61–85. A symposium arranged by the Royal Society of Tasmania, Hobart, November 1972.
- Jacobs, M.R. (1955) *Growth Habits of the Eucalypts*. Government Printer, Canberra.
- Kedharnath, S. and Vakshasya, R.K. (1978) Estimate of components of variance, heritability and correlation among some growth parameters in *Eucalyptus tereticornis*. In: *Proceedings of the Third World Consultation on Forest Tree Breeding*, Canberra, Australia, 21st–26th March 1977, pp. 667–676. CSIRO, Canberra.
- Kirkpatrick, J.B. (1977) Eucalypt invasion in southern California. *Australian Geographer* 13: 387–393.
- Kirkpatrick, J.B. (1981) A transect study of forests and woodlands on dolerite in the Eastern Tiers, Tasmania. *Vegetatio* 44: 155–163.
- Kirkpatrick, J.B. and Brown, M.J. (1984) A numerical analysis of Tasmanian higher plant endemism. *Bot. J. Linn. Soc. Lond.* 88: 165–183.
- Kirkpatrick, J.B. and Marks, F. (1985) Observations on drought damage to some native plant species in eucalypt forests and woodlands near Hobart, Tasmania. *Pap. Proc. R. Soc. Tasm.* 119: 15–21.
- Kirkpatrick, J.B. and Nunez, M. (1980) Vegetation–radiation relationships in mountainous terrain: eucalypt-dominated vegetation in the Risdon Hills, Tasmania. *J. Biogeogr.* 7: 197–208.
- Kirkpatrick, J.B., Simmons, D. and Parsons, R.F. (1973) The relationship of some populations involving *Eucalyptus cypellocarpa* and *E. globulus* to the problem of phantom hybrids. *New Phytologist* 72: 867–876.
- Ladiges, P.Y., Humphries, C.J. and Brooker, M.I.H. (1983) Cladistic relationships and biogeographical patterns in the peppermint group of *Eucalyptus* (Informal Subseries *Amygdalinae*, Subgenus *Monocalyptus*) and the description of a new species, *E. willisii*. *Aust. J. Bot.* 31: 565–584.
- Lande, R. and Barrowclough, G.F. (1987) Effective population size, genetic variation, and their use in population management. In: *Viable Populations for Conservation* (ed. M. E. Soulé), pp. 87–124. Cambridge University Press, Cambridge.
- Lawrence, M.J. (1984) The genetic analysis of ecological traits. In: *Evolutionary Ecology: The 23rd Symposium of the British Ecological Society Leeds 1982* (ed. B. Shorrocks), pp. 27–64. Blackwell Scientific Publications, Oxford.
- Levin, D.A. and Kerster, H.W. (1974) Gene flow in seed plants. *Evol. Biol.* 7: 139–220.
- Long, J.L. (1984) The diets of three species of parrots in the south of Western Australia. *Aust. Wildl. Res.* 11(2): 357–372.
- Macphail, M.K. (1980) Regeneration processes in Tasmanian forests. A long-term perspective based on pollen analysis. *Search* 11(6): 184–190.

- Marginson, J.C. and Ladiges, P.Y. (1982) Morphological and geographical disjunctions in forms of *Eucalyptus nitida* Hook.f. (Myrtaceae): with special reference to the evolutionary significance of Bass Strait, south-eastern Australia. *Proc. R. Soc. Vict.* 94: 155–167.
- Mitchell-Olds, T. and Rutledge, J.J. (1986) Quantitative genetics in natural populations: a review of the theory. *Am. Nat.* 127: 379–402.
- Moran, G.F. and Bell, J.C. (1983) Eucalypts. In: *Isozymes in Plant Genetics and Breeding: Part B* (eds S.D. Tankley and T.J. Orton), pp. 423–441. Elsevier, Amsterdam, Netherlands.
- Moran, G.F. and Hopper, S.D. (1983) Genetic diversity and the insular population structure of the rare granite rock species *Eucalyptus caesia* Benth. *Aust. J. Bot.* 31: 161–172.
- Noble, I.R. (1989) Ecological traits of the *Eucalyptus* L' Hér. subgenera *Monoclyptus* and *Symphyomyrtus*. *Aust. J. Bot.* 37: 207–224.
- Onans, J. and Parsons, R.F. (1980) Regeneration of native plants on abandoned mallee farmlands in south-eastern Australia. *Aust. J. Bot.* 28: 479–493.
- Parsons, R.F. (1969) Distribution and palaeogeography of two mallee species of *Eucalyptus* in southern Australia. *Aust. J. Bot.* 17: 323–330.
- Parsons, R.F. and Kirkpatrick, J.B. (1972) Possible phantom hybrids in *Eucalyptus*. *New Phytologist* 71: 1213–1219.
- Parsons, R.F. and Rowan, J.N. (1968) Edaphic range and cohabitation of some mallee eucalypts in south-eastern Australia. *Aust. J. Bot.* 16: 109–116.
- Phillips, R.L. and Reid, J.B. (1980) Clinal variation between *Eucalyptus viminalis* Labill. and *E. dalrympleana* Maiden. *Aust. J. Bot.* 28: 329–342.
- Potts, B.M. (1986) The population dynamics and regeneration of a hybrid zone between *Eucalyptus risdonii* and *E. amygdalina*. *Aust. J. Bot.* 34: 305–329.
- Potts, B.M. (1989) *Population Variation and Conservation Status of a Rare Tasmanian Endemic, Eucalyptus cordata*. Research Report No. 4. Tasmanian Forest Research Council, Hobart.
