Systematic Affinities, Hybridisation and Clinal Variation within Tasmanian Eucalypts

by Fred Duncan
Forestry Commission, Tasmania

Abstract

Twenty nine species of eucalypts are native to Tasmania, of which seventeen species are considered to be endemic. Affinities of Tasmanian species are indicated, and the factors contributing to the relatively high levels of hybridisation observed within the two Tasmanian subgenera (Monocalyptus and Symphyomyrtus) are discussed. Clinal variation within species, and between related species, is described and correlated with environmental gradients. Maintenance of genetic diversity, primarily by conserving representative areas of native vegetation, has potential economic and scientific benefits.

Introduction

There are currently considered to be 29 species of eucalypts native to Tasmania (Figure 1 and Appendix). This figure comprises 5 per cent of the number of eucalypt species occurring in Australia. However, variation in some morphological (i.e. physical) characteristics of eucalypts is possibly more pronounced in Tasmania than elsewhere. Australia's tallest eucalypts, *Eucalyptus regnans* reaching a height of some 90 metres in the Styx Valley, are located within a few stone throws of stunted *E. vernicosa*, flowering and fruiting at heights of less than 50 cms in the Snowy Range. Variation within an individual species (i.e. variation at the provenance level) can be almost as dramatic. Compare the towering *E. viminalis* at Evercreech Forest Reserve, rivalling in height the Styx Valley giants, with the mallee-form shrubs of the same species, which flower and fruit on the coastal dunes of the north and east.

Trees of some Tasmanian species, such as most of the ashes, can be readily identified in almost all situations. However, difficulty is often experienced in positively identifying trees, particularly in the peppermint and gum groups, because they possess morphological characteristics (e.g. bark type, fruit size, leaf shape, juvenile foliage) which do not completely match with those of species described or illustrated in texts (e.g. Curtis and Morris 1975; Hall *et al.* 1970; Boland *et al.* 1984; Kirkpatrick and Backhouse 1981, 1985; Chippendale 1988).

Major problems with identifying eucalypts arise from the large amount of genetic variability maintained in most eucalypt populations, and the ability of species to perform reproductive manoeuvres of considerable complexity. These mainly comprise hybridisation between species with systematic (i.e. taxonomic) affinities, and the clinal variation that can occur within individual species and between closely related species.

Systematic Affinity

Within the genus *Eucalyptus*, eight subgenera have been recognised (Pryor and Johnson 1971), and some consideration has been given to re-organising the eucalypts into eight genera, by raising the subgeneric groups to generic level (Johnson and Briggs 1983). However, a detailed revision along these lines awaits publication, and there may be resistance, for morphological or practical reasons, to its widespread acceptance (McAlpine 1986). The treatment of eucalypts

and angophoras in the 'Flora of Australia' series (Chippendale 1988) maintains the status quo, and *Eucalyptus* remains the genus which dominates forests and woodlands over most of Australia.

Two of the eucalypt subgenera occur in Tasmania: *Monocalyptus* comprising the ashes and peppermints, and *Symphyomyrtus* comprising the gums (Figure 1). The subgenera differ in numerous respects - reproductive, physiological, morphological and in their response to environmental stress. Interspecific hybrids between the subgenera have not been found, nor have they been artificially induced. Each of the subgenera can be further subdivided into series to indicate affinities between species. However, hybridisation can occur between species of Series *Obliquae* (ashes) and Series *Piperitae* (peppermints), and between species of Series *Ovatae* and Series *Viminales* (gums). Ashes tend to dominate wet sclerophyll forests and mixed forests, peppermints tend to dominate dry sclerophyll forests and woodlands, and gums tend to occur as subdominant or minor species, though they may dominate in specific environments (e.g. poorly drained sites).

Seventeen of Tasmania's eucalypts are endemic to the State. All seven peppermints are considered to be endemic, with the acceptance that the Forth Valley species currently known as *E. radiata* ssp. *robertsonii* differs sufficiently from the mainland species of that name, to warrant recognition as a distinct species. None of the five ash species is endemic at the species level, though the Tasmanian form of *E. delegatensis* is recognised as being sufficiently distinct from its mainland counterpart to be designated as *E. delegatensis* var. *tasmaniensis* (Boland 1985). Ten of the seventeen gum species are endemic.

Hybridisation

Although hybrids are few and relatively scattered compared to the total population of a species (Brett 1938), hybridisation between species of the same subgenera is not uncommon in Tasmania, or other areas of southern Australia. Hybridisation can occur naturally when pollen transfer, fertilisation and subsequent seed set takes place between related species. Hybridisation can also be induced artificially, for example in eucalypt breeding programmes, when barriers to natural hybridisation between species are circumvented.

