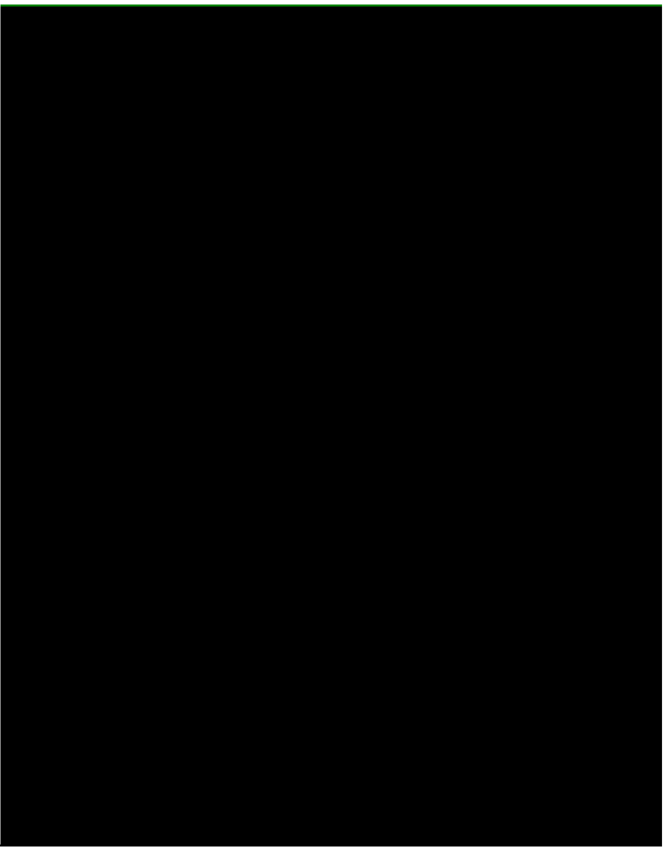
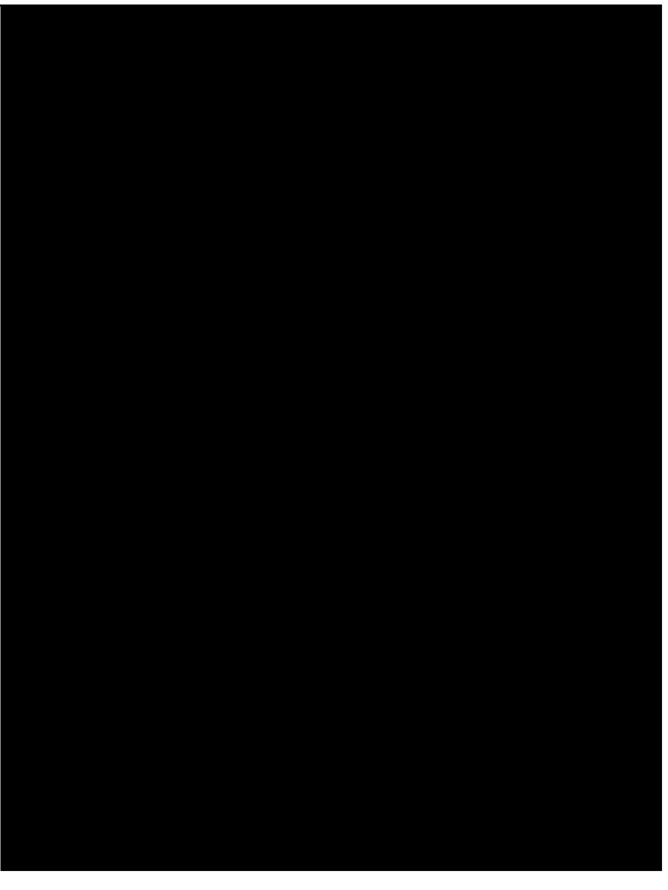


Comprehensive Regional Assessment

World Heritage Sub-theme: Eucalypt-dominated vegetation.

Report of the Expert Workshop, Canberra, 8 & 9 March,1999



The views expressed in this publication are those of the authors and not necessarily those of the Commonwealth of Australia. The Commonwealth does not accept responsibility for any advice or information in relation to this material.

Comprehensive Regional Assessment
World Heritage Sub-theme: Eucalypt-dominated vegetation

Report of the Expert Workshop, Canberra, 8 & 9 March 1999.

Table of Contents

Introduction

Comprehensive Regional Assessment

The Comprehensive Regional Assessment (CRA) process, implemented by Commonwealth and State Governments, requires an assessment of all forest values for designated forested regions. These assessments are used in the development of a Regional Forest Agreement (RFA) for each region. The Regional Forest Agreements are to ensure that the full range of obligations and interests of governments are met in relation to the protection of Australia's forest values and the sustainable use and development of its forest resources.

Australia is a State Party to the *World Heritage Convention 1972*, which means that it has an obligation to ensure that its natural and cultural heritage of outstanding universal value is identified, protected and maintained for the benefit of future generations. Identification of World Heritage values in forested areas and their protection and maintenance is an important obligation being met as part of the CRA process.

A thematic approach to identification of World Heritage values

Governments have adopted a thematic approach for the identification of World Heritage values in Australia's forested areas as part of the CRA process. The thematic approach is regarded as complementary to other approaches for the identification of World Heritage; its use should not be interpreted as replacing these other approaches or influencing the ways in which they are used.

The thematic approach is based on a methodology developed by Domicelj, Halliday and James (1992) for identification of World Heritage cultural values. The approach provides a systematic, comparative and efficient means of identifying places that meet the Criteria and Operational Guidelines of the World Heritage Convention (see Attachment 1). The use of a thematic approach is consistent with an international trend towards systematic assessment of World Heritage value.

Implementation of the thematic approach involves developing themes of outstanding universal value and then identifying potential places to represent them. Each potential place is tested by working through a series of elimination steps, which include tests drawn from the Criteria and Operational Guidelines of the World Heritage Convention. This sieving process discards any places that do not meet particular tests of significance, integrity and authenticity. Places that meet all tests are suitable for a formal assessment of potential World Heritage value. Places that meet all tests and also meet the requirements of a separate, formal assessment against the Criteria and Operational Guidelines of the World Heritage Convention are likely to have World Heritage value. A summary of the thematic approach is provided in Attachment 2.

Application of the thematic approach

Implementation of the first steps of the thematic approach has been carried out with the assistance of a World Heritage Expert Panel. The Expert Panel was convened by governments in 1996 and asked to provide advice on significant themes relating to World Heritage natural and cultural values for all terrestrial areas of Australia. It was also asked to identify the subset of the themes relevant to forested areas of Australia and, further, to advise governments of forested places that may require assessment as possible best global expressions of these forest themes.

Australian themes of outstanding universal value were identified by the Expert Panel within the broad context of the history and evolution of the continent and the development of its unique landscapes, biota and human cultures. In some cases, particular aspects of the themes were regarded by the Panel as exceptional in their own right in a global context. These aspects were described as "sub-themes" of outstanding universal value.

The Expert Panel provided its advice on themes of outstanding universal value and places that require further assessment as possible best global expressions of the themes at meetings in Melbourne on 13 and 14 June 1996 (World Heritage Report 1996), and in Canberra on 13 March 1997 (World Heritage Report 1997a) and 14, 15 and 21 October 1997 (World Heritage Report 1997b). A summary of the Australian themes and sub-themes of outstanding universal value identified by the World Heritage Expert Panel is available in the record of the Panel's meetings (for example, see World Heritage Report 1997b, Attachment 5, pp. 92-98).

One of the themes of outstanding universal value identified by the Expert Panel was "**Evolution of landforms, species and ecosystems under conditions of stress**". This theme was identified within the context of the unique, long-term isolation of the Australian continent following its separation from other land masses during the break-up of the supercontinent Gondwana. The more recent geological history of the Australian continent was regarded by the Panel as central to an understanding of the co-evolution of Australia's past and present landscapes, flora and fauna and, latterly, human societies.

This theme was also associated with the changing environmental conditions as the newly-isolated continent moved slowly northwards as a result of global plate tectonic events. With this northwards movement came greater climatic variability as the continent was influenced by altered atmospheric systems. Other important environmental factors included lower nutrient soils, increased incidence and intensity of fires, and the interaction of surface water and ground water in a landscape of predominantly low relief formed as a result of exceptionally-long periods of weathering and erosion.

Sub-themes of outstanding universal value identified by the Expert Panel in relation to this theme are concerned particularly with the ways in which Australia's landforms and vegetation evolved in response to continental isolation and these environmental conditions. The related sub-themes included:

- **Scleromorphy** - the development of a diverse range of scleromorphic characteristics (including hard, thickened leaves and pronounced cuticle development) by large sections of the Australian flora in response to low nutrient soils and a highly variable climate;
- **Arid landscapes and adaptations** - development of outstanding arid land forms and arid-adapted biota in sandy deserts, including longitudinal dune systems with the longest dunes, on the most arid, non-polar continent in the world;
- **Alpine vegetation** - evolution of globally-unusual alpine vegetation that has developed in response to maritime conditions and poor soils; and
- **Eucalypt-dominated vegetation** - evolution of the eucalypts under conditions of high climatic variability, nutrient deficiency and a variety of fire regimes including those with very short between-fire intervals and those with extreme fire intensities, and their subsequent taxonomic and geographic expansion to dominate most of the woody vegetation of an entire continent.

Places that are both forested and within designated RFA regions were identified by the World Heritage Expert Panel for further assessment to evaluate whether they are best global expressions of the sub-theme of eucalypt-dominated vegetation (see World Heritage Report 1997b, pp. 42-47, and Table 8, pp. 48-49). The eucalypt sub-theme and its representative places thus require further assessment within the context of the CRA process. Places identified by the Panel in relation to the other themes and sub-themes are either non-forested or are not directly associated with RFA regions, and their further assessment will need to take place in other contexts.

The sub-theme of eucalypt-dominated vegetation

Australia is unique in that almost all of its present-day, woody vegetation communities are dominated by only two groups, the eucalypts and the acacias (Beadle 1981). Both the eucalypts and the phyllodinous acacias have a very restricted natural distribution outside the continent (Barlow 1994). The outstanding universal sub-theme of eucalypt-dominated vegetation recognises the international significance of the eucalypts and the woody vegetation communities that they dominate on the Australian continent.

The eucalypts are widely regarded as globally outstanding and as an exemplar of the unique character and diversity of the Australia biota (eg, see Blakers 1987, Busby 1992, Mosley and Costin 1992, Kirkpatrick 1994). Factors important in contributing to the outstanding universal value of the eucalypts include their ancient Gondwanan origins and their subsequent evolution which parallels the geological and ecological history of the Australian continent, their success in dominating the majority of woody ecosystems throughout an entire continent, the diversity of their growth forms which range from the tallest hardwood forests in the world to prostrate shrub forms, the wide diversity of the communities which they dominate, and their unique ecology.

Representation of the sub-theme of eucalypt-dominated vegetation

In considering possible representation of the sub-theme of eucalypt-dominated vegetation, the Expert Panel was careful to keep in mind that a natural place must meet one or more of the criteria specified in paragraph 44 (a) of the Operational Guidelines for the Implementation of the World Heritage Convention (UNESCO 1999) and fulfil the conditions of integrity specified in paragraph 44 (b) in order to qualify for World Heritage listing (see Attachment 1 for a summary of the criteria and conditions of integrity).

The Panel also took a wider view of the genus *Eucalyptus*. For example, it commented that a best global representation of eucalypt-dominated vegetation in Australia "would necessarily be based on a series of areas. The areas would, together, represent the major types of ecological relationships exhibited by the genus *Eucalyptus* (*sensu lato*) [i.e. in the broad sense] including such taxa as *Eudesmia*, *Corymbia* and *Angophora*, the major structural types and the floristic variation in the genus." (World Heritage Report 1997b, p. 40).

The places identified by the Expert Panel in relation to possible representation of the eucalypt sub-theme are listed below in Table 1. Each of the identified places was regarded by the Panel as likely to be of sufficient size and natural condition to fulfil the conditions of integrity, either alone, or in association with adjacent listed World Heritage Areas. In identifying possible places the Expert Panel considered only "forested" areas as defined in the National Forest Policy Statement (Commonwealth of Australia 1992) and did not consider other areas with eucalypt-dominated vegetation such as woodlands or mallee. It should be noted that for some regions, governments have agreed that any potential world heritage nomination can be achieved from within the CAR Reserve System.

Further assessment of the sub-theme of eucalypt-dominated vegetation

A process for further assessment of the sub-theme of eucalypt-dominated vegetation has been put forward and is outlined in Attachment 3. In general terms, the process involves describing outstanding universal values of eucalypt-dominated vegetation, and identifying the attributes that contribute to their global significance. The outstanding universal values and their associated attributes can provide the basis for subsequent documentation and assessment of the global significance of places identified in relation to the sub-theme.

As part of the process of further assessment of the sub-theme (see Attachment 3, Figure 1) an expert workshop was held in Canberra on 8 and 9 March 1999. The expert workshop was asked to develop a description of the outstanding universal values of the sub-theme of eucalypt-dominated vegetation and to identify an agreed list of significant attributes that contribute to these outstanding universal values. The workshop was attended by experts selected from amongst Australia's foremost authorities on eucalypts and eucalypt-dominated vegetation. It was also observed by representatives from all governments involved in the CRA process. Terms of reference for the workshop are listed in Attachment 4. A list of workshop participants is included in Attachment 5. The experts who participated in finalization of the content of the workshop report included: Professor Jamie Kirpatrick (Chairman), Dr Mike Austin, Dr Bryan Barlow, Dr Ian Brooker, Dr Mick Brown, Dr Malcolm Gill, Dr Gordon Guymer, and Professor Pauline Ladiges.

Table 1. Forested places identified by the World Heritage Expert Panel in relation to the sub-theme of eucalypt-dominated vegetation (World Heritage Report 1997b)

Forested places identified by the Expert Panel in relation to the sub-theme of eucalypt-dominated vegetation	**State or Territory**
Specified south-west National Parks and associated areas	Western Australia (south-west)
The Moonee-Bindery area, including Guy Fawkes Wilderness Area	New South Wales (north-east)
Specified National Parks in the sandstone area centred on the Blue Mountains	New South Wales (central)
Natural forest areas of south-eastern Australia extending from the sea to the alps and the inland slopes	New South Wales (south-east) Victoria (east) Australian Capital Territory
The Carnarvon Ranges, including Carnarvon National Park	Queensland
Natural eucalypt forest areas on the inland slopes, and eucalypt and *Melaleuca*-dominated areas on the coastal plains, adjacent to the Wet Tropics World Heritage Area	Queensland
Cooloola National Park, adjacent to the Fraser Island World Heritage Area	Queensland
Eucalypt-dominated areas adjacent to the Central Eastern Rainforest Reserves World Heritage Area, including Bunya Mountains National Park	Queensland
Kakadu National Park World Heritage Area	Northern Territory
The Tasmanian Wilderness World Heritage Area	Tasmania

The following sections of the report provide a summary of the findings of the expert workshop concerning outstanding universal values of eucalypt-dominated vegetation, and significant attributes that contribute to these values.

Workshop Report

The Eucalypts

General description

The term "eucalypt" in its broad sense refers to certain taxa within the family Myrtaceae. These taxa include species in the genera *Eucalyptus* and *Angophora*. They also include species in the bloodwood groups *Corymbia* and *Blakella* which are often included as sub-generic groups within *Eucalyptus* (e.g. Pryor and Johnson 1971, Brooker and Slee 1996), but have also been described as a separate genus, *Corymbia* (Hill and Johnson 1995).

The following botanical descriptions of the eucalypts are based on the genera *Eucalyptus* (including the bloodwoods) and *Angophora*, and have been derived primarily from Chippendale (1988), Brooker and Slee (1996) and Mabberley (1997). Technical terminology has been defined using non-technical language wherever possible, and technical terms have been included in square brackets.

Eucalyptus L'Her. (including *Corymbia* K.Hill & L. Johnson)

Evergreen trees, shrubs or mallees. Bark smooth or rough, including fibrous, stringy or in squarish patches [tessellated]. Leaves of seedling and young plant distinct from adult leaves [heterophyllous] in shape, position and colour; adult leaf phases occurring in most species, the latter phases sometimes not achieved [neoteny] so that some species are reproductively mature while crown is in the juvenile leaf phase; oil glands present in most species. Adult leaves mostly borne singly at different levels along a stem [alternate], usually with a leaf stalk [petiolate], ovate to broadest in the lower half and tapering to the tip [lanceolate] or curved [falcate], dull or glossy, smooth and hairless [glabrous], pendulous, rarely erect, with a distinct midvein and pinnately-arranged veins [penninerved], or with parallel veins. Inflorescences borne in the angle formed by the leaf with its branch [axillary], but in some species on leafless shoots in axils of leaves at ends of branchlets [terminal pseudopanicles]. Flower buds single, or in 3s, 7s, 11s etc.; sepals and petals absent, replaced by one or two covering caps [operculae] which are shed at flower opening [anthesis]; stamens numerous, often brightly coloured; sterile stamens [staminodes] present in some species; ovary sunk into the floral tube [hypanthium], below the level of attachment of other flora parts [inferior] or partly above the level of attachment [superior], with 3 to 8 chambers [locules]; ovules many, partly inverted [hemitropous] or fully inverted [anatropous]. Fruit a capsule with a usually woody floral tube [hypanthium]; releasing contents [dehiscing] by valves which are either exserted, level with capsule rim, or inserted; seeds several to many, ellipsoid, cuboid or pyramidal but variously flattened or distorted, variously coloured; with terminal or ventral separation scar [hilum]; numerous chaff grains [ovulodes] usually included with seeds.

The most characteristic genus of the Australian landscape; includes more than 700 species, all but a few endemic to Australia; varies from dwarf shrubs to some of the tallest hardwood trees known. Main groups recognisable by their bark: gums (smooth and deciduous), boxes (rough but fibrous), peppermints (finely fibrous), stringybarks (long fibrous), ironbarks (hard, rough fissured, dark) and bloodwoods and ghost gums (included in *Corymbia*) (tessellated).

Over 200 species introduced elsewhere; the most important dicotyledon plantation trees worldwide; widely planted in other countries for timber, oils, tannins, lowering watertables etc; dominate scenery in parts of some countries e.g. California, East Africa, Sri Lanka, Portugal; aggressive and invasive in some parts.