- Potts, B.M. and Jackson, W.D. (1986) Evolutionary processes in the Tasmanian high altitude eucalypts. In: *Flora and Fauna of Alpine Australasia* (ed. B. Barlow), pp. 511–527. CSIRO, Melbourne.
- Potts, B.M., Potts, W.C. and Cauvin, B. (1987) Interbreeding and interspecific hybridization in *Eucalyptus gunnii*. *Silvae Genetica* 36: 194–199.
- Potts, B.M. and Reid, J.B. (1983) Hybridization between *Eucalyptus obliqua* L' Hér. and *E. pulchella* Desf. *Aust. J. Bot.* 31: 211–229.
- Potts, B.M. and Reid, J.B. (1985a) Variation in the *Eucalyptus gunnii*-*archeri* complex. I. Variation in the adult phenotype. *Aust. J. Bot.* 33: 337–359.
- Potts, B.M. and Reid, J.B. (1985b) Variation in the *Eucalyptus gunnii*-*archeri* complex. II. The origin of variation. *Aust. J. Bot.* 33: 519–541.
- Potts, B.M. and Reid, J.B. (1985c) Analysis of a hybrid swarm between *Eucalyptus risdonii* Hook.f. and *E. amygdalina* Labill. *Aust. J. Bot.* 33: 543–562.
- Potts, B.M. and Reid, J.B. (1988) Hybridization as a dispersal mechanism. *Evolution* 42: 1245–1255.
- Potts, B.M. and Savva, M. (1989) The crossability of *Eucalyptus globulus*. In: *Proceedings of the IUFRO meeting on Eucalyptus provenances and breeding, Thailand, 1988*. (in press)
- Prober, S.M., Tompkins, C., Moran, G.F. and Bell, J.C. (1990) The conservation genetics of *Eucalyptus paliformis* L. Johnson et Blaxell and *E. parvifolia* Cambage, two rare species from south-eastern Australia. *Aust. J. Bot.* 38: 79–95.
- Provine, W.B. (1989) Founder effects and genetic revolutions in microevolution and speciation: an historical perspective. In: *Genetics, Speciation and the Founder Principle* (eds L.V. Giddings, K.Y. Kaneshiro and W.W. Anderson), pp. 43–76. Oxford University Press, New York.
- Pryor, L.D. (1951) A genetic analysis of some *Eucalyptus* populations. *Proc. Lin. Soc. N.S.W.* 76: 140–148.
- Pryor, L.D. (1976) *The Biology of Eucalypts*. Edward Arnold, London.
- Pryor, L.D. and Johnson, L.A.S. (1971) *A Classification of the Eucalypts*. Australian National University Press, Canberra.
- Pryor, L.D. and Johnson, L.A.S. (1981) *Eucalyptus*, the universal Australian. In: *Ecological Biogeography of Australia* (ed. A. Keast), pp. 499–536. W. Junk, The Hague.
- Reddy, K. and Rockwood, D.L. (1989) Breeding strategies for coppice production in a *Eucalyptus grandis* base population with four generations of selection. *Silvae Genetica* 38: 148–151.
- Rogers, R.W. and Westman, W.E. (1979) Niche differentiation and maintenance of genetic identity in cohabiting *Eucalyptus* species. *Aust. J. Ecol.* 4: 429–439.
- Savva, M., Potts, B.M. and Reid, J.B. (1988) The breeding system and gene flow in *Eucalyptus urnigera*. In: *Pollination '88* (eds R.B. Knox, M.B. Sing and L.F. Troiani), pp. 176–182. Plant Cell Biology Research Centre, University of Melbourne.
- Shaw, M.J., Potts, B.M. and Reid, J.B. (1984) Variation within and between *Eucalyptus nitida* Hook.f. and *Eucalyptus coccifera* Hook.f. *Aust. J. Bot.* 32: 641–654.

- Singh, G., Kershaw, A.P. and Clark, R. (1981) Quaternary vegetation and fire history in Australia. In: *Fire and the Australian Biota* (eds A.M. Gill, R.H. Groves and I.R. Noble), pp. 23–54. Australian Academy of Science, Canberra.
- Tibbits, W.N., Potts, B.M. and Savva, M. (1991) The inheritance of freezing resistance in interspecific F1 hybrids of *Eucalyptus*. *Aust. J. Bot.* (in press)
- Tibbits, W.N. and Reid, J.B. (1987) Frost resistance in *Eucalyptus nitens* (Deane and Maiden) Maiden: genetic and seasonal aspects of variation. *Aust. For. Res.* 17: 29–47.
- Volker, P.W., Dean, C.A., Tibbits, W.N. and Ravenwood, I.C. (1990) Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. *Silvae Genetica* 39: 18–21.
- Wagner, W.H. Jr. (1970) Biosystematics and evolutionary noise. *Taxon* 19: 146–51.
- Watson, R.J., Ladiges, P.Y. and Griffin, A.R. (1987) Variation in *Eucalyptus cypellocarpa* L. Johnson in Victoria, and a new taxon from the Grampian Ranges and Anglesea. *Brunonia* 10: 159–76.
- Wiltshire, R.J.E. and Reid, J.B. (1987) Genetic variation in the spinning gum, *Eucalyptus perriniana* F. Muell. ex Rodway. *Aust. J. Bot.* 35: 33–47.
- van Wyk G. (1976) Early growth results in a diallel progeny test of *Eucalyptus grandis* (Hill) Maiden. I. Field study. *Silvae Genetica* 25: 126–132.