Most morphological features are subject to polygenic control, so hybrids tend to be intermediate in character between the two parents. For example, capsules of *E. ovata* x *E. globulus* hybrids are intermediate in shape and size between the capsules of the two parents, and juvenile leaves of hybrid seedlings of the same parents are intermediate in shape and glaucousness (McAulay 1938). Such hybrids are relatively easy to recognise, particularly if the putative parents are observed or known to occur in the general vicinity. Hybrids are more difficult to recognise when parents are morphologically similar (e.g. *E. viminalis* and *E. dalrympleana*) and in such situations clinal variation may also confuse the issue. Progeny testing of seed from the suspected hybrids can indicate or confirm the parent species. Seedlings of the hybrid may show a range in characteristics from one parent type to another as a result of multiple gene inheritance. In the case of seedlings of the *E. globulus* x *E. ovata* hybrid, some seedlings closely resembled those of *E. globulus*, while others closely resembled those of *E. ovata* (McAulay 1938). More time consuming experiments, involving controlled pollination, can also indicate species which have the potential to hybridise.

Figure 1 indicates the extent of natural hybridisation that has been verified (closed triangles) or reliably observed (open triangles) amongst Tasmanian species of eucalypts. It is likely that several of the 'observed hybrids' will be verified in the future, and that new hybrid combinations will be discovered in the course of surveys. Reference to the figure will in many cases suggest a reason for problems being

experienced in identification of eucalypt specimens.

Griffin *et al.* (1988) have examined patterns of natural and manipulated hybridisation within the genus *Eucalyptus*. In subgenus *Monocalyptus* they found that about 11 per cent of potential hybrid combinations (on the basis of geographical proximity of different species) had been recorded. In subgenus *Symphyomyrtus* the figure was about 6 per cent. The ratio of observed to potential hybrid combinations is much higher amongst the Tasmanian members of the subgenera (Figure 1). For Tasmanian species in subgenus *Monocalyptus* the figures range from 34 per cent (using verified hybrids only) to 51 per cent (if reliably observed hybrids are also included). The comparable figures for Tasmanian species in subgenus *Symphyomyrtus* are almost identical. The

disparity between the proportions recorded for Tasmania and Australia as a whole probably reflects the extent of botanical survey and collection in the State, and the environmental heterogeneity that occurs over relatively short distances in Tasmania. Species with substantially different environmental requirements are thereby often located close to each other.

The absence of hybridisation between *Symphyomyrtus* and *Monocalyptus* species is obvious on perusal of Figure 1. However, there are mistaken reports in some older literature of hybridisation between members of these groups, such as descriptions of *E. risdonii* x *E. viminalis* hybrids by Brett (1938). Also apparent in Figure 1 is the existence of hybrids between species such as *E. obliqua* and *E. pulchella* (Potts and Reid 1983) which do not have particularly strong taxonomic
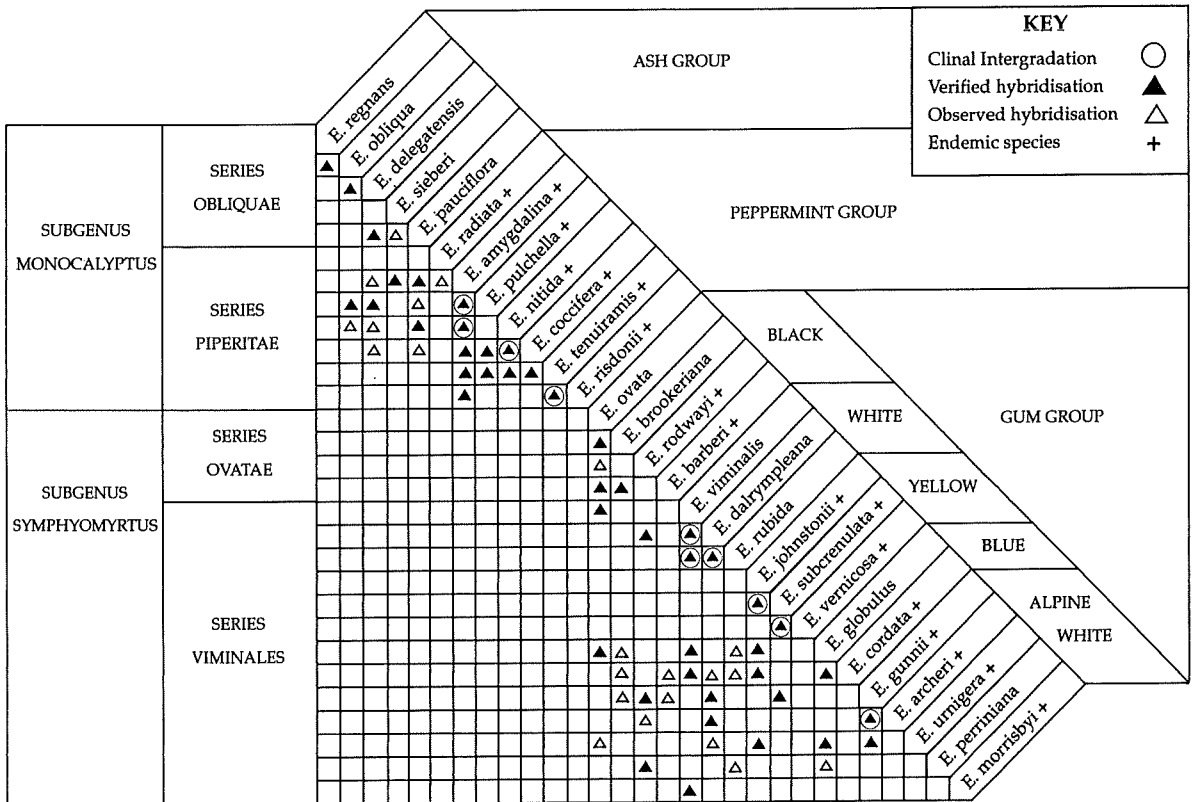