Angophora Cav.
Evergreen trees or shrubs. Bark rough or fibrous or smooth. Leaves of 2 different kinds [dimorphic]; lateral veins very close, straight and parallel; juvenile leaves borne on opposite sides of stem at the same level [opposite], heart-shaped [cordate] at base, without a stalk [sessile], often rough with stiff, bristly hairs [hispid], with raised oil glands; adult leaves opposite, lanceolate, rarely curved [falcate], stalked [petiolate], usually smooth and hairless [glabrous], with upper and lower surfaces of a different colour [discolorous]. Inflorescence a terminal aggregate of flowers [compound] comprising clusters [umbels] of 3-7 flowers borne on primary or secondary branches of the main axis [paniculate]. Flowers creamy-white to creamy-yellow, stalked [pedicellate], calyx-lobes [sepals] 4 or 5, free, reduced to persistent projections on rim of floral tube [hypanthium]; petals 4 or 5, flat and more or less circular [orbicular], overlapping [imbricate], broadly attached at the base, deciduous; stamens numerous in several whorls, free, anthers bilobed, opening by two longitudinal slits, swinging freely around the point of attachment to the filament [versatile], filaments creamy yellow, rarely pink, smooth and hairless [glabrous]; floral tube [hypanthium] extending beyond ovary which is below the level of attachment of other flora parts [inferior], usually with 3 chambers [locules], ovules partly inverted [hemitropous]. Fruit a hard, woody, longitudinally-ribbed capsule enclosed mostly by the persistent floral tube [hypanthium], releasing contents [dehiscing] by terminal valves. Seeds 1 per chamber [locule], broadly elliptic, flat, dark brown, leaves of the embryo [cotyledons] folded; numerous chaff grains [ovulodes] included with seeds.

Includes thirteen species, all endemic to eastern Australia. Closely related to *Eucalyptus* but distinguished by the petals and the bristle-like emergent oil glands that are interspersed with several-celled white hairs.

Some of these characters may be considered either relatively “primitive” or “advanced” (ie derived) in terms of whether they are associated with taxa that are basal or more recent in the eucalypt phylogenetic tree. Examples of “primitive” and “advanced” characters of the eucalypts are listed in Table 2

Table 2 Examples of "primitive" and "advanced" characters in eucalypts

"primitive" characters	**"advanced" characters**
- leaf blades horizontal, the upper leaf surface [adaxial surface] usually different in colour from the lower leaf surface [abaxial surface]	- leaf blades vertical and hanging via leaf stalk [petiole]
- flowers at tips of stems [terminal inflorescences]	- flowers in the angle between the upper surface of a leaf and the stem which bears it [axillary inflorescences]
- small numbers of buds in each flowering shoot [or unit inflorescence]	- larger numbers of buds in each flowering shoot [or unit inflorescence]
- green corolla parts [sepals] distinct from coloured corolla parts [petals] in the flower	- a single covering cap [operculum] or two covering caps replacing corolla parts [sepals and petals] in the flower
- anther attached to the filament of the stamen by a small area on its upper [dorsal] side so that it can turn freely [versatile anther]	- anther attached to the filament of the stamen along its entire length so that it is fixed in position [adnate anther]
- developing seeds [ovules] in odd number of rows	- developing seeds [ovules] in even number of rows
- ovules partly inverted [hemitropous]	- ovules fully inverted [anatropous]

Eucalypt taxonomy

The taxonomy of the eucalypts remains not fully understood despite considerable work over the past two centuries. Indeed, eucalypt taxonomy generally has been viewed as difficult (see Ladiges 1997). A number of taxonomic classifications for the eucalypts, and for *Eucalyptus* in particular, have been proposed at different times. Some have recognised the existence of separate taxon groups within *Eucalyptus* (e.g. Bentham 1867, Blakely 1934, Pryor and Johnson 1971, Chippendale 1988). Others have proposed a split of the genus into two or more genera on the basis of these groups (e.g. two genera, Carr and Carr 1962; three genera, Hill and Johnson 1995; five genera, Andrews 1913). The most common classification of the eucalypts has been into two genera, *Angophora* and *Eucalyptus* (e.g. Pryor and Johnson 1971, Chippendale 1988, Brooker and Slee 1996). In general, the comprehensive classification by Pryor and Johnson (1971) which recognises these two genera has been the most widely accepted and used.

In addition to recognising *Angophora* and *Eucalyptus*, Pryor and Johnson (1971) delineated seven groups within *Eucalyptus* which they informally recognised as subgenera. These groups included *Blakella*, *Corymbia*, *Eudesmia*, *Gaubaea*, *Idiogenes*, *Monocalyptus* and *Symphyomyrtus*. Although they considered *Angophora* as equal to the other seven groups, they chose not to include it at this stage. It has been suggested subsequently that these informal sub-generic groups may warrant full generic status (e.g. Pryor and Johnson 1981). This view is based on the possibility that at least some of the groups may have had separate origins from closely-related ancestral stocks. In this regard, two of the subgeneric groups, *Corymbia* and *Blakella*, the bloodwoods and ghost gums respectively, have recently been separated from *Eucalyptus* and described as a single new genus, *Corymbia*, by Hill and Johnson (1995). Even when *Eucalyptus* is treated in this narrower sense, there remain relatively distinct subgeneric groups such as *Symphyomyrtus* and *Monocalyptus* recognizable within the genus.

Notwithstanding the different views on the taxonomic ranking of the eucalypt groups such as *Angophora*, *Corymbia* and *Eucalyptus sensu stricto* (in the narrow sense), there is a general, strong consensus among eucalypt taxonomists that the entire stock has developed from a single lineage.

Eucalypt phylogeny

Reviews of evidence for the eucalypts, including molecular and morphological data, also support the concept of a single phylogenetic tree for *Angophora*, *Corymbia* and *Eucalyptus sensu stricto* (Ladiges *et al.* 1995, Ladiges 1997). Two major branches (clades) or lineages are evident within this monophyletic group. One clade is further differentiated into *Angophora* and the bloodwoods and ghost gums represented by *Corymbia* and *Blakella*; the other includes taxa associated with *Eucalyptus sensu stricto* (e.g. Ladiges 1997, Figure 2.2, p. 20).

A phylogenetic summary tree that includes both the eucalypts and closely-related taxa within the Myrtaceae, based on the latest published and unpublished morphological and molecular evidence including nuclear and chloroplast DNA, further supports the interpretation of a monophyletic lineage for the eucalypts (Ladiges *et al.*, unpublished). This latest tree demonstrates three major branches for the eucalypts and a close relative. One branch corresponds to *Eucalyptus*, a second is differentiated into *Angophora* and the bloodwoods *Corymbia* and *Blakella*, and the third is associated with the putative closest living relative of the eucalypts, the genus *Arillastrum*, which is extant only in New Caledonia. This evidence for three groups of eucalypts, including *Eucalyptus*, *Angophora* and the bloodwoods, is broadly consistent with the recent classification by Hill and Johnson (1995).

The existence of major groups among the eucalypts appears to be strongly supported by the evidence, and has gained general acceptance. A central issue within eucalypt taxonomy that remains to be resolved is the appropriate level or rank at which these groups should be recognised. Irrespective of how they are ranked taxonomically, it is clear that the eucalypts comprise a monophyletic stock which is exceptional in the way in which it has diversified to dominate the vegetation of an entire continent and has influenced the evolutionary moulding of an entire continental flora.

Outstanding Universal Values of Eucalypt-dominated Vegetation

Ancient origins in Gondwana and evolution of the eucalypts in Australia

The origins and evolution of the eucalypts are strongly linked to the evolutionary history of the Australian continent, including the geological events associated with its origin and the environmental conditions that subsequently shaped the continent and forged its unique identify.

Evolutionary history of the continent

"The history of Australia as an individual entity is a post-Jurassic phenomenon" (Hill 1994, p. 2). This statement provides a clear reference point in the geological time-scale of about 135 million years BP for the origin and subsequent development of the present Australian continent. Australia's origin as a continent can be traced to its separation from other landmasses that made up the southern supercontinent of Gondwana. Other major Gondwana landmasses included Antarctica, South America, Africa, Madagascar, India and New Zealand. The subsequent development of the unique identity of the Australian continent took place during its drift northwards from far southern latitudes, over many thousands of kilometres and many millions of years, to its present location.

Continental separation and tectonics

The following summary of events associated with the separation of Australia from Antarctica and its subsequent drift into more northerly latitudes is derived from reviews by Quilty (1994) and Wilford and Brown (1994) and references therein. The reconstructions of these events must be viewed as conjectural at least to some extent, based as they are on limited evidence representing only relatively small sequences of the entire time course of events.

Separation of Australia from India and Antarctica is believed to have begun about 132 million years BP. The initial break-up took place in the north-west region of what is now the Australian continent and gradually extended southwards as Australia and India separated. This event was followed closely by Australia's separation from Antarctica from about 110 million years BP, beginning in the southwest and gradually extending east along the southern margins of the continent. The land connection between the two was eventually confined to the southern parts of Tasmania by about 80 million years BP. Final separation, followed by the formation of a deep marine strait between the two continents, had taken place by about 38 million years BP. Subsequently, the Australian Plate drifted slowly northwards, eventually colliding with the Pacific Plate and the Southeast Asian Plate. The northward drift of the Australian continent continues today.

Palaeoclimates

The following summary of trends in Australian palaeoclimates has been based on reconstructions and information in reviews by Martin (1994), Quilty (1994) and Wilford and Brown (1994). Again it should be emphasised that relatively few data are available from which to infer geographical and temporal variation in climatic factors, particularly at the continent scale, but also over shorter time-scales. Therefore, reconstructions which infer trends in climate, particularly at these scales, remain largely conjectural.

Climatic conditions in Australia from about 140 million years BP are believed to have been cool and humid with some seasonality, at least for south-eastern parts of the continent, and with a gradient of increasing but still cool temperatures towards the northwest. Large parts of the continent were covered by sea during much of this period. By about 65 million years BP, conditions appear to have become much warmer and humid, and the seas had largely retreated from the continent. During the period 65 to about 45 million years BP, southern parts are thought to have experienced higher rainfall and temperate conditions, with warm temperatures in northern regions and a moisture gradient across the north of the continent which ranged from humid in the northwest to dry conditions in the northeast.

In contrast to the relative climatic stability of previous times, major variations in climate followed Australia's separation from Antarctica. This variability, which was characterised by marked fluctuations in temperature, rainfall, runoff and sea level, is thought to have resulted from the establishment of different marine and atmospheric circulation regimes as the Australian and Antarctic land masses moved further apart. A general cooling of sea temperatures in southern regions also occurred following separation of the continents, possibly associated with the development of a circumpolar oceanic flow. Antarctica is thought to have commenced its glacial phase at about this time with the development of sea ice. The cooling of Antarctica has been associated with increased temperature gradients between the polar region and the tropics, leading to increased wind strengths. Large-scale ice sheet development in East Antarctica from 38 to 36 million years BP is thought to have contributed to the onset of drier climates over much of Australia and the formation of wide-spread duricrusts (see Wilford and Brown, 1994).

From about 27 million years BP, temperatures appear to have become warmer across northern Australia, with tropical conditions evident at about the time of the collision of the Australian plate with the Southeast Asia plate. Modern circulation patterns for ocean and atmosphere appear to have become established as Australia moved closer to Asia and as the gap with Antarctica widened. In the period to about 18 million years BP, there is evidence for humid conditions in central Australia with substantial lake systems, watercourses and dense vegetation. In contrast, subsequent periods have been associated with a change to more seasonal conditions with marked dry periods. Fire is thought to have become an important element in the Australian environment at about this time (Martin 1989).

Climates during the Late Tertiary (10 to 2.2 million years BP) and the Quaternary (2.2 million years BP to present) are believed to have become increasingly variable, and there is evidence to suggest a gradual drying out of the continent (see Bowler 1982). A warm, wetter phase occurred in southern Australia in the period after about 10 million years BP. There is also evidence for a warmer period in Antarctica at about this time (see Quilty 1994). This phase was followed by a gradual return to drier conditions in Australia, which is thought to have been associated with the transition from rainforest to wet sclerophyll vegetation and eventually to more open vegetation types, including grasslands. There is evidence that relatively rapid alternations between rainforest and sclerophyllous vegetation occurred at some places (Truswell 1990). Sea temperatures to the south of Australia continued to decline during this period and Antarctica entered its present glacial phase at about 2.6 to 2.4 million years BP.

Conditions in southern and central parts of the Australian continent became more arid at about this time, with tropical conditions persisting in the north.

The present pattern of polar glaciation became established during this most recent period, with at least 17 glacial periods documented as occurring during the past 2 million years BP. Each glacial cycle has been associated with a prolonged period of increasing icecap volume at the poles and decreasing sealevel, followed by a short-term collapse of the icecap and a sudden increase in sealevel. Although the chronologies of earlier glacial cycles are poorly known, the most recent seem to have involved a glacial period of about 100,000 years, a collapse period of about 10,000 years, and a stable, interglacial period of between 5,000 and 10,000 years. The glacial periods are believed to have been associated with cold, dry and windy conditions on the Australian continent, leading to a large expansion of the continental arid zone, reduced incidence of tropical cyclones in the north, and increased snowfall with some glaciation at higher elevations. Stable interglacial periods, which includes the present time, are generally associated with warmer and less arid conditions.

Landscapes

The following summary of Australian landscapes has been derived largely from a recent review by Taylor (1994). The landscapes of Australia are predominantly ancient, although younger formations occur in some parts. In general, the western two thirds of the continent is dominated by older landscapes of lower relief and the eastern third includes younger and higher relief landscapes, particularly associated with the Eastern Highlands. Australia's ancient landscapes include some that are considerably older than the breakup of Gondwana, including examples dating back as far as Precambrian times (prior to 570 million years BP).

Much of the Australian continent is dominated by landscapes of low relief. Many of these comprise younger sedimentary basins partly overlying much older rocks. The Eastern Highlands include older rocks superimposed by younger landscapes, such as those formed by basalt flows. With some exceptions, basalt landscapes along the eastern margins of the continent exhibit a general north-south trend of decreasing age, ranging from Late Cretaceous (before 65 million years BP) in the north, to Holocene (10,000 years BP to present) in the south. Marine inundation has also affected parts of the continent at different times. Many of the higher elevation areas are thought to have been separated by shallow seaways at these times, which is likely to have contributed to increased spatial and habitat diversity (Wasson 1982).

The land surfaces of a large part of the continent comprise a regolith (ie material overlying bedrock) of either sedimentary deposits derived from weathering or erosion of older surfaces, or deeply weathered *in situ* material derived from the underlying parent rocks. These ancient landscapes have undergone deep weathering and soil formation over very long periods associated with Australia's exceptionally stable tectonic conditions.

The soils of the majority of Australian landscapes are characteristically highly-leached and infertile. Humid periods from the Cretaceous to the Pliocene are believed to have contributed to widespread deep weathering and the formation of leached acid soils of low nutrient status that are characteristic of large parts of the continent. Drier conditions in the Quaternary led to a change in weathering processes and the formation of the alkaline soils with a high salt or carbonate content that are widespread throughout the drier parts of central and southern Australia.

Tertiary and Quaternary phytogeography

The following overview of phytogeography in Australia during the Tertiary (65 to 2.2 million years BP) and Quaternary (2.2 million years BP to present) has been drawn largely from recent reviews by Martin (1994), Kershaw *et al.* (1994), Macphail *et al.* (1994) and Hope (1994). Their reconstructions of the phytogeography of the Australian continent during these periods have been based on the fossil pollen record. It should be noted that generalisations that form the basis of these reconstructions neither encompass the actual spatial diversity of vegetation that may be present in the landscape nor deal comprehensively with its temporal variation. As Martin (1994) points out, reconstructions relate to the dominant types of vegetation in the landscape and they largely exclude small areas of different types of vegetation.

In general, the spatial variation exhibited by past vegetation in Australia is thought likely to have been comparable with the present-day vegetation (Martin 1994). All the fossil evidence shows that the flora was not uniform at any time (Martin 1994). In this regard, Macphail *et al.* (1994) also commented that "there is no compelling evidence for a pan-Australian flora ...". Temporal change in the vegetation was also likely to have been ongoing and gradual, with occasional periods of drastic change, probably associated with times of major climate change (Martin 1994).

The Australian landscape was largely forested throughout the Tertiary (Martin 1994). Palaeocene (65 to 54 million years BP) vegetation in southeast Australia is believed to have been dominated by coniferous wet forests that were able to withstand the long, dark winters of southern latitudes (Macphail *et al.* 1994). A gradient from wetter coastal areas to drier inland areas is thought to have persisted across the continent for much of this period (Martin 1994, Kershaw *et al.* 1994). Inland areas were probably dominated by rainforest-type vegetation with angiosperm dominants. Little is known of the vegetation of northern and western Australia at this time.

The conifer-dominated rainforest of southeast Australia appears to have been replaced by angiosperm-dominated rainforest during the Eocene (54 to 38 million years BP. Rainforest with *Nothofagus* species is thought to have become a dominant vegetation type during the Late Eocene, at least for southern parts of the continent (Martin 1994), and was possibly associated with a phase of global cooling (Macphail *et al.* 1994). There is some evidence of eucalypt-dominated vegetation in the Early to Middle Miocene, but its distribution appears to have been limited and there is little evidence of grassland and open sclerophyllous vegetation (Kershaw *et al.* 1994).

Mid to Late Miocene vegetation has been associated with the disappearance of *Nothofagus* from many areas and an increase in Myrtaceae, but with some rainforest taxa still present. It has been suggested that the vegetation at this time may have been predominantly wet sclerophyll, perhaps with a rainforest understorey (Martin 1994). Macphail *et al.* (1994) have also suggested there was a marked contrast between coastal and inland environments.

An increase in charcoal content in the fossil record occurred during the Miocene, possibly reflecting a change to an increased incidence of fires (Kershaw *et al.* 1994, Martin 1994). Kershaw *et al.* (1994) also discussed the possibility that increasing temperatures in the Mid Miocene associated with an effective reduction in precipitation may have contributed to this change in fire regime. A paucity of pollen evidence from the very Late Miocene is also consistent with drier or to more variable climatic conditions (Kershaw *et al.* 1994).

Rainforest vegetation increased again in the Early Pliocene, although the spatial incidence of this was extremely variable, which may reflect vegetation mosaics of rainforest in wetter habitats and wet sclerophyll in drier habitats. By the Mid to Late Pliocene a dominant Myrtaceae component of the vegetation was again evident.

The Late Pliocene to Pleistocene record demonstrates further substantial vegetation change, particularly associated with an increasing component of herbs and grasses. The increased herbaceous component is believed to reflect a transition towards vegetation with a more open structure, such as woodland and grassland (see Martin 1994). This change is first evident in the northwest of the continent, extending later to southern regions (Kershaw *et al.* 1994). There is little evidence for the presence of open-canopied vegetation in the period prior to the Miocene, suggesting this vegetation type was either absent or very restricted (Kershaw *et al.* 1994).