Figure 1
Species of eucalyptus native to Tasmania, showing those species forming clines and natural hybrids. For each species, follow horizontal and vertical axis. For example, *Eucalyptus barberi* is known to hybridise with *E.ovata* and *E.brookeriana* (horizontal axis) and possibly hybridises with *E.gunnii* and *E.cordata* (vertical axis).

affinities, and the absence of records of natural hybrids between species which appear to be closely related (e.g. *E. perriniana* and *E. morrisbyi*). In such cases barriers exist which inhibit hybridisation, or limit its extent, between species which have close taxonomic affinities.

The most obvious barrier to hybridisation is that imposed by geography. Pollen transfer between eucalypts is primarily by insects and birds, and species which are located, by distance or other physical features, beyond the normal range of pollen transfer are unlikely to hybridise. A good example is the absence of hybrids between *E. radiata* ssp. *robertsonii*, which is restricted in distribution to the Forth Valley, and species of peppermints which are largely confined to south eastern Tasmania (*E. pulchella*, *E. tenuiramis*, *E. risdonii*). Hybridisation between *E. radiata* ssp. *robertsonii* and the co-occurring *E. amygdalina* has been observed by Davies (1988). Within the gum group it is useful to look at the closely related species, *E. perriniana* and *E. morrisbyi*, both of which are rare in Tasmania (but are often horticulturally planted). The absence of natural hybridisation between the species is a function of their populations being small and geographically isolated from each other. At the same time, hybridisation is occurring between *E. perriniana* and adjacent *E. rodwayi*, and *E. morrisbyi* and adjacent *E. viminalis*. In the former case the *E. perriniana* genotype appears relatively stable, with little morphological difference existing between the two populations at Tunnack and Strickland, and *E. rodwayi* genes not being incorporated into either gene pool, possibly because of reduced viability of second generation hybrids (Wiltshire and Reid 1987). On the other hand, pollen migration from *E. viminalis* is in danger of swamping the only reserved population of *E. morrisbyi*, comprising about twelve adults and numerous saplings in the East Risdon Nature Reserve (Brown and Bayly-Stark 1979).

Other barriers to hybridisation involve season of flowering (phenology) and lack of reproductive compatibility. Some species exhibit strong seasonality of flowering, while considerable variation exists amongst other species. For example, *E. pauciflora* mainly flowers in spring to early summer, whereas *E. delegatensis*, with which it rarely appears to hybridise despite considerable overlap in range, flowers in late summer to autumn (Willis 1980). A seasonal barrier to hybridisation also exists between the winter flowering *E. urnigera* and the spring-summer flowering *E. gunnii* (Davidson *et al.* 1981). At Snug Plains (600m a.s.l.) gene flow between *E. pulchella*, *E. coccifera* and *E. delegatensis* was facilitated by atypical late flowering of *E. pulchella*, resulting in overlap of flowering periods of the three species (Davidson *et al.* 1987). Physiological barriers may prevent successful interspecific fertilisation and development of viable seed. Obviously, reproductive barriers exist between members of the different subgenera, but complete or partial incompatibility can also occur between closely related species. An example of the latter is provided by *E. globulus* and the non-indigenous but increasingly planted *E. nitens* (Tibbits 1986, Potts and Savva 1988). The stigma in *E. globulus* is too long to allow its ovule to be reached by the pollen tube of *E. nitens*, thus fertilisation does not take place. However, fertilisation can occur in the other direction, i.e. *E. globulus* pollen can fertilise an ovule of *E. nitens*.

The presence of hybrid individuals is generally associated with ecological boundaries or change. Pryor (1976) considers that increases in the number of hybrid individuals are largely due to ecological disturbance of natural plant communities, mainly as a result of European settlement, either by partial clearing or the use of fire. However, similar increases in hybrid densities may be caused by natural phenomena, such as prolonged drought. Hybrids may appear vegetatively vigorous when selection pressures have been reduced by disturbance, but in natural forests hybrids often exhibit reduced vegetative and reproductive vigour when competing with parental forms (Davidson *et al.* 1981).

Natural hybrids are often associated with sharp changes in ecological boundaries. In the Hobart area *E. pulchella* x *E. tenuiramis* hybrids are largely confined to the contact between mudstone sediments (supporting *E. tenuiramis*) and dolerite (supporting *E. pulchella*). Interestingly, the strong substrate fidelity shown by peppermints in the vicinity of Hobart (*E. amygdalina* is strongly associated with siliceous sites) breaks down over a relatively short distance. For example, *E. tenuiramis* is common on sandstone in the New Norfolk area, and is found on dolerite on Tasman Peninsula and the Eastern Tiers.

Hybrid swarms may develop where extensive back crossing between parents, hybrids and their progeny results in the survival of whole populations of hybrid individuals. An example is the hybrid complex involving *E. risdonii*, *E. tenuiramis* and *E. amygdalina* in the Risdon Hills (Potts and Reid 1985a). Although a change in fire frequency resulting from European settlement may have played a part in the extent of hybridisation in this area, the severe climate of the dry, insolated Risdon Hills may also be a major contributor (Hogg and Kirkpatrick 1974, Kirkpatrick and Nunez 1980). In the Falmouth area, disturbance was associated with the development of hybrid swarms involving *E. sieberi* and *E. amygdalina* (Jackson 1958).

Hybridisation between eucalypts in Tasmania is likely to become more common and more complex. The genus *Eucalyptus* is still actively speciating, in a relatively unstable natural environment, limiting the development of reproductive isolating mechanisms. Evolutionary processes within the genus are described by Johnson (1972), and for Tasmanian highland eucalypts by Potts and Jackson (1986). The continuing process of environmental disturbance will further favour the establishment of hybrid individuals or swarms. The sowing or planting of species not indigenous to an area increases the possibility of hybrid combinations with compatible on-site species. For example, hybridisation between *E. nitens* and native gums is made more likely by

disturbance associated with forestry operations. Hybridisation is also possible between widely planted exotics (e.g. *E. camaldulensis*, *E. leucoxylon*) and Tasmanian species with which they are known to form hybrids (e.g. *E. viminalis*, *E. ovata*), particularly in disturbed agricultural or urban areas. Further confusion to eucalypt identification in Tasmania may result from the development of three-way crosses. Such a scenario is possible where gene flow occurs between local species and hybrids planted for production purposes. Three-way hybrids (e.g. *E. gunnii* x *E. ovata* x *E. macarthurii*) are being currently trialled in France (Potts and Potts 1986, Potts *et al.* 1987). Elsewhere, spontaneous hybrids have developed, which in some cases are being used for production purposes, following hybridisation between species which have non-overlapping natural distributions (Pryor 1976, Griffin *et al.* 1988).

Clinal Variation

The physical environment of a species which has a wide distribution will vary throughout that species' range. It is likely that the provenance (or population form) occupying a particular site is best adapted to the conditions operating at that site. Thus, in the example of *E. viminalis* given previously, progeny of the Evercreech giants are unlikely to thrive, or even survive, in the harsh coastal environment occupied by mallee-form *E. viminalis*, while progeny of the coastal form may be competitively disadvantaged in the moist and fertile streamside environment of Evercreech Creek.

Clinal variation occurs when morphological and physiological differences within a species are correlated with particular changes in the physical environment (Pryor 1976). Usually clines involve gradients in altitude (as a surrogate of temperature or rainfall), latitude (as a surrogate of temperature or day length) or environmental stress (such as moisture availability or frost susceptibility). Clinal variation within Tasmanian species has been demonstrated along altitudinal gradients for *E. urnigera* (Barber and Jackson 1957, Thomas

and Barber 1974 a,b) and *E. gunnii* (Potts 1985, Potts and Reid 1985 b,c), with juvenile leaf glaucousness being positively correlated with frost susceptibility of sites. Clinal variation along a moisture gradient has been inferred for *E. cordata* in south eastern Tasmania, with forms of the species having angular stems and more rapid growth rates being found in the western (wetter) part of the species' range (Potts 1988, 1989).

Clinal variation can also involve closely related species. Gradation in morphological characteristics along a cline can contribute to difficulty in identifying eucalypts, or at least assigning individuals to a particular species. Clinal variation involving several species of Tasmanian eucalypts has been demonstrated. Considerable variation in height and form, or other morphological characteristics, can be observed in the altitudinal clines involving *E. johnstonii - E. subcrenulata - E. vernicosa* (Jackson 1960) and *E. viminalis - E. dalrympleana* (Phillips and Reid 1980). In eastern Tasmania, clinal variation involving *E. amygdalina* and *E. pulchella* is related to site dryness (Kirkpatrick and Potts 1987). A similar situation exists in the Meehan Range area, with *E. tenuiramis* and *E. risdonii* (Davidson *et al.* 1981). The frequently broad transition zones which separate populations of *E. amygdalina* and *E. nitida* also tend to be clinal in the gradual change in seedling and adult morphology which occurs from relatively fertile substrate in the east (where *E. amygdalina* is found) to relatively infertile substrate in the west (where *E. nitida* is found). Another cline, from lowland to subalpine environments, also exists between *E. nitida* and *E. coccifera* (Shaw *et al.* 1984).