The present-day vegetation types that occur in Australia are believed to have developed by the end of the Pliocene (Kershaw *et al.* 1994), although marked changes in their distribution and relative contribution to the flora would have occurred as a result of the climate changes of the Pleistocene and Holocene periods.

In summary, major changes in Australia's vegetation occurred during the Tertiary and Quaternary which involved a transition from coniferous and rainforest dominated vegetation to a predominantly open-sclerophyll vegetation with rainforest confined to wetter localities. As part of this transition, eucalypt-dominated vegetation expanded greatly in distribution at the expense of other vegetation types, including the drier rainforests, Casuarinaceae-dominated forests, and wet sclerophyll forests with non-eucalypt dominants from the family Myrtaceae. These changes were also associated with an increased grassy understorey component in more open eucalypt-dominated communities and the development of temperate grasslands in some areas (see Kershaw *et al.* 1994). Factors thought to have been important in influencing these changes to the vegetation include increased climatic variability, a transition to drier climatic conditions, the effects of the extreme glacial/interglacial cycles of the past 2 million years, and an increased incidence of fires. The latter may also have been influenced in more recent times by the arrival of humans on the continent.

Evolution of the eucalypts

The fossil record

The fossil record of the eucalypts, including both macrofossils and pollen, is poor with relatively few specimens that have been reliably identified and dated (Hill 1994). The earliest records of eucalypt-type pollen in Australia are of Late Paleocene age (to 54 million years BP) (see Martin 1994). Pollen types with close affinities to extant eucalypt taxa first appear in the Late Oligocene (to 27 million years BP). For example, pollen with close affinities to the extant species *Eucalyptus spathulata* has been identified at sites of Pliocene age (10 to 2.2 million years BP) from both the southeast and southwest of the continent (Martin and Gadek 1988); in the southeast, this fossil pollen type extends well into the Pleistocene (after 2.2 million years BP). The more recent pollen record tends to exhibit a greatly increased abundance of eucalypt pollen compared with previous periods (see Martin 1994). This is often associated with increased amounts of charcoal. It has been suggested that the increased charcoal may reflect an increased incidence of fires, perhaps associated with a drying climate (Hill 1994), and also with the influence of humans (Singh *et al.* 1981, Kershaw 1986).

Reliably-dated eucalypt macrofossils are mostly from the south-east of the continent. Well-preserved eucalypt-like fossils have been found in central Australia (e.g. Lange 1978), but their age is uncertain (Ambrose *et al.* 1979). The oldest accurately-dated eucalypt macrofossil is estimated as 21 million years BP (Bishop and Bamber 1985). Other reliably-identified eucalypt fossils, including fruits and leaves comparable to extant taxa, have been dated from the Middle Miocene (17 to 14 million years BP) (e.g. Holmes *et al.* 1982), and the Pliocene (10 to 2.2 million years BP) (e.g. Pole *et al.* 1993). Fossil flower remnants of Late Miocene age (10 to 5 million years BP) represent the earliest evidence of the eucalypt subgenus *Monocalyptus*; these deposits also include specimens associated with the subgenus *Symphyomyrtus* (Blazey 1994).

Macrofossils with affinities to the eucalypts have also been reported from other countries which have no extant eucalypts in their natural floras. These extra-Australian records include fossilised fruits and leaves of Early Miocene age from New Zealand (Pole 1989, 1993) and fossilised fruits from sediments of Miocene age in Patagonia on the South American continent (Frenguelli 1953). In addition, fossilised leaf material with affinities to the eucalypts has been collected more recently in Patagonia by Romero (see Hill 1994). The New Zealand fossils have been described by Hill (1994) as more reliable that those from South America, although Ladiges (1997) notes that without definitive characters none of this material can be reliably attributed to *Angophora* or *Eucalyptus*. Hill (1994) also draws attention to the records of eucalypt-type pollen in New Zealand, listed by Mildenhall (1980) as having a stratigraphic age of Miocene to Early Pliocene.

Present distribution

Extant eucalypt species are nearly all endemic (confined in their natural distribution) to the Australian continent. Exceptions include four species that occur in tropical parts of Asia, but are not found in Australia. These are *Eucalyptus deglupta* which is endemic to parts of Indonesia, northern New Guinea, New Britain and the southern Philippines, and *E. urophylla*, *E. orophyla* and *E. wetarensis* which occur in Timor and the nearby Lesser Sunda islands (Pryor *et al.* 1995). A further ten species are common to Irian Jaya and Papua New Guinea and areas of northern Australia (Eldridge *et al.* 1993).

The closest living relatives of the eucalypts include the genera *Arillastrum* which is endemic to New Caledonia, *Eucalyptopsis* which occurs in northern Australia and New Guinea, and *Allosyncarpia* and *Stockwellia*, both of which occur in northern Australia.

Origin of the eucalypts

The palynological record for the family Myrtaceae, to which the eucalypts belong, indicates a Late Cretaceous distribution that included Borneo (90 to 85 million years BP), Africa (85 to 80 million years BP), South America (70 to 65 million years BP) and Antarctica (80 to 65 million years BP). The Antarctic records are earlier than the first records for the Myrtaceae in Australia and New Zealand (65 to 54 million years BP).

As mentioned above, the earliest records for eucalypt-like pollen in Australia date from about 54 million years BP, and the earliest fossil evidence of pollen with strong affinities to extant eucalypt species occurred about 27 million years BP. The palynological evidence therefore supports the presence of eucalypts in Australia and New Zealand during at least the early Tertiary.

The available macrofossil evidence raises the possibility that there may have been eucalypts in New Zealand and South America during the middle of the Tertiary. Hill (1994) and Ladiges (1997) discuss hypotheses to explain these more remote, though unconfirmed records, in terms of the origins and distribution of the eucalypts. Two hypotheses have been proposed, viz: either the fossils represent an ancient lineage for the eucalypts which was more widely distributed in Gondwana prior to the break-up or, alternatively, the fossils resulted from long-distance dispersal either from Australia or from some other part of the natural distribution of the eucalypts. Either hypothesis might explain the New Zealand fossils, whereas verification of the South American fossils as eucalypts would constitute stronger support for the former explanation. There is no clear fossil evidence to support either of these explanations to date.

In considering the biogeographic evidence, it is important to note that *Angophora*, *Corymbia* and *Eucalyptus sensu stricto* are most closely related to *Arillastrum*, which is endemic to New Caledonia. The split between these two groups may therefore be as old as the split of New Caledonia from the Australian land mass, which formed part of Gondwana. This evidence suggests the eucalypts may date back at least to the Late Cretaceous (about 80 million years BP), which is older than the fossil record indicates (Ladiges 1997, Ladiges pers. comm. 1999).

Although the actual origins of the eucalypts remain uncertain, it is clear that Myrtaceous taxa, which may have included eucalypt precursors, were present in the landmasses that comprised Gondwana prior to its breakup. It is also clear that the eucalypts have been present on the Australian continent since the early Tertiary, prior to its final separation from Antarctica. The natural distribution of extant eucalypt taxa, which are almost all confined to the Australian continent and with only very few taxa occurring naturally in other, nearby parts of the world, is consistent with either a Gondwanan or Australian origin for the eucalypts. In this regard, Barlow (1981) referred to evidence in Gill (1975) and Martin (1981) when he commented "For phytogeographical reasons alone there can be little doubt that *Eucalyptus* is of ancient Australian origin, although the genus does not appear definitely in the fossil record until the Oligocene" (p. 58).

Evolutionary considerations

The following discussion of the evolution of the eucalypts builds on the few factual data available concerning historical distributions of the eucalypts, and also draws upon the reconstructions of past geological events, landscapes, palaeoclimates and vegetation discussed in previous sections. There is little direct evidence available as yet from which the evolution of the eucalypts can be reconstructed with any degree of certainty.

Within the context of reconstructed changes in Australian environments and vegetation, it seems that the eucalypts or their ancestral forms persisted and evolved through the transition from the relatively predictable moist climates and closed vegetation that characterise the early Tertiary, to the highly variable and drier climates and more open vegetation of the late Tertiary and the Quaternary.

Lange (1980) proposed that the vegetation of the Mid Tertiary may have comprised predominantly wetter non-eucalypt vegetation around the margins of the continent and drier vegetation with eucalypts in central regions. Under this scenario, the transition to drier climates may have ultimately resulted in displacement of the eucalypts to the continental margins, and restriction of non-eucalypt vegetation to the wettest areas and its loss altogether from parts of the continent. Hill (1994) commented that the available fossil evidence is not inconsistent with this hypothesis.

The most-recently-evolved component of the Australian flora is called the "autochthonous" element and is readily distinguished from the ancient "Gondwanan" or "relict" and the recently-invaded "tropical" elements of the flora (see Burbidge 1960, Barlow 1981, Martin 1994, Wardell-Johnson *et al.* 1997). Barlow (1981) described the autochthonous element as comprising "those elements of the flora which have undergone considerable evolutionary change, under conditions of geographical isolation, to produce typically Australian taxa with high levels of endemism" (p. 44). The eucalypts comprise an important part of the autochthonous element of the flora (Martin 1994).

Scleromorphy has been described as one of the more striking aspects of the autochthonous flora (Barlow 1981). Scleromorphs, as the name suggests, have hard, stiff leaves that are heavily cutinized (called sclerophylly). Sclerophyllous vegetation typically comprises woody plants with hard, tough and generally smaller leaves and is characteristic of dry places (see Usher 1979), particularly of Mediterranean-type climates. It has also been interpreted as a response to low nutrient soils (e.g. Beadle 1966). Scleromorphy is strongly represented in Australia by a number of plant families including Myrtaceae, Proteaceae, Rutaceae, Epacridaceae, Mimosaceae, Fabaceae, Goodeniaceae and Casuarinaceae (Barlow 1994).

It has been proposed that the scleromorphic element of the Australian flora, which includes the eucalypts, may have originated on the margins of areas dominated by rainforest, perhaps as an adaptation to low soil fertility (see Andrews 1913, 1916, Beadle 1981). Specht's (1981) observation, that sclerophyllous heath communities are part of Australia's moist tropical ecosystems today, where they form a mosaic with closed forest communities in response to deep, infertile, sandy soils, is consistent with this view. If the above hypothesis is correct, the characteristics of the eucalypts may have constituted a pre-adaptation rather than a direct adaptation to environmental factors favouring scleromorphic vegetation, such as increasing aridity or an increased incidence of fires (see Barlow 1981).

Johnson and Briggs (1981) similarly proposed that scleromorphy in Australia may have evolved in the early Tertiary on nutrient-deficient forest sites. Radiation of scleromorphic taxa would have occurred as the soils of large parts of the continent became impoverished and the climate became drier. The pollen record is generally consistent with this view, showing progressive transitions from rainforest to wet sclerophyll forest to dry sclerophyll vegetation followed by a relatively sudden transition to open sclerophyll vegetation during the period from the Mid Miocene (17 million years BP) to the Late Pliocene/Pleistocene (about 2.2 million years BP) (Martin 1994).

The high degree of adaptation by species to the presence of fires, through different fire regimes, amongst the sclerophyllous element may also be indicative that fire has been an important factor in the evolution of this component of the Australian flora. The charcoal record in pollen cores supports the hypothesis that fire was present in Australian environments throughout the Tertiary, and that its activity increased in association with the changes towards drier climates and increased seasonality of rainfall that occurred subsequently (Kershaw *et al.* 1994).

Hill (1994) noted both that there has been a dramatic increase in abundance of eucalypt pollen in recent sediments and that has this occurred in association with increased charcoal levels. This has been interpreted as consistent with the geographic expansion of the eucalypts to dominate the continent (see Hill 1994). The possibility that Aborigines may have played a role in increasing the incidence of fires and therefore in promoting the current dominance of the vegetation by the eucalypts has also been raised (e.g. Singh *et al.* 1981, Kershaw 1986). In this regard, Martin (1994) noted that rainforest vegetation requires exceptionally dry conditions to burn and that Aboriginal burning by itself would be insufficient to cause a widespread decline of rainforest. Drier climates are also likely to have contributed to the recent expansion of the eucalypts due to an increased incidence of fires (Hill 1994). The changing temperature and rainfall patterns associated with the glacial cycles over the past 2 million years would also have had pronounced effects on eucalypt distribution.

***Outstanding universal value*: Ancient origins in Gondwana and evolution in Australia**

The eucalypts have outstanding universal value as an ancient, monophyletic lineage that has evolved and persisted on the Australian continent and nearby islands and is now unique to these areas. The origins of the eucalypts were on landmasses that formed part of the supercontinent of Gondwana, and their evolution took place subsequent to its breakup and the separation of these landmasses.

The evolution of the eucalypts is intimately linked to the Australian continent, having been influenced by its ancient, flat landscapes of unusual tectonic stability, its heavily-leached, nutrient-poor soils, and also by the environmental changes that resulted during the northwards drift of the continent to reach its present position. These environmental changes included a broad transition from a wet, stable climate at higher latitudes to a variable but drier climate with increasing periods of aridity at lower latitudes. The drier periods may also have been associated with increased incidence of fire in some areas. While maintaining a general drying trend, these climatic changes appear to have oscillated to some extent between wetter and drier climates at different times.

At the broadest scale, these past changes in environmental conditions have been associated with a transition of the dominant vegetation types of the continent from conifer-dominated rainforest to angiosperm-dominated rainforest, to wet sclerophyll forest, and then to progressively more open sclerophyll forest and woodland with an increasing grassy component. The eucalypts are believed to have originated on the margins of rainforest patches, and to have evolved in response to low nutrient soils that were seldom waterlogged, a drying climate and an increased incidence of fires.

The pollen record shows that the eucalypts have played an increasingly prominent role in the vegetation, often dominating the sclerophyll vegetation types as they increased in distribution, and eventually expanding to dominate almost all of the woody vegetation of the entire continent. The eucalypts are therefore one of the most important components of the recently-evolved, or autochthonous, element of the Australian flora. Their evolution has paralleled that of the continent, and their particular adaptations and characteristics reflect this history as well as contributing in a major way to the unique character of Australia's present environments and vegetation.

Current understanding of evolutionary relationships and ongoing evolutionary processes

Evolutionary relationships

A recent review by Ladiges (1997) provides a summary of current understanding of evolutionary relationships amongst the eucalypts based on morphological and molecular studies. As discussed previously, the evidence that the eucalypts represent a monophyletic lineage is strong (see eucalypt phylogeny section above). Moreover, within this single lineage, it is also clear that there are a number of eucalypt groups which have been classified as genera, or informally as sub-genera, based on morphological evidence.

Recent molecular evidence based on DNA data (Udovicic *et al.* 1995) shows two major evolutionary lineages (branches or clades) amongst eucalypt taxa currently in the genera *Angophora* and *Eucalyptus sensu lato* (including the bloodwoods). One clade comprises *Angophora* and the bloodwood sub-genera *Corymbia* and *Blakella*, and the other includes the remaining subgenera within *Eucalyptus sensu stricto*. A summary tree of phylogenetic relationships of the major groups of eucalypts, based on both morphological and molecular data, has been published (see Ladiges 1997, Figure 2.2, p. 20) and characters diagnostic to these eucalypt groups listed (Ladiges 1997, pp 18-22 and Table 2.1). The analyses also indicate that some of the morphological features used in previous taxonomic classifications of *Eucalyptus* have evolved more than once.

The *Angophora* lineage shows a further division into two branches, corresponding with *Angophora* and the bloodwoods. Three lineages are evident amongst the non-bloodwood eucalypts included in *Eucalyptus sensu stricto*; these include an older lineage comprising the sub-genus *Eudesmia* (20 species) and two others represented by the large sub-genera *Symphyomyrtus* (>300 species) and *Monocalyptus* (>120 species) (see Ladiges 1997, Figure 2.2). Basal taxa associated with the *Symphyomyrtus* and *Monocalyptus* lineages have been identified. The species *Eucalyptus guilfoylei* and *E. microcorys* are basal both to *Symphyomyrtus* and to the closely-related sub-genus *Telocalyptus*. Taxa basal to the *Monocalyptus* lineage include *Eucalyptus curtisii*, *E. tenuipes*, *E. cloeziana* and *E. rubiginosa* (Ladiges 1997, P. Ladiges personal communication).

Biogeography of the major eucalypt groups

The major eucalypt groups differ in their biogeographic distributions within Australia, and these differences may be relevant to understanding evolutionary relationships amongst the eucalypts as well as inferring historical distributions and interpreting the implications of physiological constraints and tolerances. Overviews of the distributions of the major eucalypt groups may be found in Gill *et al.* (1985) and Ladiges (1997). A brief summary of these distributions follows.

Taxa of the *Angophora*-bloodwood group occur widely in tropical, sub-tropical and warm-temperate regions of the continent but are not found in the cooler southern regions (Ladiges 1997). The major concentration of the bloodwoods is in the northern, tropical savannah regions (Gill *et al.* 1985). Some taxa in *Corymbia* extend into southern areas, with particular species exclusive either to the east or the west of the continent. Ladiges (1997) noted that this east-west division may be evidence for an older lineage that pre-dates the ancient biogeographic isolation of the two parts of the continent or, alternatively, it may reflect more recent long-distance dispersal.

The *Telocalyptus* group occurs only in northern latitudes. This group, which is closely related to *Symphyomyrtus,* includes one species confined to the northwest of Australia, and two species restricted to the northeast. In addition, there is a fourth species, *E. deglupta*, which is endemic to New Guinea, New Britain, Ceram, Sulawesi and Mindinao in the southern Philippines, and probably reflects an early dispersal event from Australia or New Guinea perhaps associated with tectonic events (see Ladiges 1997).

The *Symphyomyrtus* group is the most widespread of the eucalypts as it occurs throughout the Australian continent, including the drier areas, and also has taxa common to northern Australia, Indonesia and New Guinea. Within the *Symphyomyrtus* lineage, the oldest, basal taxa also show an east-west division, with *E guilfoylei* (yellow tingle) occurring in the southwest and *E. microcorys* (tallowwood) in the east of the continent (Ladiges 1997).

The *Monocalyptus* group shows a predominantly southern distribution, extending also up the east coast. It also includes taxa confined to either the west or the east of the continent (Gill *et al.* 1985). The oldest basal taxa within the *Monocalyptus* lineage, including *E. curtisii*, *E. tenuipes*, *E. cloeziana* and *E. rubiginosa* are all found in the northeast of Australia. Interestingly, these basal taxa or "living fossils" also occur together with representatives of all the other sub-genera at Isla Gorge in southeast Queensland. Ladiges (1997) noted that this unusual combination is suggestive of relictual taxa (only remaining species of particular lineages) and an early biogeographic separation of northern areas from southern parts of the continent.

Evolutionary processes

A recent review of patterns of eucalypt genetics and breeding systems provides an overview of mechanisms for promoting gene flow and genetic mixing amongst eucalypts (see Potts and Wiltshire 1997). These mechanisms include divergence, hybridization and introgression and the establishment of reproductive barriers between small populations (Potts and Wiltshire 1997).