Identification of eucalypts along a cline is relatively easy at geographic or environmental extremes, but can become difficult in intermediate locations or environments. The white gum group provides a good example. *Eucalyptus viminalis*, characterised by lanceolate juvenile leaves, invariably represents the group in coastal areas. *Eucalyptus dalrympleana*, with ovate juvenile leaves, can be readily identified

in highlands such as the Central Plateau. However, in many upland areas (e.g. 400 to 700m a.s.l.), the presence of ambiguous characteristics makes it difficult to assign white gums to either species, and they are frequently referred to as '*E. vim-dal*'. Identity crises can also occur over much shorter distances. For example, in the Eastern Tiers *E. amygdalina* (with rough bark and relatively broad and somewhat glaucous leaves) grades into *E. pulchella* (with smooth bark and fine, non-glaucous leaves) in the course of a transect from a valley to a ridgeline, with trees and seedlings having ambiguous characteristics typically being present on sites (e.g. mid-slopes) intermediate in stress between the valley and ridgeline environments (Kirkpatrick and Potts 1987).

The ash species (*E. regnans, E. obliqua, E. delegatensis*) occupying moist environments over an extensive geographic range in Tasmania exhibit less pronounced within-species variation and less intergradation between species than is the case with the peppermints and gums. Natural selection in such habitats tends to be density dependent following wildfire, resulting in severe competition for dominance amongst even-aged regeneration. In more severe environments, occupied by uneven-aged stands dominated by peppermints or gums, selection tends to be density independent, with selection amongst the pool of seedlings and saplings in the understorey being a response to stresses, such as drought or frost, imposed by the physical environment (Davidson *et al.* 1981). Such selection is more likely to favour the development of clines.

Conclusion: The Importance of Conserving Genetic Resources

In recent years, the variation in production and environmental tolerances of different species and provenances has received a great deal of attention, both within Australia and overseas. Selection of eucalypts with desirable characteristics of growth, wood quality, site adaptation etc. is important in production forestry, and is certain to assume

greater importance in the future, as pressure increases to maximise returns (whether they be for timber, reforestation, horticulture or other reasons).

Genetic manipulation, with the aim of maximising wood production, has been successfully undertaken in many overseas countries, both temperate and tropical (see for example Potts and Potts 1986, Brandao *et al.* 1984, Davidson 1988). In Australia, variation in morphology, environmental tolerance, growth and wood quality have been examined for several species. Apart from those mentioned previously, they include *E. nitens* (Pederick 1976, 1979; Tibbits and Reid 1987; McKimm and Ilic 1987), *E. regnans* (Eldridge 1972, Rook *et al.* 1980, Griffith *et al.* 1982, Harris *et al.* 1985), *E. viminalis* (Paton 1972, Ladiges 1974, Ladiges and Ashton 1974), *E. globulus* (Kirkpatrick 1974, Turner *et al.* 1983, Volker and Orme 1989), *E. camaldulensis* (Rudman 1970, Grunwald and Karschon 1982), *E. obliqua* (Green 1971, Matheson *et al.* 1986), *E. pauciflora* (Pryor 1957, Green 1969) and *E. delegatensis* (Ohmart *et al.* 1984).

Some hybrid populations display superior form and vigour. The Otway messmate, now regarded as a natural *E. obliqua* x *E. regnans* hybrid, occurs throughout the Otway Ranges near the junction of stands of the two parents. A relatively uniform stand in the Wye River catchment appears to be a stable intermediate form, which has the potential to improve productivity on high quality sites (Pederick 1976).

In Tasmania isolated or remnant *E. globulus* populations on the West Coast and on King Island have good growth and pulping characteristics (Turner *et al.* 1983, Volker and Orme 1989) but populations in both areas are vulnerable because of their small sizes. The endemic *E. gunnii* is being extensively used in plantations in frost susceptible areas of France (Potts *et al.* 1987), but some of the most frost resistant individuals known to occur in Tasmania have been recently cleared (B. Potts, pers. comm.).

The above examples are far from isolated, and illustrate the need to maintain genetic diversity across the range of a species. Conservation of representative areas of native vegetation is the most realistic way of achieving this aim and is being addressed by research programmes and government and industry initiatives in many areas of Australia, including Tasmania. Conserved areas of forest and woodland, if sufficiently large and heterogeneous, can be considered as natural laboratories, which will permit gene flow to occur within and between species, and will allow the forces of natural selection to take place. The potential benefits are scientific and economic. Ideally, conservation of natural areas should be coupled with establishment of genetic storehouses, comprising seed banks and orchards. These would enable a range of genotypes to be stored and maintained, including local genotypes which might be eliminated by habitat modification or natural selection in the wild.

Acknowledgements

References

Barber, H.N. and Jackson, W.D. (1957). Natural selection in action in *Eucalyptus. Nature* 179 : 1267-1269.

Boland, D.J. (1985). Taxonomic revision of *Eucalyptus delegatensis* R.T. Baker (Myrtaceae). *Aust. For. Res.* 15 : 173-181.

Boland, D.J., Brooker, M.I.H., Chippendale, G.M., Hall, N., Hyland, B.P.M., Johnston, R.D., Kleinig, D.A., Turner, J.D. (1984). *Forest Trees of Australia.* Thomas Nelson and CSIRO, Melbourne.

Brandao, L.G., Campinhos, E. and Ikemori, Y.K. (1984) Brazil's new forest soars to success. *Pulp and Paper International* 26 : 38-40.

Brett, R.G. (1938). A Survey of *Eucalyptus* species in Tasmania. *Pap. Proc. Roy. Soc. Tasm.* 1937 : 75-109.

Brown, M.J. and Bayly-Stark, H.J. (1979). The plant communities of the East Risdon Nature Reserve. *Tasm. Nat.* 58 : 1-11

Chippendale, G.M. (1988). *Eucalyptus, Angophora* (Myrtaceae). *Flora of Australia, Vol. 19.* A.G.P.S., Canberra.

Curtis, W.M. and Morris, D.I. (1975) *The Student's Flora of Tasmania, Part 1* (Second edition). Govt. Printer, Hobart.

Davidson, J. (1988). Breeding eucalypts in tropical countries. Proceedings of the International Forestry Conference for the Australian Bicentenary. A.F.D.I., Albury-Wodonga.

Davidson, N.J., Potts, B.M. and Reid, J.B. (1981). Eucalypts. In: (Editor: W.D. Jackson). *The Vegetation of Tasmania.* Aust. Acad. Sci., Canberra.

Davidson, N.J., Reid, J.B. and Potts, B.M. (1987). Gene flow between three eucalypt species at Snug Plains. *Pap. Proc. Roy. Soc. Tasm.* 121 : 101-108.

Davies, J.B. (1988). Pre-logging Survey Report No. 26 : Moina 9A and Moina 10A. Unpublished report to the Tasmanian Forestry Commission.

Eldridge, K.G. (1972). Genetic variation in growth of *Eucalyptus regnans. Aust. For. Timb. Bur. Bull.* No. 46.

Green, J.W. (1969). Temperature responses in altitudinal populations of *Eucalyptus pauciflora. New Phytol.* 68 : 399-410.

Green, J.W. (1971). Variation in *Eucalyptus obliqua* L'Herit. New Phytol. 70 : 897-910.

Griffin, A.R., Williams, E.R. and Johnson, K.W. (1982). Early height growth and frost hardiness of *Eucalyptus regnans* provenances in twelve field trials in south-east Australia. *Aust. For. Res.* 12 : 263-80.

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.

Grunwald, Clara and Karschon, R. (1982). Leaf xylem water potentials and water saturation deficits as related to seed origin of *Eucalyptus camaldulensis* Dehn. *Aust. For. Res.* 12 : 175-81.

Hall, N., Johnston, R.D. and Chippendale, G.M. (1970). *Forest Trees of Australia*. A.G.P.S., Canberra.

Harris, J.A., Kassaby, F.Y., and Smith, I.W., (1985). Variations in mortality in families of *Eucalyptus regnans* caused by *Phytophthora cinnamomi*, up to 5 years after planting. *Aust. For. Res.* 15 : 57-65.

Hogg, A. and Kirkpatrick, J.B. (1974). The phytosociology and synecology of some southern Tasmanian eucalypt forests and woodlands. *J. Biogeog.* 1 : 227-245.

Jackson, W.D. (1960). Clinal variation in *Eucalyptus vernicosa*. Part 1. Taxonomic treatment. Ph.D. Thesis, Univ. of Tasmania.

Johnson, L.A.S. (1972). Evolution and classification in *Eucalyptus*. *Proc. Linn. Soc. N.S.W.* 97 : 11-29.

Johnson, L.A.S. and Briggs, B.G. (1983). Myrtaceae. In : (Editors: B.D. Morley and H.R. Toelken). *Flowering Plants in Australia*. Rigby.

Kirkpatrick, J.B. (1974). Geographical variation in *Eucalyptus globulus*. *Aust. For. Timb. Bur. Bull.* No. 47.

Kirkpatrick, J.B. and Backhouse, S. (1981). *An Illustrated Guide to Tasmanian Native Trees*. Mercury Walch, Hobart.