The observed patterns of biogeographic distribution for eucalypts are generally consistent with a model of evolutionary divergence based on a combination of differentiation along ecological gradients and speciation in geographical isolation (allopatric speciation) (see Ladiges 1997). Closely-related eucalypt species tend to display patterns of spatial separation from each other which may be the effect of processes of variation and adaptation to environmental change, culminating in genetic divergence and speciation. The observed partitioning of closely-related species along major environmental gradients, such as climate, topography, and soils, is consistent with this model (Austin *et al*. 1997). Marked genetic variation reflecting adaptation divergence along steep environmental gradients has been demonstrated amongst co-occurring taxa over relatively short distances and within continuous stands. Morphological and physiological studies also suggest close adaptation of populations to local conditions for many characters (see Potts and Wiltshire 1997). Adaptive changes in response to habitat factors may also lead to genetic divergence within a species and ultimately to speciation.

Broader patterns of spatial separation between related taxa may reflect geographical isolation, leading to divergence and speciation. Patterns of genetic diversity between populations of some eucalypt species are consistent with this interpretation. For example, a high proportion of the observed genetic variation for widespread species such as *E. delegatensis* and *E. nitens* has been shown to correspond to major geographic disjunctions within their range (Moran 1992).

Hybridisation is an active and ongoing process amongst potentially-interbreeding eucalypt species which increases genetic variability and thereby facilitates adaptive change. Some eucalypt species are able to hybridize where they come into contact, although other species are genetically isolated. The frequency of natural hybrid combinations tends to decrease with increasing taxonomic distance (Griffin *et al.* 1988). Genetic isolation is also characteristic of higher taxonomic levels amongst the eucalypts. A possible exception is the recorded hybridization between species of two closely related subgenera *Idiogenes* (*E. cloeziana*) and *Monocalyptus* (*E. acmenoides*) (Brooker and Kleinig 1994), although recent DNA analyses have raised concerns about the subgeneric classifications of the species involved (see Potts and Wiltshire 1997).

Natural hybrids tend to occur at habitat boundaries between parent species. Where these boundaries are sharp, hybrids may be absent, or occur as isolated individuals; where the boundaries are gradual, many hybrids may occur in a "hybrid swarm", sometimes including progeny beyond the first hybrid generation. Hybrid swarms that persist and become geographically isolated from one or both of their parent taxa are known as "phantom hybrids" (see Pryor and Johnson 1971, Potts and Wiltshire 1997).

Hybrids may also occur as zones of introgression (see Potts and Wiltshire 1997). Introgression is the introduction of genes from one species into the population of a closely-related species during hybridization. In this case, hybridization may provide a mechanism for adaptive or neutral gene flow to occur. Introgression may also result in resurrection and dominance of the phenotype of the pollen parent.

Hybridisation has the potential to increase genetic variability amongst eucalypts, but there may also be a subsequent loss of this increased genetic variability from a population; for example, as a result of reduced vigour, fitness or reproductive capacity in hybrid progeny compared with parent types (see Ladiges 1997, Potts and Wiltshire 1997, Wardell-Johnson *et al.* 1997).

Reproductive barriers to prevent hybridisation and inhibit gene flow are found in natural eucalypt populations. These barriers are important in maintaining genetic integrity of populations, and may play a major role in the survival of rare or relict species. Reproductive barriers in eucalypts include spatial separation of potentially-interbreeding populations, and temporal separation involving different flowering times for species. The use of different pollinators by different species may constitute a reproductive barrier, although this has yet to be investigated. Structural and physiological barriers which interfere with fertilization processes also occur in some species (see Potts and Wiltshire 1997 and references therein).

Divergence, hybridization and introgression are active processes that are ongoing amongst the eucalypts. Although there is no definitive evidence that ongoing speciation is occurring amongst the eucalypts at the present time, these mechanisms may be of major importance in contributing to the wide genetic variation observed amongst eucalypt populations and species.

Genetic diversity

The overall level of genetic diversity of the eucalypts is high (Moran 1992). Similar high levels of genetic diversity are common among many widespread tree species (see Potts and Wiltshire 1997). The average percentage of genetic diversity between populations for eucalypts has been estimated at more than twice the average diversity for both wind-pollinated conifers and wind-pollinated angiosperms in the northern hemisphere (Moran 1992). This difference appears to be consistent with taxa that have animal pollination and poor seed dispersal and which show increased genetic differentiation between populations (see Potts and Wiltshire 1997). Eucalypts also exhibit high levels of genetic diversity within populations, comparable with gymnosperms and other long-lived woody perennials (see Potts and Wiltshire 1997).

The eucalypts themselves vary widely in terms of overall levels and distribution of genetic diversity. Widespread eucalypt species tend to have greater levels of between- and within-population genetic diversity compared with more localised species (Potts and Wiltshire 1997). Genetic diversity between populations tends to be higher in species with disjunct distributions compared with those with continuous distributions. This may be due to increased genetic differentiation in populations which are smaller and have been isolated over long time periods (Moran 1992). Populations of some rare species have also been shown to be genetically depauperate (see Crisp 1988, Potts and Wiltshire 1997). The relationship between genetic diversity within eucalypt populations and population size is not clear, with some studies showing a correlation, but others showing no relationship (see Potts and Wiltshire 1997). There is also no indication that populations that are outliers in the distribution of eucalypt species have reduced genetic diversity compared with those located centrally.

***Contribution to outstanding universal value*: Evolutionary relationships and processes**

The evolution of the eucalypts in Australia is reflected in the phylogenetic relationships among and within the main eucalypt groups. These groups appear to reflect ancient branches of the eucalypt family tree and they are central to the story of the evolution of the eucalypts on the Australian continent, contributing to its outstanding universal value.

The current biogeographic distributions of the main eucalypt groups are also important in shedding light on aspects of the evolution and historical biogeography of the eucalypts. The larger of these groups have predominantly northern, southern or widespread distributions, probably resulting from different evolutionary pathways and historical constraints.

Sites of co-occurrence of the main groups and also of particular taxa that are basal on the main branches of the evolutionary tree of the eucalypts are likely to represent important, relictual sites associated with ancient biogeographic distributions. The restriction of certain taxa to the west or to the east in the southern parts of the continent is also thought to be important in representing aspects of past biogeographic distributions of the eucalypts. These and other disjunct aspects of distribution may also be important in reflecting the impact of changes in climate and environmental conditions resulting in long-term isolation of taxa in different parts of the continent and their subsequent evolutionary divergence to form distinctive components of the present-day flora.

The eucalypts have a high level of genetic diversity and also exhibit a range of active processes for increasing genetic diversity, including divergence, hybridisation and introgression. These processes may be important in the continuing evolution of the eucalypts, although there is, as yet, no definitive evidence that speciation is occurring under present-day conditions.

Eucalypts have been described as globally outstanding in an evolutionary context in relation to their wide and rapid radiation, adaptation, and hybridisation (Costin 1989, p. 16). It is likely that the high levels of genetic diversity of the eucalypts have been crucial in their evolutionary diversification and the success of their geographic expansion to dominate a wide range of environments across the entire continent.

Taxonomic diversity of the eucalypts

The eucalypts are highly diversified (Pryor and Johnson 1971), currently including more than 700 species (Brooker and Kleinig 1994). The species are distributed amongst the major eucalypt groups as follows: *Angophora* (11-13 species); *Corymbia* gen.nov (102+ species) and *Eucalyptus sensu stricto* (600 species) (see Ladiges 1997, Table 2.1, pp. 18-19). All but four of these species occur in Australia.

Although the overall taxonomic differentiation amongst the eucalypts is very high, there are other taxa world-wide of dominant woody genera with similar or higher levels of taxonomic diversity. Amongst these other large genera of dominant woody species, *Acacia* has an estimated 1200 species world-wide, including about 900 species in Australia, *Ficus* includes 750 species (although not all of these are either dominant or woody species), *Quercus* has 400 species, *Salix* includes 400 species, *Shorea* includes 357 species, *Dipterocarpus* includes 69 species, and *Pinus* has 93 species (Mabberley 1997).

An unusual feature of the eucalypts is related to the fact that they represent a large taxonomic group of woody dominants which has diverged almost entirely on a single continent. Although *Acacia* is more taxonomically diverse than the eucalypts and also has more species within Australia, particularly including the phyllodinous species (those with leaves reduced to expanded petioles, or phyllodes), the genus has a much wider distribution globally than the eucalypts. With the possible exception of *Dipterocarpus*, other taxonomically-diverse dominant woody genera also tend to have much wider distributions globally (see Mabberley 1997).

The Australian autochthonous flora has been described as "predominantly temperate and arid-adapted, showing massive evolutionary diversification from the more labile of the ancestral Gondwanan stocks and characterised by scleromorphy and high endemism" (Barlow 1981, p. 44). The eucalypts are an exemplar of these aspects of the autochthonous flora, exhibiting very high levels of evolutionary diversification, development of scleromorphy and high levels of regional endemism within the Australian continent. Their extraordinary taxonomic diversity has resulted from this “massive” evolutionary diversification (Barlow 1981).

Eucalypt-dominated vegetation exhibits relatively high levels of diversity of eucalypt species. In general, the richness of eucalypt species within particular community samples, called within-habitat or "alpha" diversity (see Whittaker 1975), is variable and often low. The alpha diversity of eucalypts depends strongly on habitat type. In contrast, the degree of change in species composition of eucalypts along an environmental gradient, called between-habitat or "beta" diversity (see Whittaker 1975), is often high. The diversity of eucalypts in a region, called "gamma" diversity (see Kikkawa 1986), is therefore often high due to the high levels of alpha or beta diversity (or both) (see Wardell-Johnson *et al.* 1997).

Some regions of the continent display exceptionally high gamma diversity for eucalypts. For example, Beadle (1981) noted that the areas of greatest eucalypt species diversity on the continent include eastern New South Wales, and semi-arid to arid parts of southwestern Western Australia. Studies by Gill *et al.* (1985) and Kelly and Robson (1993) (based on analyses of records for eucalypt taxa recorded per 1:250,000 mapsheet, or per 1° latitude and longitude grid cell) identified three regions, including the east and southeast of the continent, the southwest of the continent extending into semi-arid regions, and the north and northeast of the continent, as having exceptionally high species diversity of eucalypts (see Gill *et al.* 1985, Table 2, p. 4 and Figure 2, p. 5; Kelly and Robson 1993, Map 7). The following summaries of eucalypt diversity for these three regions is largely derived from Wardell-Johnson *et al.* (1997) with reference to Gill *et al.* (1985).

The southeast of the continent, and particularly the sub-coastal region of central New South Wales including the Blue Mountains area, has one of the highest regional diversities for eucalypts of any part of the continent. For example, Gill *et al.* (1985) recorded 220 taxa with 111 endemic for the broader southeast region. Wardell-Johnson *et al.* (1997) recorded 84 taxa with 13 endemics for the sub-coastal region of central New South Wales bounded by the Hunter River valley to the north, the Blue Mountains area to the west and the Shoalhaven River area to the south. This area includes part of three biogeographic regions defined by Thackway and Cresswell (1995) including the Sydney Basin, the Southeast Corner and the East Coast and Ranges. Rates of eucalypt species changeover across the landscape (beta diversity) are particularly high for this region due to its topographic complexity and high levels of environmental heterogeneity, which result in a complex mosaic of habitats and environmental gradients.

The southwest region of the continent also displays exceptionally high gamma diversity for eucalypt species. Gill *et al.* (1985) recorded 223 eucalypt taxa for the broader southwest region, including 167 taxa and 75 endemics for the inland part which extends into the semi-arid and arid zones, and 56 taxa and 5 endemics for the far southwest corner extending from Albany to Perth. Wardell-Johnson *et al.* (1997) recorded 101 taxa with 31 endemics for the southwest corner of this broader region, defined by the Swan Coastal Plain, Jarrah Forest and Warren biogeographic regions of Thackway and Cresswell (1995). Heterogeneity of soil types rather than topographic factors is thought to be an important factor contributing to the high diversity of eucalypts in this region, resulting in a complex spatial mosaics of habitats. This complexity is reflected in the distribution of eucalypt species which include many endemic species and also some taxa that are largely peripheral to the region. The high regional diversity of eucalypts for the broader southwest of the continent occurs despite the fact that large parts of the region are dominated by vegetation which has relatively low diversities of eucalypts, such as the jarrah forest areas (see Bell and Heddle 1989).

The northeast of the continent is another region with high gamma diversity for the eucalypts. For example, Gill *et al.* (1985) recorded 130 eucalypt taxa with 31 endemics for the broader northeast part of the continent. Wardell-Johnson *et al.* (1997) recorded 65 taxa with 5 endemics for the central part of this region, defined as including parts of five of the biogeographic regions of Thackway and Cresswell (1995): the Wet Tropical Coast in the north, the Einasleigh Uplands in the west, the Brigalow Belt in the southeast, the Central Mackay Coast in the far southeast and the Desert Uplands in the far southwest. A combination of varied topographic features and climatic conditions has resulted in the wide range of habitats and high number of eucalypt species recorded for the northeast. These high levels of variation in habitat factors across the region are also associated with a high beta diversity for the eucalypts (Wardell-Johnson *et al.* 1997).

Factors that contribute to the exceptional diversity of each of these three regions include large numbers of eucalypt hybrids, endemics and rare species as well as the high levels of species diversity for particular eucalypt groups associated with each region. The eucalypt groups that contribute substantially to this diversity include: for the southeast - *Monocalyptus* and *Symphyomyrtus* (Section *Maidenaria*); for the southwest - *Symphyomyrtus* (Section *Bisectaria*); and for the northeast - *Corymbia* and *Symphyomyrtus* (Section *Adnataria*). In terms of rare species and endemics, the southwest region has 84 rare taxa and 31 endemic taxa amongst its eucalypt species, compared with 56 rare taxa and 13 endemic taxa for the southeast central region and 39 rare taxa and 5 endemic taxa for the northeast region (Wardell-Johnson *et al.* 1997, Table 5.2, p. 105). Estimates of numbers of hybrid taxa for these regions have also been made by Wardell-Johnson *et al.* (1997); these include 22 hybrid taxa for the southwest region, 74 for the southeast central region and 65 for the northeast region (see Table 5.2, p. 105)

The major eucalypt groups display high diversity, in terms of numbers of groups in a region, in parts of the northeast of the continent. For example, five of the informal subgenera of *Eucalyptus sensu stricto*, *Angophora*, and the two informal subgenera of *Corymbia* are found in the northeast (at Isla Gorge, Queensland). This high northeast diversity for eucalypt groups compares with 4 eucalypt subgenera and *Angophora* in the southeast, and 4 subgenera in the southwest (Wardell-Johnson *et al.* 1997).

Contribution to outstanding universal value: Taxonomic diversity

An important aspect in the evolutionary development of the eucalypts associated with their persistence and geographic expansion on the Australian continent is their extraordinary divergence, forming a monophyletic group of woody, dominant species of very high taxonomic diversity. The diversity of the eucalypts is comparable to the most diverse woody taxa found in the world and is also globally unusual in that it is almost entirely contained within one continent. Taxonomic diversity is an important aspect contributing to the outstanding universal value of the evolution of the eucalypts in Australia.

Places with exceptional regional diversity of eucalypt species are found in the southeast, southwest and northeast of the continent. The high regional diversity of these places results from very high levels of species replacement along environmental gradients, reflecting extraordinary levels of adaptation and evolutionary divergence of the eucalypts across catenae and complex spatial mosaics of changing environmental factors including soils, topography or microclimate. High levels of endemism, rarity, and hybridization, and also the retention of relictual taxa or “living fossils”, are important contributing factors to this exceptional regional diversity.

The outstanding success of the eucalypts in dominating most of the woody vegetation of an entire continent

The fossil record provides evidence of major expansions in the eucalypt component of the vegetation during the Quaternary Period (2.2 million years BP to present) associated with environmental change, particularly drier climates. Expansion of the eucalypts is thought to have been largely at the expense of drier rainforest and Casuarinaceae-dominated vegetation and to have been associated with a general transition to sclerophyll forest and woodland of increasingly open structure (Kershaw *et al.* 1994). The charcoal content of the fossil record is consistent with an increased incidence of fires accompanying the expansion of the eucalypts during this time.

Repeated glacial cycles during the Quaternary resulted in large, relatively rapid shifts in climatic conditions, especially temperature and rainfall. The eucalypts are believed to have persisted in sheltered sites through the cold, dry extremes of the glacial periods, and to have expanded their distribution again during the warmer interglacial periods. Hope (1994) has suggested that increased climatic variability associated with the glacial cycles is likely to have favoured generalists such as the eucalypts over species requiring greater environmental stability.

Repeated expansion and contraction of eucalypt distribution associated with climatic cycles is likely to have contributed to disjunctions in the distributions of eucalypt taxa and the creation of relictual populations, such as those observed amongst the eucalypts today (Wardell-Johnson 1997). Alteration of natural fire regimes by Aborigines is believed to have occurred during the last 50,000 years or more, but the implications of this for past and present composition and structure of Australia's vegetation are unknown (see Hope 1994). It has been suggested that Aboriginal burning may have resulted in an increased incidence of fires which may have favoured the expansion of the eucalypts (Singh *et al.* 1981, Kershaw 1986). The Holocene (the last 10,000 years), which comprises the present interglacial period, has seen the continuing geographic expansion and taxonomic radiation of the eucalypts to dominate most of the woody vegetation of the continent.

At the present time, eucalypts dominate the majority of Australia's woody vegetation, except in the wettest and the driest areas of the continent. Analyses by Gill *et al.* (1985) of herbarium records associated with each of 541 (1:250,000) mapsheets for the Australian continent have demonstrated the presence of eucalypts in 502 mapsheets, or about 93% of the total. The inclusion of eucalypt records made subsequent to the analyses of Gill *et al.* (1985) would, in all probability, confirm the presence of eucalypts associated with every mapsheet for the entire continent (A.M. Gill, M.I.H. Brooker, CSIRO, personal communication). Although herbarium data may amount to only very few records for some of the map sheets, particularly those associated with the arid centre of the continent, the analyses of Gill *et al.* (1985) confirm the present, ubiquitous distribution of the eucalypts throughout the entire Australian continent.

When considered at the continental scale, the distribution of the eucalypts within Australia encompasses an exceptionally broad range of latitudinal, altitudinal and rainfall environments. For example, eucalypts occur throughout both the tropical and the temperate zones, extending across all latitudes and longitudes covered by the continent. Their distribution extends along the rainfall gradient from the high rainfall area associated with the mountain and coastal regions of the continent to its arid interior. Eucalypts also occur along the complete altitudinal sequence from sea-level into the alpine zone (see AUSLIG 1990).