Kirkpatrick, J.B. and Backhouse, S. (1985). *Native Trees of Tasmania*. Sue Backhouse, Hobart.

Kirkpatrick, J.B. and Nunez, M. (1980). Vegetation - radiation relationships in mountainous terrain : Eucalypt dominated vegetation in the Risdon Hills, Tasmania. *Pap. Proc. Roy. Soc. Tasm.* 107 : 197-208.

Kirkpatrick, J.B. and Potts, B.M. (1987). Isolated intermediates - products of long distance gene dispersal; phantom hybrids or convergent evolution? The case of the half-barked *Eucalyptus amygdalina*. *Pap. Proc. Roy. Soc. Tasm.* 121 : 15-22.

Ladiges, P.Y. (1974). Differentiation in some populations of *Eucalyptus viminalis* Labill. in relation to factors affecting seedling establishment. *Aust. J. Bot.* 21 : 81-102.

Ladiges, P.Y. and Ashton, D.H. (1974). Variation in some central Victorian populations of *Eucalyptus viminalis* Labill. *Aust. J. Bot.* 22 : 81-102.

McAlpine, D.K. (1986). Up a gum-tree or taxonomic changes in the eucalypt alliance. *Search* 17 : 170-171.

McAulay, A.L. (1938). Evidence for the existence of a natural hybrid between *Eucalyptus globulus* and *Eucalyptus ovata*. *Pap. Proc. Roy. Soc. Tasm.* 1937 : 45-46.

McKimm, R.J. and Ilic, Y. (1987). Characteristics of the wood of young fast-grown trees of *Eucalyptus nitens* Maiden with special reference to provenance variation. III. Anatomical and physical characteristics. *Aust. For. Res.* 17(1) : 19-28.

Matheson, C.A., Turner, C.H. and Dean, G.H. (1986). Genetic variation in the pulp qualities of *Eucalyptus obliqua* L'Herit. *Appita* 39 : 205-212.

Ohmart, C.P., Thomas, J.R. and Stewart, L.G. (1984). Differential defoliation by insects among provenances of *Eucalyptus delegatensis*. *J. Aust. Ent. Soc.* 23 : 105-111.

Paton, D.M. (1972). Frost resistance in *Eucalyptus*: A new method for assessment of frost injury in altitudinal provenances of *E. viminalis*. *Aust. J. Bot.* 20 : 127-139.

Pederick, L.A. (1976). The genetic resources of the Victorian eucalypts. *For. Comm. Vict. Bull. No.* 22.

Pederick, L.A. (1979). Natural variation in Shining Gum (*Eucalyptus nitens*). *Aust. For. Res.* 9 : 41-63.

Phillips, R.L. and Reid, J.B. (1980). Clinal variation between *Eucalyptus viminalis* Labill. and *E. dalrympleana* Maiden. *Aust. J. Bot.* 28 : 329-42.

Potts, B.M. (1985). Variation in the *Eucalyptus gunnii - archeri* complex. III. Reciprocal transplant trials. *Aust. J. Bot.* 33 : 687-704.

Potts, B.M. (1986). Population dynamics and regeneration of a hybrid zone between *Eucalyptus risdonii* Hook.f. and *E. amygdalina* Labill. *Aust. J. Bot.* 34 : 305-329.

Potts, B.M. (1988). The distribution and type locality of *Eucalyptus cordata* Labill. - an historical account. *Pap. Proc. Roy. Soc. Tasm.* 122 : 31-38.

Potts, B. M. (1989). Population variation and conservation status of a rare Tasmanian endemic, *Eucalyptus cordata. Res. Rep. No. 4.* Tas. For. Res. Council, Hobart.

Potts, B.M. and Jackson, W.D. (1986). Evolutionary processes in the Tasmanian high altitude eucalypts. In: (Editor : B. Barlow). *Flora and Fauna of Alpine Australasia : Ages and Origins.* CSIRO, Melbourne.

Potts, B.M. and Potts, W.C. (1986). Eucalypt breeding in France. *Aust. For.* 49 : 210-218.

Potts, B.M., Potts, W.C. and Cauvin, B. (1987). Inbreeding and interspecific hybridisation in *Eucalyptus gunnii. Silvae Genetica* 36 : 194-199.

Potts, B.M. and Reid, J.B. (1985a). 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. (1985b). 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. (1985c). 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. (1986). Hybridisation between *Eucalyptus obliqua* L'Herit. and *E. pulchella* Desf. *Aust. J. Bot.* 31 : 211-229.

Potts, B.M. and Reid, J. (1988). Hybridisation as a dispersal mechanism. *Evolution* 42 : 1245-1255.

Potts, B.M. and Savva, M. (1988). The crossability of *Eucalyptus globulus*. Proc. of the IUFRO Meeting on *Eucalyptus* Provenances and Breeding, Thailand, 1988.

Pryor, L.D. (1957). Variation in snow gum (*Eucalyptus pauciflora* Sieb.). *Proc. Linn. Soc. N.S.W.* 81 : 299-305.

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*. A.N.U., Canberra.

Rook, D.A., Wilcox, M.D., Holden, D.G. and Warrington, I.J. (1980). Provenance variation in frost tolerance of *Eucalyptus regnans* F.Muell. *Aust. For. Res.* 10 : 213-238.

Rudman, P. (1970). The influence of genotype and environment on wood properties of juvenile *Eucalyptus camaldulensis* Dehn. *Silvae Genetica* 12 : 49-54.

Thomas, D.A. and Barber, H.N. (1974a). Studies on leaf characteristics of a cline of *Eucalyptus urnigera* from Mount Wellington, Tasmania. I. Water repellancy and the freezing of leaves. *Aust. J. Bot.* 22 : 501-512.

Thomas, D.A. and Barber, H.N. (1974b). Studies on leaf characteristics of a cline of *Eucalyptus urnigera* from Mount Wellington, Tasmania. II. Reflection, transmission and absorption of radiation. *Aust. J. Bot.* 22 : 701-707.

Tibbits, W. (1986). Frost resistance of *Eucalyptus nitens* (Deane & Maiden) Maiden. Ph.D. Thesis, Univ. of Tasmania.

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.

Turner, C.H., Balodis, V. and Dean, G.H. (1983). Variability in pulping quality of *E. globulus* from Tasmanian provenances. *Appita* 36 : 371-376.

Volker, P.W. and Orme, R.K. (1989). Provenance trials of *Eucalyptus globulus* and related species in Tasmania. *Aust. For.* 51 : 257-265.

Willis, J.H. (1972). *A Handbook to Plants in Victoria. Volume 2. Dicotyledons.* Melbourne University Press, Melbourne.

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.

Appendix: List of Species of *Eucalyptus* Mentioned in Text

Currently valid scientific names and authorities are given, following Chippendale (1988). Common names for many species vary throughout the State, and it is possible that local names for some species have not been included. Synonyms sometimes used in Tasmania are also given; these mainly comprise names which have been superseded.

Species Native to Tasmania

E. amygdalina Labill.	Black peppermint
E. archeri Maiden & Blakely	Archer's gum, Alpine cider gum
E. barberi L.Johnson & Blaxell	Barber's gum
E. brookeriana A.M.Gray	Brooker's gum, Marrawah gum
E. coccifera J.D.Hook.	Snow gum
E. cordata Labill.	Heart-leaved silver gum
E. dalrympleana Maiden	Mountain white gum
E. delegatensis ssp. *tasmaniensis* Boland	Gum-topped stringybark, White-top
E. globulus Labill. ssp. *globulus*	Blue gum
E. globulus ssp. *bicostata* (Maiden, Blakely & J.Simm.) Kirkpatr.	
E. gunnii J.D.Hook	Cider gum
E. johnstonii Maiden	Yellow gum
E. morrisbyi Brett	Morrisby's gum
E. nitida J.D.Hook.	Smithton peppermint
E. obliqua L'Herit.	Stringybark, Brown-top
E. ovata Labill.	Black gum, Swamp gum
E. pauciflora Sieber ex Sprengel	Cabbage gum, Weeping gum
E. perriniana F.Muell. ex Rodway	Spinning Gum
E. pulchella Desf.	White peppermint
E. radiata ssp. *robertsonii* (Blakely) L.Johnson & Blaxell	
E. regnans F. Muell.	Swamp gum, Stringy gum

E. risdonii J.D.Hook.	Risdon peppermint
E. rodwayi R.Baker & H.G.Smith	Swamp peppermint
E. rubida Deane & Maiden	Candlebark, Ribbon gum
E. sieberi L.Johnson	Ironbark
E. subcrenulata Maiden & Blakely	Alpine yellow gum
E. tenuiramis Miq.	Silver peppermint
E. urnigera J.D.Hook.	Urn gum
E. vernicosa J.D.Hook.	Varnished gum
E. viminalis Labill.	White gum, Manna gum

Species Not Native to Tasmania

E. camaldulensis Dehnh.	River red gum
E. leucoxylon F.Muell.	Yellow gum
E. macarthurii Deane & Maiden	Paddys River box
E. nitens (Deane & Maiden) Maiden	Shining gum

Synonyms for Tasmanian Species

E. amygdalina	[syn. *E. salicifolia*]
E. brookeriana	[syn. *E. brookerana*]
E. delegatensis ssp. *tasmaniensis*	[syn. *E. gigantea*]
E. globulus spp. *bicostata*	[syn. *E. bicostata*]
E. nitida [syn. *E. simmondsii*]	
E. pulchella	[syn. *E. linearis*]
E. radiata spp. *robertsonii*	[syn. *E. robertsonii*]
E. sieberi	[syn. *E. sieberana*]
E. tenuiramis	[syn. *E. tasmanica*]

Tasforests