At the wetter margins of the continent, eucalypts dominate most of the woody vegetation with the exception of tropical rainforest and cool-temperate rainforest in the wettest areas. In areas where mean annual rainfall falls below 200 mm, and particularly towards the arid centre of the continent, other woody dominants such as *Acacia* or non-woody taxa such as the hummock grasses or the tussock grasses replace the eucalypts as the dominants in the vegetation. Within the broad environmental range between these extremes, eucalypts are the dominant taxon, spanning an exceptionally-wide diversity of habitats (see Doing 1981, Figure 1.1, pp. 10-11, AUSLIG 1990, p. 9 and p. 14).

Flexibility of response to environmental variation is a feature exhibited by some species of eucalypts (Wardell-Johnson *et al.* 1997). Clinal variation has been shown for a range of phenotypic and genetically-linked characters and across a number of species in relation to environmental gradients such as altitude (see Potts and Wiltshire 1997) and is regarded as relatively common amongst eucalypt species (see Pryor 1976). Genetic variation and adaptation associated with environmental gradients such as topography, soils and climate has also been documented for eucalypt species, and marked genetic differentiation has been shown, even over short distances in response to steep environmental gradients (see Potts and Wiltshire (1997, p. 74).

It should be noted that most eucalypt species are unable to dominate environments characterised by extremes of aridity, low temperature, low light, soil infertility, high salinity or waterlogging (Wardell-Johnson *et al.* 1997). For example, in some of the drier parts of the arid interior of the continent the eucalypts are only a relatively minor component of the vegetation or may be absent. Similarly, while eucalypts dominate at the margins of rainforest vegetation, they are uncommon in the heavily shaded environments under closed rainforest canopies (Kirkpatrick 1997). As well, eucalypts only rarely regenerate within rainforest vegetation except in response to broad-scale disturbance. Eucalypts are also found in vegetation types dominated by non-eucalypt taxa. For example, eucalypts occasionally occur as canopy emergents in rainforest communities, as infrequent shrubs in some vegetation types, and even as prostrate, creeping shrubs in alpine communities (e.g. *E. vernicosa*) and at the seaward margins of some coastal communities.

The capacity of the eucalypts to dominate such a wide range of environments and habitats is not demonstrated by any other taxon in the world, even amongst closely-related ecosystems. For example, sclerophyllous vegetation types comparable to eucalypt-dominated vegetation are found in the Mediterranean regions of Europe, in southern Africa, and on the west coast of the American continents, including California and Chile. Together with regions of eucalypt-dominated vegetation in Australia, these have been classified by Udvardy (1975, 1984) in the "evergreen sclerophyllous forests, scrubs or woodlands biome". This is one of fourteen principal biomes that, together, represent the major types of terrestrial ecosystems on earth. In contrast to eucalypt-dominated vegetation, other vegetation types characteristic of this biome are mostly confined in their distributions to the western or southern margins of continents (Udvardy 1975, Busby 1992). Eucalypt-dominated vegetation is exceptional, even amongst closely-related ecosystems in its wide distribution across an entire continent. There are no other cases in the world of the domination of most of the woody vegetation of an entire continent by a single phylogenetic lineage.

***Outstanding universal value*: Domination of an entire continent**

The geographic expansion and taxonomic radiation of the eucalypts to become an increasingly dominant component of Australia's vegetation has occurred during the past 2 million years or more. The geographic expansion of the eucalypts is thought to have been facilitated by climate changes affecting the Australian continent, particularly the transition to drier climates. Other factors likely to have favoured this increasing dominance of the eucalypts include the widespread soil infertility resulting from previous wetter periods, an increased incidence of fires associated with drier conditions, and climatic instability associated with the glacial cycles during the Quaternary. In very recent times, fire regimes may also have been influenced by Aboriginal use of fire.

Eucalypts are a characteristic feature of most present-day Australian landscapes. They dominate most of the woody vegetation on the continent. Their distribution extends throughout the tropical and temperate zones, from the wetter fringes of the margins of the continent to its arid interior, and from sea-level to the alpine zone. Within this broad range of environments the eucalypts also span an unusually wide diversity of habitats associated with their exceptional flexibility in coping with environmental change and habitat variation.

Domination of the majority of the environments of an entire continent by a single phylogenetic group, as exemplified by the eucalypts in Australia, is unique in a global context and the eucalypts have become universally associated with Australia and its landscapes. The differentiation amongst eucalypts that underpins this dominance by a single taxon is also exceptional, and is probably unparalleled amongst other dominant woody plant taxa in the world.

The diverse range of growth forms expressed by the eucalypts

As a group, the eucalypts include an unusually wide range of growth forms, varying from the world's tallest hardwood trees to prostrate shrubs and spanning a height range of more than two orders of magnitude (<1 m to >100 m). Individual species also exhibit exceptional flexibility in their growth responses and are capable of adopting a wide range of growth forms depending on habitat conditions. For example, the same species (e.g. *Eucalyptus obliqua*) may occur as a tall forest tree in favourable habitats, but also exist nearby as a low shrub in response to unfavourable habitat conditions. Ground-creeping or procumbent forms of some eucalypts also occur; for example, at the seaward edges of coastal communities in Western Australia (M.I.H. Brooker, CSIRO, personal communication).

Certain species of eucalypts can attain great size in response to the high rainfall conditions and the deep, relatively fertile soils of the continent's most resource-rich environments. These exceptional species constitute the tall open eucalypt forests of Australia. They have been described as the "supreme expression of the genus *Eucalyptus sensu lato.*" (Ashton 1981a). One of the dominant species of the tall forests in the southeast of the continent, mountain ash (*Eucalyptus regnans*), has been documented as including the tallest hardwood trees in the world with recorded heights exceeding 100 metres (Penfold and Willis 1961, Mabberley 1997). For example, in the last century a specimen of mountain ash was recorded as reaching 110 metres (Hardy 1935). Other eucalypt species that attain exceptional heights include alpine ash (*Eucalyptus delegatensis*), manna gum (*E. viminalis*) which occurs in the southeast, and karri (*E. diversicolor*) which occurs in the southwest of the continent.

Under adverse conditions, many eucalypt species can adopt a low, multi-stemmed habit known as "mallee". The mallee growth habit is characterised by multiple stems arising from a partly buried, woody organ called a "lignotuber" (Kerr 1925). In some species, the mallee habit is characteristically expressed as the adult life form, in others it is adopted opportunistically. Mallee eucalypts range in structure from larger forms with few stems and heights of up to 9 metres or more (bull mallees) to dwarf forms with many stems of only one to several metres in height (whipstick mallees) (see Parsons 1981, Wardell-Johnson *et al.* 1997).

In non-mallee species, the lignotuber is important during the seedling stages, but is not retained in the adult tree except under exceptionally adverse conditions. In the latter case, these non-mallee species adopt the mallee habit. Some eucalypt species do not have the capacity to develop a lignotuber; for example, some of the "ash" species in the subgenus *Monocalyptus*. Other species, known as "marlocks" (Burbidge 1952), occur as single-stemmed, low growth forms in which the lignotuber is absent or only poorly developed (Parsons 1981).

Eucalypts generally occupy the tallest stratum of the vegetation in which they occur, constituting the main canopy species. In many vegetation types, they dominate the canopy exclusively. Non-dominant eucalypt species may also occur occasionally as understorey species, although this is relatively rare. Usually, eucalypt species present in the understorey are also the canopy dominants of the community (Kirkpatrick 1997).

The wide structural variation that occurs in eucalypt-dominated vegetation can be interpreted as forming a continuum, reflecting the response of the vegetation to gradients of resource availability or environmental factors such as altitude. The major structural characteristics (height and canopy density) of eucalypt-dominated vegetation are determined by this response to environment. As a general rule, eucalypt-dominated vegetation becomes progressively shorter in stature and has a more open canopy structure as environmental conditions become less favourable, for example due to low rainfall, high altitude, high salinity, waterlogged soils.

The structural continuum of eucalypt-dominated vegetation in Australia therefore extends from the world's tallest hardwood forests (see Ashton 1981a) to low, multi-stemmed mallee (see Parsons 1981). The tall open forests at one extreme of this structural continuum form a discontinuous arc extending from southern Queensland (latitude 25° S) to southern Tasmania (latitude 42° S) to southwest Western Australia (latitude 35° S) (Ashton 1981a). Shrublands dominated by mallee eucalypts at the other end of the structural continuum are typical of Australia's semi-arid environments, particularly those regions with a Mediterranean-type climate on the southern, eastern and western margins of the arid centre of the continent. Mallees are also found in other regions of the continent, including throughout the arid zone. As well, there are outliers of mallee species in the higher rainfall zones; these usually occur as isolated patches interspersed amongst other vegetation types. These mallee outliers are often associated with infertile soils or other adverse environmental conditions. It has been suggested that the mallee outliers may be relictual, reflecting a former, wider distribution of this vegetation type (Hope 1994).

The jarrah forest in south-west Western Australia is a unique example of a tall open forest in a region with a Mediterranean-type climate (Dell and Havel 1989). Elsewhere in the world, these areas are dominated by sclerophyllous shrub-dominated communities.

Structural growth forms intermediate between the extremes of tall open forest and low mallee shrublands are defined on the basis of height and percentage foliage cover, and include various categories of open forest, woodland and shrubland (see Table 4, also Specht 1970, Carnahan 1976, AUSLIG 1990, National Forest Inventory 1998). These intermediate structural forms constitute the majority of Australia's eucalypt-dominated vegetation, which occurs throughout the north, east, southeast and southwest regions of the continent (see AUSLIG 1990, map p. 14).

The structural continuum evident in eucalypt-dominated vegetation is most pronounced amongst the altitudinal sequences that run almost unbroken from near sea-level on the east coast to the alpine areas of the Great Divide in the south-east of the continent. The structural continuum is also starkly evident along the gradients of decreasing rainfall and increasing evapotranspiration that extend inland from the coastal and mountain regions at the margins of the continent towards the arid regions at its centre.

<u>Outstanding universal value</u>: Diverse range of growth forms

The eucalypts exhibit a globally-outstanding variety of growth forms, ranging from the world's tallest hardwood trees to procumbent or ground-creeping shrubs. The existence of such a broad range of growth forms, spanning two orders of magnitude in height, is exceptional within a single phylogenetic group of woody taxa. The wide diversity of these growth forms is also expressed to a large extent within some individual species (e.g. *Eucalyptus obliqua*) as well as amongst the phylogenetic group as a whole.

Eucalypt forests include the world's tallest angiosperms or flowering plants, *Eucalyptus regnans, E. delegatensis* and *E. viminalis* in the southeast and *E. diversicolor* in the southwest of the continent. Under adverse conditions, a low, multi-stemmed shrub habit called "mallee" is commonly adopted. Procumbent shrub forms can also occur in extreme alpine and coastal environments. A large range of growth forms occurs between these extremes of tall forests and low shrublands.

This unusual flexibility of growth form means that eucalypt-dominated vegetation forms a structural continuum of varying height and canopy density in response to environmental variation in many parts of the continent. This structural continuum is best expressed along the altitudinal gradients which extend from near sealevel to the alpine zone in the southeast of the continent, and along the rainfall gradients that extend from the wetter margins towards the arid centre of the continent.

The wide diversity of eucalypt-dominated communities

The eucalypt overstorey

Overviews of the phytogeography of Australian vegetation at the scale of the continent have included various descriptions of the major vegetation types and their distribution (see Specht *et al.* 1974, Carnahan 1976, Beard 1980, Beadle 1981, Groves 1981, 1994, Bridgewater 1987, AUSLIG 1990 and Specht *et al.* 1995). The majority of these have been based on classifications using structural classes of the vegetation, with secondary reliance on floristic information related to the overstorey, including eucalypt species assemblages (or associations). Others (for example, Beadle 1981) have placed more emphasis on biogeographic regions and floristic alliances with secondary emphasis on structural classes and habitat factors. Limited consideration, or none, has been given to the understorey in most continental-scale descriptions of Australian vegetation and its phytogeography. Brief summaries of three descriptions, from Beadle (1981), Groves (1981, 1994) and Bridgewater (1987), for eucalypt-dominated vegetation are included in Attachment 6.

The phytogeography of the genus *Eucalyptus sensu lato* has also been examined by Gill *et al.* (1985) using an explicit approach based on the Australian Map Grid 1:250,000 mapsheet series. Available herbarium records for the occurrence of eucalypt species were aggregated for each cell of the 1.0 º latitude x 1.5 º longitude mapgrid covering the entire continent. Quantitative pattern analysis techniques were used to identify and map patterns in the distribution of similar taxa using the grid cells. This approach allowed areas with similar species (defined as "zones"), areas with species that tend to co-occur and therefore have similar distribution ("taxon groups"), and areas with similar taxon density (number of taxa per grid cell) at the species and subgeneric level to be identified at the scale of the continent (Gill *et al.* 1985).

Eleven major zones each characterised by particular assemblages of eucalypt species were recognised by Gill *et al.* (1985). These occupied 95% of the area of distribution of *Eucalyptus sensu lato* in Australia. The largest zone (zone A) comprised the central arid regions of the continent. Other major zones were located around the northern, eastern and southern margins of the arid zone. The largest of these were the northern zone (zone C), the northeastern zone (zone D), two south-eastern zones including a northerly (zone O) and southerly zone (zone P), a southern zone extending across the continent (zone (I) and two larger south-western zones (zone K and zone L). The remaining zones occupied much smaller areas and were predominantly in the south-east and south-west of the continent (Gill *et al.* 1985, Figure 2).

Twenty-five taxon groups of co-occurring species were also identified. The taxon groups ranged in numbers of species from 101 (group a) to 1 (groups f, k, y). The taxon groups could be divided broadly into those with predominantly northern (group a), eastern (groups m, n), north-eastern (group d), central-eastern (groups e, f, l, u, v, w), south-eastern (groups b, c, o, p, q, r, s, t, x, y) and south-western (groups g, h, i, j, k) distributions. A detailed summary of the taxon groups is available in Gill *et al.* (1985, Figure 4 and Appendix 4).

Relationships between patterns in the distribution of eucalypt vegetation described by Beadle (1981), Groves (1981, 1994), Bridgewater (1987) and Gill *et al.* (1985) are summarised in Table 3. Within the context of the major biogeographical regions of the continent identified by Beadle (1981), a broad correspondence is evident between the patterns in eucalypt vegetation described in these different studies (see Table 3). At the broadest level, the general continental-scale pattern in eucalypt distribution corresponds to the tropical wetter areas in the north, the temperate wetter areas in the south, east and west, and the drier areas in the centre. At a finer scale, it is evident that major differences occur between the east and west regions in the south, separated by the drier centre of the continent. The far northeast region also has greater affinity to the east coast than to the wet-dry tropics region which extends across the top of the continent. The pattern of eucalypt distribution down the east coast can be differentiated into northern, central and southern components.

Within these broad biogeographic patterns of eucalypt distribution, an exceptionally wide diversity of eucalypt communities can be delineated, representing the extraordinary structural and floristic variation of this vegetation. For example, in their recent assessment of the conservation status of plant communities in Australia, Specht *et al.* (1995) identified a total of 297 major and minor communities for eucalypt open forest and woodland overstoreys and 62 major and minor communities for mallee open-scrub within 17 biogeographic regions across the continent (Specht *et al.* 1995, Table 3, p. 8).

It should be noted that the identification of pattern in vegetation, and therefore the identification of eucalypt communities within the vegetation, is study-dependent. The actual patterns identified depend upon a range of factors including scale of resolution, attributes used for description, availability of data, types of classification or other methods used, and subjective interpretation. For example, in comparison with Specht *et al.* (1995), Beadle (1981) identified 89 vegetation alliances containing a further 63 suballiances within the eight broad biogeographic groupings to describe eucalypt-dominated vegetation across the continent. In other studies, AUSLIG (1990) used 57 groups of eucalypt vegetation types within nine broad structural classes to describe and map eucalypt-dominated vegetation. Similarly, Bridgewater (1987) used 16 classes of eucalypts (based on *Angophora* and the informal subgenera within

Eucalyptus sensu lato) within three broad biogeographic and structural categories for describing broader patterns amongst eucalypt-dominated vegetation.

The wide variation in eucalypt vegetation is particularly evident at regional and local scales and may involve patterns of considerable complexity at these scales. As discussed previously, the eucalypts show exceptional diversity in terms of their responses to environmental variation and this often results in both a high alpha diversity and a high beta diversity. For example, the open forests of the southeast of the continent can exhibit very high species diversity in some parts, with up to 10 eucalypt species per hectare recorded for some areas, and also with a very high species turnover across the landscape (see Wardell-Johnson *et al.* 1997). These changes in eucalypt species composition can occur over relatively short distances, depending on the steepness of environmental gradients. Marked structural changes over short distances also occur in response to changing environmental conditions. The effect of these can have a major influence on the structural and floristic composition of the eucalypt overstorey, resulting in highly-complex spatial mosaics of eucalypt communities.

Table 3 Continental-scale patterns in the distribution of eucalypt-dominated vegetation types

Biogeographic regions (Beadle 1981)	**Eucalypt-dominated vegetation types (Beadle 1981)**	**Eucalypt-dominated vegetation types (Groves 1981, 1994)**	**Mapping unit class, & [vegetation types] (Bridgewater (1987)**	**Zones with similar eucalypt taxa (Gill *et al.* 1985)**
Wetter Tropics	Eucalypt communities of the Tropics	Open-forests	Tropical/Subtropical evergreen wooded vegetation [1, 2, 5]	A, C, E, F
		Woodlands		
Eastern Coastal Lowlands (east coast)	Tall eucalypt forest on high fertility soils	Tall open-forests (wet sclerophyll)	Tropical/Subtropical evergreen wooded vegetation [6, 8, 9]	D, O
	Eucalypt forests and woodlands on lower fertility soils	Open-forests	Temperate forests, grasslands and shrubland [21]	O
		Woodlands		
Eastern Inland Lowlands (inland slopes, and northern Great Divide)	Ironbark forests and woodlands	Tall open-forests (river red gum)	Tropical/Subtropical evergreen wooded vegetation [1, 7, 9]	B, C, D, E
	Box woodlands	Woodlands	Temperate forests, grasslands and shrubland [23, 24, 28]	D, I, O, P
Eastern Highlands (southern Great Divide)	Eucalypt communities of cooler climates	Tall open-forests (Wet sclerophyll)	Temperate forests, grasslands and shrubland [26, 28]	O, P
		Open-forests		
		Woodlands		
Tasmania	Eucalypt communities of cooler climates	Tall open-forests (Wet sclerophyll)	Temperate forests, grasslands and shrubland [27, 28]	O, P
		Open-forests		
		Woodlands		
Mallee	Mallee and marlock communities	Scrubs and shrublands	Semi-arid grassland and shrubs [18]	I
			Temperate forests, grasslands and shrubland [22, 28]	I, P
South-western Australia	Eucalypt forests and woodlands of the south-west	Tall open-forests (wet sclerophyll)	Semi-arid grassland and shrubs [18]	I
		Open-forests	Temperate forests, grasslands and shrubland [22, 29, 30]	K, L
		Woodlands		
Semi-arid, Arid	Mallee communities	Scrubs and shrublands	Tropical/Subtropical evergreen wooded vegetation [5, 8]	A, C, D
			Semi-arid grassland and shrubs [18]	I, K,

Understorey vegetation

The understorey component of eucalypt-dominated vegetation also varies widely in response to the extraordinary geographic and environmental range of the eucalypts in Australia. Taller forests often have dense understoreys of one to several layers of shrubs and small trees and, in the wetter areas, often include large numbers of treeferns, ferns and bryophytes. Forests and woodlands of the drier areas and in the north of the continent tend to have simpler shrub understoreys, and sometimes have an understorey of grasses or herbs. Forests and woodlands on poorer soils have predominantly shrubby or heathy, herbaceous or grassy understoreys or sedge understoreys (ie Cyperaceae, Restionaceae). The vegetation typical of mallee understoreys also ranges widely from scleromorphic shrubs, to semi-succulent saltbush, to perennial grasses, including hummock or spinifex grasses.

Examples of major understorey types associated with eucalypt forest, woodland and mallee vegetation are listed in Table 4. These broad understorey types are based on a combination of structural, physiognomic and taxonomic information. They have been derived largely from the descriptions of Australian vegetation in AUSLIG (1990) based on the classification system of Carnahan (1976).

Table 4 Major types of understorey vegetation associated with eucalypt forest, woodland and mallee (derived from AUSLIG 1990)

Understorey	**Overstorey**						
Height range: **Cover range:**	**> 30 m** **30-70%**	**10-30 m** **30-70%**	**< 10 m** **30-70%**	**10- >30 m** **10-30%**	**10-30 m** **<10%**	**<10 m** **<10-30%**	**<5 m** **<10-70%**
Understorey dominants	**Tall open forest**	**Open forest**	**Low open forest**	**Woodland**	**Open woodland**	**Low woodland**	**Mallee shrubland**
rainforest species	•						
broad-leaved shrubs	•						
ferns	•	•					
cycads	•	•					
small-leaved shrubs	•	•	•	•	•	•	•
heath species		•	•	•	•	•	•
sedges		•	•	•	•	•	•
herbs, annual grasses		•	•	•	•	•	•
perennial tussock grasses		•	•	•	•	•	•
perennial hummock grasses				•	•	•	•
semi-succulent saltbushes					•	•	•

Within these broad types, the understorey of eucalypt-dominated vegetation encompasses a wide range of communities. For example, Specht *et al.* (1995) described 110 types of major and minor communities within four broad structural classes for the understoreys of all Australian vegetation. These structural classes, together with the total number of communities recorded in each, were: sclerophyll (heathy) understoreys (21 communities), hummock grass understoreys (20 communities), savanna (grassy) understoreys (39 communities) and forested wetland vegetation (30 communities) (see Specht *et al.* 1995, Table 3, p. 8). A large proportion of the understorey communities described by Specht *et al.* (1995) occur within eucalypt-dominated vegetation.

The understorey component of eucalypt-dominated vegetation is also outstanding in terms of species diversity. With the exception of rainforest (tropical and cool-temperate), alpine and some swamp vegetation and arid-zone communities, the eucalypts dominate most other vegetation throughout the continent. Australia has a high species diversity in the global context with an estimated total of about 25,000 species of native vascular plants; a large proportion of these species occur within the understoreys of eucalypt-dominated communities (see Kirkpatrick 1997), including perhaps as much as 60-70% of the entire vascular flora of the continent.

Eucalypt-dominated vegetation has also been described as including some of the most species-rich understoreys in the world (Kirkpatrick 1997). Examples of species-rich eucalypt-dominated communities include: 93 species of vascular plants in a 128 m^2 sample area in grassy woodlands in Victoria (Lunt (1990); 86 vascular plant species in a 1 x 10 m sample area in grassy woodlands in Tasmania (Kirkpatrick *et al.* 1988); 52 plant species including bryophytes in a 75 x 75 cm sample area in eucalypt-dominated vegetation at Wog Wog in New South Wales (M.P. Austin, CSIRO, personal communication). The understorey of eucalypt-dominated communities can also vary widely in species richness and some extremely species-poor understoreys have been recorded. In one example, as few as 3 species were recorded for sample areas of 100 m^2 in mixed species callidendrous closed-forest with eucalypts emergent over *Nothofagus cunninghamii* in Tasmania (Kirkpatrick 1997).

The relationship between the overstorey and understorey components of eucalypt-dominated vegetation appears to be complex. In some instances, eucalypt species are associated with a wide variety of understorey communities. In other cases, an understorey community may also be associated with a wide range of overstorey dominants. Overall, the available evidence suggests that the extent of correlation between overstorey eucalypt species and understorey species varies between regions and, in many instances, the relationship is either weak or non-existent (Kirkpatrick 1997). In contrast, at the scale of the individual tree, there is often an association between eucalypts and understorey species, with patterns of variation in the understorey clearly dependent on position in relation to the canopy or the root zones of eucalypt trees.

In terms of diversity of understorey communities, eucalypt-dominated vegetation is outstanding compared with any other ecosystem in the world dominated by a single phylogenetic group of woody overstory taxa. The structural diversity of eucalypt understorey communities is also at least as diverse those of other comparable vegetation in the world.

Fauna

A large part of the Australian fauna is taxonomically distinct from the fauna of other continents. This distinctiveness results both from the persistence of ancient elements in the fauna, and also from adaptive radiation and evolutionary change associated with the long period of isolation and environmental change that followed the separation of the continent from Gondwana (see Heatwole 1987). An outstanding example of this distinctiveness relates to the unique character of the mammal component of the Australian fauna. The mammals include the monotremes, of which two of the world's three extant species occur in Australia. They also include the marsupials, a large and diverse group thought to have originated in North or South America and subsequently to have dispersed into Antarctica and Australia where they radiated into a great diversity of different forms rivalling that of placental mammals in other continents (see Heatwole 1987).

The vertebrate fauna of the Australian continent displays high levels of species diversity with 282 species of mammals, including 141 species of marsupials, over 770 species of birds, approximately 750 species of reptiles and about 200 species of amphibians including frogs (DEST 1994). The diversity of the invertebrate fauna of the continent is also high, with overall estimates in the vicinity of 225,000 species, half of which are undescribed and at least one third have yet to be discovered (E. Neilsen 1993 personal communication quoted in DEST 1994). Australian fauna groups with exceptionally high diversity on a global scale include the marsupials, reptiles, ants and cockroaches. For example, the latter two invertebrate groups have been estimated to include about 15 per cent and 12 per cent respectively of the world's taxa for each group (Naumann *et al.* 1991, Groombridge 1992).

The Australian fauna also has very high levels of endemism. For example, overall endemism amongst the mammals is about 82 per cent, including the following levels for the terrestrial groups: monotremes (50%), marsupials (93%), bats (58%), rodents (88%). Levels of endemism amongst the other major vertebrate groups is also high, including: birds (more than 40%), reptiles (89%) and frogs (93%) (see DEST 1994).

A substantial proportion of the Australian fauna is found within eucalypt-dominated ecosystems. Woinarski *et al.* (1997) calculated relative percentage of mammals, birds and reptiles occurring in broad vegetation types in Australia. Eucalypt formations, together with estimates of the proportional representation of the main vertebrate groups in each, included: eucalypt open forest - mammals (20%), birds (19%), reptiles (7.5%); eucalypt woodland - mammals (35%), birds (32.5%), reptiles (29%); and mallee - mammals (2%), birds (2.5%), reptiles (6%) (Figure 13.7, p. 323). To a large extent, the fauna of eucalypt-dominated vegetation can be seen as broadly representative of the Australian fauna as a whole. This results, in part, because of the extraordinary domination by the eucalypts of the majority of woody vegetation communities throughout large parts of the Australian continent. Eucalypt-dominated ecosystems also provide the habitat for many taxa which extend widely in distribution beyond eucalypt vegetation, as well as those with strong association with the eucalypts.

Expansion of the eucalypts to dominate the continent is thought to have influenced the geographic extent of particular elements of the fauna, greatly increasing their opportunities to expand their distributions while restricting the opportunities of others. The elements of the fauna with strong associations with eucalypt-dominated vegetation have been described as "providing much of the ecological distinctiveness of the Australian biota" (Woinarski *et al.* 1997).

In terms of overall species diversity, the vertebrate fauna of eucalypt-dominated vegetation is broadly similar to other, non-eucalypt vegetation in Australia, and is also comparable to vegetation with similar structure to eucalypts on other continents. (Woinarski *et al.* 1997). Exceptions include the species diversity of nectarivorous birds which is higher in Australia compared to other continents and frugivores which are almost absent. Other differences include the absence of large mammals and a higher species diversity for nocturnal mammals in Australia. For some groups, particularly for the mammals and birds, there are generally fewer taxa overall in Australia compared to other continents. Woinarski *et al.* (1997) suggest that the reasons for this and for the relative homogeneity of the vertebrate fauna over large parts of Australia may be associated with the combination of low relief, shallow environmental gradients, and the dominance by the eucalypts of large parts of the continent, resulting in extensive areas of relatively similar environments compared with other countries.

Variation in vertebrate species diversity in eucalypt-dominated vegetation, measured on a regional scale (gamma diversity), is summarised by Woinarski *et al.* (1997, Table 13.1, p. 313). These data, derived from a limited number of the regions, show greatest species diversity on a regional scale for mammals in eastern Australia (113 species, including 53 in the southeast and 68 in the northeast) and northern Australia (59 species). High levels of gamma diversity for reptiles occur in northern Australia (106 species), eastern mallee areas (89 species), the northeast (85 species) and the jarrah forests of the southwest (45 species, see Nichols and Muir 1989). Regions with highest species diversity for frogs included the northeast (31 species), the north (24 species) and the southeast (21 species). Other data show that regional species diversity of birds is greater in the southeast than the southwest of the continent and also Tasmania (Woinarski *et al.* 1997).

The species diversity of the invertebrate fauna of eucalypt-dominated ecosystems at the regional scale is also high (Majer *et al.* 1997). For example, recent estimates indicate that the diversity of canopy arthropods in eucalypt forest is intermediate between the exceptionally high levels characteristic of rainforest and the much lower levels of temperate deciduous forest (Majer *et al.* 1997). As well, the invertebrate fauna of eucalypt vegetation is characterised by the combination of many rare species and only a limited number of species with high abundance (Recher *et al.* 1996).

There is also evidence that there are major differences in the taxonomic composition of the invertebrate fauna of eucalypt canopies compared to temperate forests in the northern hemisphere. In general, eucalypt canopies are dominated by sap-sucking and gall-forming psyllids and leaf-eating beetles, compared with the domination of northern hemisphere trees by sap-sucking aphids and leaf-eating caterpillars (Majer *et al.* 1997).

The distribution of fauna within eucalypt-dominated vegetation varies widely over a range of scales. At broader scales, environmental factors such as latitude, altitude, rainfall, and temperature are important determinants of fauna distribution. In a broad regional context, there is good correspondence between the major zoogeographic regions for vertebrates and the continental distribution of eucalypt forests and woodlands (Schodde and Calaby 1972). This correspondence is thought to reflect the broad influence of climate and also the evolutionary history of the eucalypts and the vertebrate fauna (Woinarski *et al.* 1997). Continental-scale regional patterns may also reflect the influence of isolation and extinction, leading to regional divergence amongst particular groups.

At finer regional and local scales, factors such as topography, disturbance regimes and particularly the fire regime, vegetation communities and structure, and soil characteristics are known to be important. For some groups of fauna, including birds and bats, there is a strong similarity in species composition across a range of eucalypt-dominated vegetation communities. For other groups, particularly arboreal and terrestrial mammals, a rapid species turnover across the landscape is evident in response to change in both the structure and floristic composition of the vegetation. In some cases, there is little similarity in the composition of these fauna groups between adjacent eucalypt communities with different canopy dominants (see Woinarski *et al.* 1997). There may also be marked discontinuities between vertebrate fauna associated with the canopy and fauna associated with the understorey and, in some instances, little or no relationship has been found between the distribution of understorey fauna and the distribution of eucalypt species in the canopy (Gullan and Robinson 1980). At the scale of individual trees, combinations of co-occurring eucalypt species may also play an important role in determining distributions of some fauna groups, particularly invertebrates.

Interactions between eucalypts and the fauna (both vertebrate and invertebrate) are important in influencing or regulating ecological processes in eucalypt-dominated ecosystems. These processes include predator population dynamics, pollination rates, effectiveness of seed dispersal, the success of seedling regeneration, and rates of plant growth, litter turnover, and nutrient cycling (see Woinarski *et al.* 1997, Majer *et al.* 1997).

The majority of studies of vertebrates in eucalypt-dominated vegetation have been concerned with birds and mammals (see Woinarski *et al.* 1997). Specialist vertebrate groups dependent on the eucalypts, for example as a food source, include arboreal mammals and foliage-gleaning and nectarivorous birds (e.g. Keast 1981). Studies in eastern Australia indicate that eucalypt-dominated communities of greatest structural complexity and floristic diversity tend to occur in response to high resource availability, particularly the combination of nutrient-rich soils and higher rainfall (Woinarski *et al.* 1997). These resource-rich sites display a particularly high diversity and species diversity of birds and arboreal mammals. In the case of birds, it has been postulated that abundance of invertebrates may also mediate a link between foliar nutrients and vertebrate abundance (Majer *et al.* 1992).

It should be noted that the relationship between nutrients and the diversity and abundance of fauna is not a simple one. For example, the vertebrate fauna of karri forest in Western Australia does not reflect the relatively higher nutrient status of its soils compared with surrounding laterite or sandy soils. Some nutrient poor sites also display exceptional diversities of vertebrate fauna; for example, associated with an abundance of hypogeal fungi (Johnson 1994), or nectar-rich plant species (Milewski 1986). Diversity of understorey plant species and recent disturbance history may also play important roles in determining diversity and abundance of fauna (Woinarski *et al.* 1997).

Disturbance regimes in eucalypt ecosystems may have a marked effect on the fauna, both directly through mortality, and indirectly through effects on resources, habitat cover and breeding habitat. Many components of the fauna of eucalypt communities show specific adaptations to recurrent disturbances such as fires, enabling them to exploit different stages in the post-disturbance regeneration of the community (Christensen *et al.* 1981, Bridgewater 1987).

The composition and dynamics of the invertebrate fauna of eucalypt-dominated ecosystems is known to vary considerably, both spatially, at a range of scales, and temporally. There is evidence that diversity and abundance of invertebrates in eucalypt communities may be influenced by nutrient levels of the foliage of host plants, as well as other factors such as canopy structure, and leaf biochemistry. For example, the most nutrient-rich sites support vegetation with high levels of foliar nutrients and also include the most diverse and abundant canopy arthropod communities (Majer *et al.* 1997). The eucalypt subgeneric group to which the host tree belongs is another important factor that may influence canopy arthropod composition at the tree scale. At a larger scale, there is also some evidence that invertebrate diversity may be largely independent of the species diversity of the vegetation (Majer *et al.* 1997).

Evolutionary dependencies and co-evolutionary relationships have been shown between the eucalypts and both vertebrate and invertebrate fauna (see Woinarski *et al.* 1997, Majer *et al.* 1997, Landsberg and Cork 1997). For example, the folivores are adapted to cope with the low levels of nitrogen typical of eucalypt leaves, and especially with well-developed chemical defences such as high tannin levels in eucalypt tissues to prevent attack by herbivores. The koala (*Phascolarctos cinereus*) is an outstanding example of a vertebrate species with an evolutionary dependence on eucalypts, adapted as it is to a diet that is almost exclusively confined to eucalypt foliage (Lee and Martin 1988). Common ringtail possums (*Pseudocheirus peregrinus*) and greater gliders (*Petauroides volans*) are also dependent on eucalypt foliage as their main food source (Kavanagh 1984, Pahl 1984, also see Landsberg and Cork 1997).

The mallee moths (Oecophoridae) provide an outstanding example of co-evolution between the eucalypts and the invertebrate fauna. The group as a whole is extremely well adapted to utilise eucalypt foliage as a food source, especially dry leaves which are normally very slow to break down on the forest floor. The mallee moths play an important ecological role in breaking down dry foliage, and thereby in facilitating the recycling of nutrients. For example, of 2000 species examined, 88 per cent were found to feed on eucalypt foliage, and 56 per cent of these on dry eucalypt foliage (Common 1990). Some taxa are further specialized in that they use eucalypt leaf remains in possum and koala faeces (Horak 1994).

***Outstanding universal value*: Wide diversity of eucalypt-dominated communities**

Eucalypt-dominated vegetation encompasses an exceptionally wide diversity of vegetation and fauna communities associated with its distribution throughout the continent. This diversity, defined on the basis of overstorey species, is expressed broadly at the scale of the continent by patterns in eucalypt vegetation which correspond to the major biogeographic zones including tropical wetter areas in the north, temperate wetter areas in the south, east and west, and the drier areas in the centre. With the exception of the drier parts, these areas include the major centres of taxonomic, structural and ecological diversity of the eucalypts and therefore form the main expression of the sub-theme of eucalypt-dominated vegetation in Australia.

Finer scale patterns in the vegetation are evident within these continental-scale zones, dividing the west from the east, and the east into northern, central and southern parts. Further differentiation of eucalypt-dominated communities at finer regional and local scales is recognisable on the basis of structure, physiognomy and taxonomy of both overstorey and understorey vascular plant species. Exceptionally high rates of species change across the landscape, very high species diversity in some areas, marked structural gradients in the vegetation, complex mosaics of environmental factors and a variable relationship between understorey and overstorey all contribute to very high levels of diversity of eucalypt-dominated communities at regional and local scales.

The overall effect at landscape, regional and continental scales is an exceptional diversity of eucalypt-dominated communities that is globally-outstanding, encompassing many hundreds of communities and perhaps as much as 60-70% of the estimated 25,000 species that comprise the vascular flora of the continent.

Eucalypt-dominated vegetation also includes a large proportion of Australia's fauna. The fauna of eucalypt vegetation is broadly representative of the continental fauna as a whole. The eucalypt fauna demonstrates exceptional levels of endemism characteristic of some Australian groups, particularly amongst the marsupials, birds and reptiles. It also displays high levels of diversity for faunal groups, including the marsupials, some of the reptiles, and parts of the invertebrate fauna.

The species diversity of the vertebrate fauna of eucalypt vegetation at regional scales (gamma diversity) is broadly comparable to other vegetation types in Australia, and also to vegetation types on other continents. The invertebrate fauna of eucalypt vegetation demonstrates levels of gamma diversity which are intermediate between the very high levels typical of rainforest vegetation and the relatively low levels that characterise temperate deciduous forests of the northern hemisphere. The invertebrate fauna of eucalypt-dominated vegetation differs markedly in its major functional groups or guilds compared with similar faunas in the northern hemisphere.

Regional differences in species diversity are evident for some vertebrate fauna groups in eucalypt vegetation, with higher gamma diversity for mammals and birds in the eastern regions of the continent and higher gamma diversity for reptiles in north and southeast and southwest.

Distribution of the fauna in eucalypt-dominated vegetation varies widely depending on environmental factors. At the broad, continental scale, there is good correspondence between the vegetation and the vertebrate fauna in terms of bioregional variation. At finer scales, there appears to be less regional variation amongst birds and bats compared with arboreal and terrestrial mammals. Local-scale variation and species turnover across the landscape can be high for the latter groups. Invertebrates also show high levels of distributional variation at fine scales, including marked differences between adjacent canopies involving different eucalypt taxa.

Many fauna groups, such as koalas and the possums, exhibit an evolutionary dependence on the eucalypt component of the vegetation. There is also evidence of substantial co-evolutionary relationships between the eucalypts and some faunal groups; for example, the mallee moths.

The unique ecology of eucalypt-dominated communities

As discussed above, the evolution of the eucalypts is believed to have been influenced by the environmental changes that took place on the Australian continent as it drifted slowly northwards. Factors such as declining soil fertility, increasing climatic variability, periods of aridity, and increases in the incidence and intensity of fires are thought to have had a major influence on the evolutionary development of the eucalypts (Florence 1981). The ecological and evolutionary responses of the eucalypts to these factors are likely to have been important in enabling them to exploit an increasingly-wide range of habitats and environments across the continent over time and, eventually, to dominate most of its woody vegetation communities. The ecology of eucalypt-dominated communities, which encompasses their adaptations to Australia's environments and their interrelationships both amongst themselves and with the other biota that make up these communities is both unique and outstanding in the global context.

An unusual and important feature of the Australian continent is the widespread absence of steep environmental gradients. This feature derives, in part, from the exceptionally low relief of the ancient landforms that dominate much of the continent, and also from the gradually-changing nature of climatic gradients that commonly occur across the landscape. Although there are exceptions, environmental variation over much of Australia tends to occur gradually and over relatively large distances, resulting in large areas of relatively similar or gradually varying environments.

This gradual expression of environmental variation is also manifest in a very gradual transition from closed forest formations typical of the wetter areas to the grassland communities of the drier parts of the continent. The transitional zone between these extremes of the vegetation is particularly broad in Australia, extending over large distances and dominating large parts of the continent. The transitional zone occurs throughout the latitudinal extent of the continent, and also extends over a large part of the range of altitudes, rainfall zones and landscape and soil types. In contrast, landscapes such as those in Indonesia, Timor, Papua New Guinea, and South Africa tend to exhibit relatively sudden transitions between closed forest and grassland associated with much steeper environmental gradients. Keast (1981) has described continental Australia as characteristically "flat, open and dry" compared with New Guinea which is "tropical, largely rain forest covered and with high mountains" (p. 1589). The transitional zone therefore forms a much smaller component of these landscapes compared with Australia.

The eucalypts are the dominant vegetation of the transitional zone between closed forest and treeless vegetation in Australia. The environments that characterise this transitional zone generally have poor soils and are subject to periodic drought and recurrent disturbance, particularly due to fire. The eucalypts exhibit a wide range of ecological and morphological adaptations which have enabled them to persist and to dominate in these types of environments. These adaptations are discussed in the following sections.

Fire regimes

Fire is an important ecological factor which affects the majority of ecosystems in Australia. Described as an ecological "agent of change" (Gill 1997), fire has a wide range of forms, intensities, frequencies and times of occurrence (Gill 1975). The impacts of fire may have a profound influence on the ecology of vegetation communities, both directly through effects on regeneration processes, plant growth and competition, and mortality, and also indirectly, for example, via effects on populations of predators, pathogens and pollinators.

Fires commonly occur in eucalypt-dominated ecosystems in Australia. Gill (1997) commented that “All eucalypt species are subject to fires but the nature, frequency and season of occurrence of those fires varies widely across Australia” (p. 152). This results in part from the exceptionally wide range of environments and habitats dominated by the eucalypts, spanning much of the rainfall gradient of the continent from the wetter coastal fringes to the drier interior, and extending from the tropical northern regions of the continent to the cool-temperate parts of the southeast and southwest. Climate, soil, terrain and vegetation are among the important determinants of fire regimes in eucalypt communities. The influence of these factors is particularly significant in terms of their effect on rates of production of biomass and also on the accumulation and breakdown of litter which acts as fuel for fires (Walker 1981, Gill 1997).

High intensity, summer fires which occur at intervals of up to one to several centuries are typical of the wetter forests in southern parts of the continent (Ashton 1981b). In contrast, dry season fires of low intensity occur every one to several years in the wet-dry tropical savannas of the north (Braithwaite and Estbergs 1985). Fires of high intensity, but with widely-varying intervals and seasonal incidence determined by factors such as productivity, rates of litter accumulation and ignition sources, are more typical of the eucalypt formations of the drier regions (Gill 1997); these include the jarrah forests of the southwest (Abbott and Loneragan 1986, Bell *et al.* 1989). The fire regimes in eucalypt-dominated communities in Australia therefore exhibit an enormous variation throughout the continent (Gill 1997).

Eucalypt fuels

Eucalypts produce large quantities of litter which includes leaves, woody fruits, twigs, small branches and bark. These dead tissues are produced as a result of the natural growth and canopy replacement processes of eucalypts (see Jacobs 1955). Eucalypts demonstrate continual growth of apical buds and also lack the terminal control and pre-determined growth shown by most other woody taxa, contributing to high rates of growth and litter production.

Eucalypt litter is highly flammable and is an important component of the fuels which carry fires in eucalypt-dominated communities. Other types of fuels are also important in eucalypt-dominated communities, including some live fuels associated with shrubs and small trees. The major types of fuel in a eucalypt-dominated community depends on a range of factors associated with its physical environment, particularly climate and soils, and also factors associated with the vegetation, including its structure, and species composition. Variation in the major types of fuel in eucalypt communities has been discussed by Gill (1997). These major fuel types are summarised in Table 5 below.

Table 5 Fuel types in eucalypt-dominated communities (from Gill 1997)

Forest type	Fuel types
northern savannas	- coarse-leaved grasses - eucalypt litter
southern wet forests	- eucalypt litter, - living shrubs and small trees
southern open forests	- eucalypt litter - bark on the stems of eucalypts
southern woodlands	- fine-leaved grasses - eucalypt litter, - living shrubs and small trees
mallee	- eucalypt litter, - living shrubs, - hummock grasses

The dynamics of fuels in selected Australian vegetation types including eucalypt-dominated vegetation has been considered by Walker (1981). He noted that the components of fuel in eucalypt-dominated communities include mainly leaf, twig and branch litter, and also some bark material (Walker 1981). For example, the work of Ashton (1975) showed the litter standing crop in mature *Eucalyptus regnans* forest in southeast Australia was composed of leaves (approximately 23% by weight), bark (13%) and wood (60%) (see Walker 1981, Table 5, p. 110). Leaf fall measured in this *E. regnans* forest was approximately 56% by weight of the annual litter fall per unit area compared to 26% for the non-leafy woody components of the litter (Ashton 1975, Walker 1981)

The importance of branch shedding in the maintenance of the eucalypt crown has been described by Jacobs (1955) who outlined mechanisms that promote the rapidity of this process. These mechanisms are associated with the development of a brittle zone which ensures that lower branches are shed rapidly and at relatively small sizes (up to about 2.5 centimetres diameter). In contrast, for most trees of the world, branch shedding is mediated by indirect factors such as fungal attack and is a much slower process, requiring up to several years before branches become brittle enough to break off. Rapid shedding of smaller branches from the eucalypt canopy therefore is unusual and is an important source of the high proportion of woody material in eucalypt litter.

Bark shedding is also important in contributing to the fuel of many eucalypt-dominated communities. In some species, the old bark is shed in small plates or patches. In other species such as *Eucalyptus viminalis* the bark is shed in long strips. Larger strips of bark in the litter can blow around considerably in high winds, and bark of this type that has been recently shed often represents a significant component of the fuel in some eucalypt communities (Jacobs 1955). Eucalypt bark often has a high phenolic content, contributing to litter accumulation by slower rates of break-down.

The amount of woody material in eucalypt fuel is also influenced by the different residual times of the components of the litter. For example, the half life of leaf litter may be less than one year compared with nearly five years for woody components (Walker 1981). Despite higher proportions of leaf material in annual litter fall, the relative proportion of the woody components of the litter standing crop in eucalypt-dominated communities therefore will tend to increase over time with respect to the non-woody components. As a result, the fuel of eucalypt-dominated vegetation has a relatively high proportion of woody material.

As well as providing a substantial proportion of the fuel in eucalypt communities, woody components of the litter, particularly the branches and larger twigs, also influence the extent of aeration of litter on the forest floor. The presence of branches tends to reduce the extent of packing of leaves and bark remnants, thereby contributing to the presence of many air spaces and a greater overall volume of the litter on the ground surface.

Rapid canopy growth, high rates of production of litter including woody tissues such as small branches, the accumulation of large quantities of litter on the ground and also the presence of dead twigs, woody fruits, bark etc in the canopy together constitute an unusual and characteristic feature of most eucalypt communities. The litter of eucalypt-dominated communities is unusual in the global context, particularly in relation to its high proportion of woody material. In comparison, the litter of most other woody ecosystems comprises most leaf material with some bark components, but fewer twigs and branches.

Long-distance propagation of fire

Fire spread in most cases can be seen as a process of continual ignition due to flame contact with unburnt fuel. The rapid spread of fires can be facilitated by ignitions occurring metres to kilometres ahead of the flame front as a result of burning brands being generated in the flames, lofted by convection, and cast downwind in a process which is called “spotting” (Cheney 1981). The fuel types of eucalypt-dominated communities provide an abundant supply of material for firebrands, especially bark. The eucalypts with loose fibrous bark or stringybark are regarded as having the greatest potential for short-distance spotting (Cheney 1981). In the case of stringybarks, Jacobs (1955) noted that fires tend to run up the fibrous strands of the outer bark and that pieces of the burning bark break off and can blow considerable distances.

Spotting over long distances has been described as a “characteristic unique to eucalypt fires” (Cheney 1981). Long-distance spotting greatly facilitates fire spread. It is typically associated with high intensity fires and commonly occurs in eucalypt communities with species that have bark decorticating in strips or ribbons. Jacobs (1955) described an example of spotting over distances of 24 kilometres (15 miles) due to burning *Eucalyptus pauciflora* (snow gum) bark blowing from the distant ranges into Canberra City during the 1939 fires. Cheney (1981) also noted that long-distance spotting can occur up to 30 kilometres ahead of the main fire in eucalypt vegetation. These characteristics of eucalypt-dominated vegetation that facilitate long-distance propagation of fire are both unique and outstanding in the global context.

Survival and reproduction

Recurrent disturbance is an important factor influencing the ecology of eucalypt-dominated communities. Disturbance may have a profound influence on the dynamics of eucalypt communities through effects on regeneration processes, growth and competition, and mortality. Fire is a common disturbance in eucalypt-dominated vegetation (Gill 1978) although there are other types of disturbance that periodically affect these communities, including insect predator outbreaks (Abbott 1992), drought (Pook 1967), severe frosts (O'Brien *et al.* 1986), and cyclones (Unwin *et al.* 1988).

The major ecological effects of fire on eucalypts are those that influence the survival of individuals, the survival of seeds, dispersal of seeds, production of seeds and the success of regeneration both from seed and also vegetative buds (Gill 1997). There are two basic types of ecological response to fire amongst the eucalypts associated with species that have relatively fire sensitive populations, and species that have relatively fire resistant populations (Gill 1981). Gill (1997) has termed these as "seeders" and "sprouters" respectively (p. 162). Fire sensitivity relates to the capacity of individuals to survive the effects of fire. It is largely determined by the extent to which the tissues essential for growth and vegetative regeneration are protected from fire. Seeders are killed by fires that kill all the leaves and small twigs in the crown, and regeneration is necessarily by seedling establishment. Sprouters are not killed by such fires; regeneration is largely from dormant buds, but sometimes also includes successful seedling establishment.

Eucalypts exhibit a range of characteristics that avoid or moderate the effects of fire, and therefore facilitate survival and reproduction under different fire regimes. In general terms, these characteristics afford protection to buds and other generative tissues, seeds, and stored food reserves. The combination of characteristics may vary markedly between eucalypt communities depending on factors such as the constituent species, type of environment and fire regime (Gill 1997). Characteristics of the eucalypts that are important for survival and reproduction are summarised in the following sections.

The lignotuber

The majority of eucalypts develop a regenerative organ called a "lignotuber" (Kerr 1925). The lignotuber begins to develop during the early seedling stage and forms a swollen, woody structure located at the base of the stem. It contains reserves of dormant buds and food and may be partly buried. With these reserves and its relatively protected position, the lignotuber represents an important mechanism by which the eucalypts are able to persist in difficult environments and to survive disturbances such as those caused by fire (see Jacobs 1955). Lignotuberous species are sprouters (*sensu* Gill 1997); they occur widely in favourable as well as harsh environments.

In most eucalypt tree species, the lignotuber is present in the early, seedling life stages but ceases to develop in the later sapling and adult stages. In these species, the lignotuber is eventually incorporated into the main stem or trunk which continues to grow around it. This is not always the case. Adverse conditions may result in the lignotuber continuing to develop in the later life stages, ensuring its persistence in adult plants. For example, in the mallee growth form typical of eucalypts in adverse environments, the lignotuber reaches its maximum expression as a dominant component of plant form and may attain sizes of up to several metres in diameter.

Rhizomes or root suckers represent another means of vegetation regeneration in eucalypts although this is relatively uncommon. Rhizomatous regeneration has been documented for several eucalypt species in the tropical savanna woodlands of northern Australia (Lacey 1974, Lacey and Whelan 1976, Gillison 1994).

Some eucalypt species do not develop lignotubers or rhizomes at all. These non-lignotuberous species are typically seeders (*sensu* Gill 1997) and have populations that are killed by fires which burn the crown. The majority of these, such as some species in the Ash group of eucalypts, occur in environments characterised by relatively high levels of resource availability and where the probabilities of successful seedling regeneration after fire are likely to be high (see Jacobs 1955). Some non-lignotuberous species also occur in less benign environments; for example, the marlocks and the mallets which occur in dry environments in Western Australia that more commonly support mallee eucalypts.

Lignotubers have been recorded in other plant taxa. For example, Gardner (1957) noted the occurrence of lignotubers in taxa of the families Casuarinaceae, Dilleniaceae, Leguminosae, Proteaceae, Sterculiaceae and Tremandraceae in Australia, but the incidence of lignotubers within these families is much less common than in the eucalypts. Estimates indicate that lignotubers occur in all but forty or so (Pryor and Johnson 1981) of the more than 700 species of eucalypts (Brooker and Kleinig 1994). The development of lignotubers in such a large number of species within one phylogenetic group is highly unusual.

Epicormic growth

The eucalypts have four principal ways of producing leafy shoots, and all are significant in their growth and survival (Jacobs 1955). These include: shoots from naked buds in the leaf axils, shoots from accessory buds, shoots from dormant buds, and shoots from lignotubers. The first two provide the mechanisms for normal canopy growth processes in which the naked buds develop into new growing tips, and the accessory buds provide a backup if the naked buds are lost; for example, due to insect attack or frost damage (Jacobs 1955). As discussed above, the lignotuberous buds also provide an important mechanism for vegetative regeneration available to most eucalypts during the early seedling stage and, for some species growing in adverse environments, in the later sapling and adult stages.

Many species of eucalypts have numerous dormant buds, also called "epicormic" buds (Jacobs 1936). Each dormant bud develops from the accessory bud associated with a leaf. Large numbers of dormant buds occur in each eucalypt tree, usually with one bud for each leaf that has developed during the growth of the tree. After a leaf is lost, its dormant bud persists and continues to grow radially outwards at the same rate as the diameter growth of the stem (Jacobs 1955). The dormant buds are distributed throughout the trunk and branches. They are protected at least to some extent from damage, for example due to fire, by the outer bark layers which are either relatively thick but dead, or thinner, but living and moist. Any death or damage to part of the crown may result in the release of dormancy of a large number of these buds, producing a flush of "epicormic growth". The buds therefore can provide new stems and leaves to replace the old canopy. Release of dormancy and subsequent growth of the epicormic buds is an important mechanism by which eucalypts are able to re-establish their crown following a disturbance which damages the growing tips.

Under low nutrient conditions, epicormic growth may also provide a mechanism for increased turnover of canopy tissues through the continuous processes of canopy growth and dieback, allowing the rapid recycling of nutrients (Florence 1981).

Dormant buds as a mechanism for vegetative regeneration are not uncommon amongst other woody taxa throughout the world. However, when considered in conjunction with lignotuberous buds, the presence of these mechanisms in the majority of the estimated 700 species of eucalypts is both highly significant and unusual. Their combination enables the persistence by vegetative regeneration of the eucalypts in an exceptionally wide range of habitats throughout the continent.

Regeneration from seed

With the possible exception of some woodland communities, eucalypt regeneration from seed is almost always cued by a disturbance, particularly by fire. In the case of seeders, regeneration from seed is an obligate response to fires which kill the canopy since the population becomes dependent on seedlings for its continuing survival (see Gill 1997). For sprouters, regeneration from seed mostly follows a fire, but does not necessarily follow all fires or other disturbances. In many Australian environments, regeneration of eucalypts from seed is a relatively infrequent event, requiring a particular combination of pre- and post-disturbance conditions for its success.

A reliable seed supply and conditions suitable for seedling establishment are prerequisites for regeneration from seed. Eucalypts in southern parts of the continent retain their seeds in woody capsules in the canopy for up to several years. This characteristic protects the seed and ensures a continuous supply of canopy seed store is available for regeneration. In contrast, many eucalypts of the tropical savannas of northern regions, notably the ghost gums, release their seed soon after it is mature (Setterfield and Williams 1996). The wet-dry tropical environments of northern regions are typically subject to fires, often on an annual basis, and also have reliable wet seasons each year, both of which may be important in relation to this phenomenon.

Eucalypt seed is relatively short-lived once dispersed (see Gill 1997). Rapid removal of newly-released seed by predators occurs widely in eucalypt-dominated communities, particularly by seed harvesting ants (see Jacobs 1955, Ashton 1979, Andersen 1982, O'Dowd and Gill 1984, Wellington and Noble 1985), and also by vertebrate predators (Stoneman and Dell 1994). In the case of mallee eucalypts, the half-life of isolated seeds on the soil surface has been estimated to be only about 5 days (Wellington and Noble 1985). Eucalypt seed that escapes predators and becomes stored in the soil apparently does not persist for long periods, with estimated longevities of one year or less (e.g. Grose 1960, Wellington 1989).

A disturbance such as a fire in a eucalypt-dominated community may stimulate the relatively sudden release of all eucalypt canopy seed stores over a period of a few weeks. This phenomenon of mass seed release following fire has been demonstrated for some species of eucalypts in the forests of the south-west of the continent (Christensen 1971, Burrows *et al.* 1990), in the tall eucalypt forests in the wetter parts of the southeast (O'Dowd and Gill 1984) and in mallee shrubland in the drier regions of the southeast (Wellington, unpublished data).

Sudden, large changes in seed availability have been shown to occur in other plant taxa around the world; for example, associated with “mast” flowering years, and the effects of these sudden changes in seed availability in overcoming seed predators has been termed “predator satiation” (Janzen 1971). Mass release of canopy seed stores in response to fire is believed to be an important mechanism enabling some species of eucalypts to overcome the effects of seed predators. This mechanism provides an outstanding example of the way in which plant seed dynamics may interact with disturbance regimes to overcome the effects of predators and thereby maximise opportunities for reproduction from seed.

Seedling establishment

Seedling establishment of eucalypts most commonly follows fire (see Gill 1997) although for some species, such as *Eucalyptus camaldulensis* (river red gum) which occurs in riverine environments, seedling establishment typically follows a flood (Jacobs 1955). Post-fire seedling establishment has been demonstrated for a range of eucalypt-dominated communities in Australia, including eucalypt forests of the southeast (Grose 1960, Ashton 1976, O’Dowd and Gill 1984) and southwest (Abbott and Loneragan 1986), eucalypt woodlands (Withers 1978) and mallee (Wellington 1989).

Effects of fire that are important for seedling establishment include removal of litter which acts as an impediment to seedling growth, particularly in relation to the development of the root system (Jacobs 1955), and the creation of an ashbed (Mott and Groves 1981). The “ashbed effect” (Renbuss *et al.* 1973) promotes rapid germination and seedling growth and has been associated with the effects of heating and the burning of litter and plant tissues. Factors believed to be significant in the ashbed effect include: an increase in nutrient availability due to the addition of ash to the soil (Humphries and Craig 1981), changes in soil conditions that may inhibit seedling growth (Florence and Crocker 1962), changes in the presence of allelopathic substances (e.g. May and Ash 1990), increases in the wettability of the soil (Wellington 1981), and microbiological changes (Renbuss *et al.* 1973,) which affect populations of pathogens and also of organisms beneficial to seedling growth such as mycorrhizal fungi (see Warcup 1981).

Other important effects of fire in facilitating seedling regeneration may result from changes to the physical and competitive environments faced by seedlings in the early stages. These changes can include reduced competition for water (e.g. Wellington 1984), and increased light levels (Jacobs 1955) and elevated temperatures (Raison *et al.* 1986) at the forest floor associated with the loss of leaves from the canopies of the adult trees.

Adaptation to a wide range of soil nutrient availability and moisture regimes

The wide distribution of the eucalypts in Australia encompasses a diverse range of conditions of soil type, nutrient availability and moisture regimes. The eucalypts demonstrate an extraordinary ability to cope with this range of environmental variation, persisting and growing in severe environments as well as benign, despite limiting nutrient supplies and recurrent periods of high soil and atmospheric water deficit.

A classification of the major Australian soil types has been made by Stace *et al.* (1968). Brief descriptive summaries of the 44 Great Soil Groups for the continent may also be found in Beadle (1981, Table 1.4, pp. 24-29). Some of these Great Soil Groups are very widely distributed and occur over a range of different climatic zones; others are more limited in extent. For example, the distribution of the Red Earths extends from the arid centre to the wet tropics (Beadle 1981). The wetter regions which support eucalypt forests in the southeast, southwest, east and north of the continent encompass a broad range of different soil types reflecting the wide variation in parent materials in these areas. The majority of the soils are highly leached. Soils of the drier areas associated with eucalypt woodlands and shrubland are also very diverse. The majority of these are formed from fine to medium textured alluvial parent materials, and many show incomplete leaching. Soils of the mallee regions also include large areas of aeolian dunes, often with a high calcareous content (see Keith 1997).

Australian soils generally have a low to very low nutrient status on a world scale, especially in terms of their concentrations of organic carbon (C), nitrogen (N) and phosphorus (P) (Beadle 1981). Areas with soils of moderate to high nutrient status also occur in Australia but these are of relatively limited extent. They are usually associated with areas of recent geological activity, such as the basaltic soils derived from volcanic activity in the east of the continent, particularly on the Great Divide (see Beadle 1981, Keith 1997). The very low nutrient status of Australian soils is associated with the great age of the majority of the landscapes, a long-term absence of geological activity leading to soil rejuvenation (see Keith 1997), and the extensive leaching and laterization (Wild 1958, Prider 1966) and repeated cycles of weathering and erosion (Stewart 1959) that have affected many soils. Phosphorus, which has an average concentration of about 0.03% (Keith 1997) but ranges down to 0.003% (e.g. Mulligan and Patrick 1985), was regarded by Beadle (1981) as the most important limiting element in Australian soils. These concentrations are low in comparison to other soils in the world; for example, North American soils exhibit a range for P of 0.04 to 0.09% (Wild 1958).

The ability to cope with wide variations in soil properties is an unusual feature of the eucalypts (see Beadle 1981, Keith 1997). Individual species vary considerably in their response to soil nutrient status; some are limited to relatively fertile soils but many demonstrate remarkable tolerances to low nutrients. Under conditions of high nutrient supply associated with fertile soils, many eucalypt species demonstrate high growth rates. Reduction in growth rate is an important mechanism allowing eucalypts to reduce nutrient requirements and therefore to persist on relatively infertile soils. Most eucalypts show a capacity to respond to low nutrient conditions by reducing their growth rate, even among species which are potentially fast growing (Mulligan and Patrick 1985).

Extreme soil properties such as high calcareous content, acidity, large concentrations of salt or amounts of certain elements such as aluminium (Al), molybdenum (Mo) and manganese (Mn), or the presence of a lateritic duricrust are also important factors limiting the distribution of many eucalypts. In most situations, however, there are species able to tolerate even these conditions and therefore exploit these more extreme environments. Examples include: *Eucalyptus saligna* which can tolerate highly acidic soils and Mn concentrations toxic to many other eucalypt species (Winterhalder 1963); species such as *E. microtheca* which are able to grow on highly calcareous soils that few other species can tolerate (Eldridge *et al.* 1993); *E. camaldulensis* which includes ecotypes that have an unusual tolerance to high salinity; and *E. marginata* which is able to thrive on duricrusts, persisting in a lignotuberous form with a minimum of above-ground development (Dell and Havel 1989) until its roots are able to penetrate to the deeper soils via channels in the duricrust (Abbott *et al.* 1989, Schofield *et al.* 1989), contrasting markedly with species such as *E. diversicolor* which is unable to persist in areas where the duricrust is intact (McArthur and Clifton 1975) (also see Keith 1997).

Moisture regimes across the continent vary widely. A large part of the continent (over one third), including the arid central regions, receives less than 250 mm mean annual rainfall. The extensive semi-arid regions surrounding the arid centre receive up to 500 mm mean annual rainfall. The humid areas towards the northern, eastern and southern margins of the continent receive in excess of 500 mm. Moisture regimes are also influenced by rainfall seasonality, particularly the extreme seasonality in the wetter areas (Fitzpatrick and Nix 1970). In general, seasonal rainfall patterns vary with latitude, with summer rainfall predominating throughout the northern regions and winter rainfall in southern regions. Average moisture index values mapped for the continent for both summer and winter clearly demonstrate this strong seasonality (see Fitzpatrick and Nix 1970, Figure 1.7, p. 13 and Figure 1.8, p. 14). Coastal and montane areas tend to exhibit a more even seasonal distribution of rainfall (see Beadle 1981). Rainfall variability is very high for most areas of the continent and tends to increase as mean annual rainfall decreases towards the centre of the continent (Beadle 1981).

Eucalypts are found in most rainfall environments throughout the continent except for extreme environments, which include the driest parts of the arid regions of the centre and also areas of permanent inundation such as swamps. Many eucalypts are able to persist and grow in areas with pronounced seasonal drought and also in areas with low mean annual rainfall. The majority of eucalypts also have to cope with drought periods associated with the high variability of annual rainfall experienced in many parts of the continent.

The ability of the eucalypts to cope with soil water deficits that develop in these situations is directly dependent on their capacity either to tolerate or avoid the onset of high plant water deficits (Stoneman 1994). In general, the eucalypts postpone development of high plant water deficits via a range of mechanisms to maintain turgor (the normal state of the cells resulting from pressure of the cell contents against the cell wall). These involve either maintaining water uptake through changes to the root system, reducing water losses by changes in leaf function or form, or slowing water losses by increasing solute concentrations in a process known as osmotic adjustment. A recent review of these mechanisms may be found in Stoneman (1994).

Important adaptations exhibited by the eucalypts that enable them to maintain water uptake by the root system include: the capacity to develop deep root systems (Gibson *et al.* 1994) which is particularly pronounced in species from drier environments; development of higher root/shoot ratios in drier environments (Zimmer and Grose 1958); and flexibility of growth response resulting in the capacity to reduce shoot growth in response to increasing water deficits, effectively increasing the root/shoot ratio (Pereira and Kozlowski 1976, Stoneman 1994). The exceptional ability of the eucalypts as water scavengers is evident in some overseas plantings, for example in India, where they have been observed to lower the water table, causing wells, springs and marshes to dry out.

The eucalypts also exhibit a range of mechanisms to reduce leaf water losses associated with photosynthesis and leaf temperature regulation. These mechanisms may involve variations in physiological response including reduction in stomatal conductance in response to increasing plant water deficit or to high vapour pressure deficits, and diurnal patterns of midday depression or decreasing stomatal conductance (see Stoneman 1994). Leaf orientation may also be important in avoiding temperature effects due to insolation in the hotter periods of the middle of the day, with the majority of eucalypts having a predominantly vertical orientation of adult leaves (Jacobs 1955), and some also demonstrating passive leaf movement associated with increased verticality due to leaf wilting (Stoneman 1994).

Other mechanisms of the eucalypts to reduce water losses involve reducing leaf area either through flexibility of growth response and the slowing of growth rates, or by producing smaller leaves. Leaf shed is a common mechanism which rapidly reduces leaf area at the onset of higher plant water deficits. Osmotic adjustment is also an important mechanism shown to occur commonly amongst the eucalypts which enables them to maintain the turgor necessary for normal physiological function despite increased plant water deficits. As well, some eucalypts have been found to be able to increase the elasticity of cell walls formed during drier conditions, effectively postponing dehydration by decreasing the amount of water that will be lost per unit plant water deficit for those cells (see Stoneman 1994).

In summary, the eucalypts display an extraordinary capacity to survive and grow under a wide range of soil types, soil nutrient conditions and moisture regimes. This very wide ecological amplitude within a single phylogenetic group of vegetation dominants is outstanding in the global context.

Adaptation to low nutrients

The eucalypts also demonstrate an exceptional ability to maintain high growth rates under a wide range of soil nutrient conditions, and to develop large biomass even under the low nutrient conditions associated with of many Australian soils (see Bowen 1981, Hingston *et al.* 1989, Keith 1997). Adaptations that enable the eucalypts to maintain high growth rates despite conditions of low nutrient availability rely primarily on enhancement of nutrient uptake or efficient nutrient recycling. In extreme situations, however, nutrient limitations also have a marked influence on eucalypt productivity and species distribution despite these adaptations.

Mechanisms that enable eucalypts to increase nutrient uptake involve the development of root characteristics that increase efficiency of uptake. As discussed in relation to moisture regimes, most eucalypts develop large root systems. As well, the eucalypt root system includes a much higher proportion of finer roots and well-developed root hairs compared with many other species, maximizing the surface area available for nutrient uptake per unit investment of root biomass (e.g. Barrow 1977). Symbiotic associations between eucalypt roots and mycorrhizal fungi are a major mechanism enabling many eucalypts to enhance absorption of nutrients from the soil (Bowen 1981). Some eucalypt species also have adaptations enabling them to extract nutrients that are generally unavailable to non-eucalypts, for example, by extracting P from insoluble aluminium and iron phosphates (Mullette *et al.* 1974).

Flexible response of the eucalypts to temporal variation in environmental conditions is important in allowing eucalypts to grow in situations of limiting nutrient availability. Many species show a capacity to maintain themselves with little growth for considerable periods, responding to the onset of favourable conditions with a rapid growth flush (see Keith 1997). This type of response is particularly important in drier environments where the availability of soil water is a major factor influencing nutrient availability. Many species of eucalypts are also able to maintain high rates of water usage; this may be associated with their capacity for high growth rates under appropriate conditions.

Mobilization of nutrients within the plant and the re-translocation of these nutrients from older tissues to sites of active growth is an important mechanism in eucalypts for reducing nutrient requirements while maintaining growth. For example, redistribution of nutrients from heartwood to sapwood is higher in eucalypts than in other trees growing on more fertile soils (Keith 1997). However, re-translocation of nutrients from senescing leaves in eucalypts is generally similar to other species, with values for eucalypts ranging up to 80% for P and up to 66% for N (Keith 1997).

Differential allocation of nutrients amongst tissues is another mechanism whereby the eucalypts are able to increase their relative efficiency of nutrient use. The maintenance of low nutrient concentrations in certain tissues means that smaller quantities of nutrients need to be tied up in biomass. For example, eucalypts maintain an overall high ratio of non-living to living biomass associated with large amounts of dead heartwood in the trunk; this reduces the overall requirement for nutrients while retaining a high biomass in organs important for structural support. As well, eucalypt leaves have relatively low nutrient concentrations per unit weight; this is associated with sclerophylly and also reflects a lowered metabolic requirement for nutrients (see Keith 1997).

The eucalypts also show a pronounced capacity for opportunistic uptake of nutrients at times of higher availability and storing them if necessary until conditions favourable for growth occur. This phenomenon occurs in response to seasonal variation in soil moisture availability, but can also be important in environments with high variability of annual rainfall. The presence of nitrogen-fixing species including legumes in eucalypt understoreys is another important factor that may influence nutrient availability. Nutrient storage is typically very well developed in eucalypts growing on low nutrient soils (Mulligan and Sands 1988). Important nutrient storage sites in eucalypts include sapwood, twigs, lignotubers and roots (Grove 1988).

The majority of the eucalypts are capable of relatively high growth rates under appropriate environmental conditions, and can also show a rapid growth in response to the onset of good conditions. This phenomenon is associated with their unusual feature of having naked buds (Carey 1930) in the leaf axils of the canopy (Jacobs 1955). The naked buds provide a mechanism for rapid growth response, allowing the eucalypts to build up a large crown very quickly, with the trunk growing in proportion to produce a high biomass (Jacobs 1955). In most situations in Australia, new growth is quickly regulated by insect attack of new bud and leaf tissues. In situations where insect attack is reduced or eliminated, including in overseas countries, the eucalypts show an extraordinary growth potential.

The high growth potential of the eucalypts and their exceptional ability to optimise productivity and to develop large biomass under conditions of low soil nutrient availability in Australia results from various combinations of these mechanisms for nutrient acquisition and recycling. In general, the relative importance of different mechanisms tends to vary at different life stages, with seedlings and saplings being more reliant on uptake mechanisms, and mature eucalypts on recycling (Keith 1997).

Formation of hollows

Eucalypts have a striking capacity to produce hollows in their larger branches and trunks. These tree hollows provide an important ecological resource utilised by a wide range of the fauna of eucalypt-dominated ecosystems including both vertebrates and invertebrates (Gibbons 1994).

Hollow formation is a normal part of the processes of crown development and senescence in eucalypts. The large, dead branches that occur in the healthy, mature eucalypt crown as it ages (Jacobs 1955) are important sites for hollow formation. The breakage of these large branches in mature individuals, or other damage including by fire, exposes the heartwood and provides entry points for the organisms responsible for hollow formation. The shedding of epicormic branches also provides sites for invasion by these organisms (see Jacobs 1955).

Hollows may be present over a relatively long period in the life span of a eucalypt. Formation of hollows most commonly occurs in older individuals in a eucalypt population (Gibbons 1994), although hollows may develop in eucalypt secondary tissues at any stage associated with damage and invasion by organisms that break down wood, such as termites and wood-rotting fungi.

Hollows are a particularly prominent feature of the "over-mature stage" of the eucalypt crown. Branch breakage leading to hollow formation is accelerated by the fungal attack which is present in most older eucalypts and which progressively weakens both the trunk and branches in senescent individuals. The more horizontal orientation of older shaping branches in the crown also increases their tendency to break. Several cycles of branch break and replacement commonly occur in senescent individuals leading to the formation of many hollows (Jacobs 1955).

A wide range of the vertebrate fauna of eucalypt-dominated communities use tree hollows in eucalypts, for example for shelter and nesting. Vertebrates recorded using tree hollows in eucalypts include birds (parrots, cockatoos, owls, treecreepers, pardalotes), mammals (possums, dasyurids, rodents, bats), arboreal reptiles and frogs (see Woinarski *et al.* 1997). In some cases, tree hollows represent an important resource for a significant proportion of the species in these fauna groups of eucalypt-dominated ecosystems. For example, Wardell-Johnson and Nichols (1991) estimated 20% of the bird fauna of eucalypt forests in southwest Western Australia use tree hollows.

Hollow-dependent vertebrate fauna in Australia rely on the availability of natural hollows rather than creating their own (see Woinarski *et al.* 1997). Suitable habitat for these taxa is therefore dependent of the presence of hollows which may be an important factor limiting these fauna, for example in eucalypt populations dominated by young individuals (Saunders *et al.* 1982). The availability of hollows has been shown to have a significant influence on the richness and species composition of the bird fauna of wet eucalypt forests in the southeast of the continent (Loyn 1985). In the case of some species of possums, the presence of suitable hollows is confined to very old trees (Inions *et al.* 1989) or to particular seral stages in a fire regeneration cycle (Lindenmayer *et al.* 1993) and is a significant factor influencing their populations.

The exceptional capacity of the eucalypts to produce hollows in their larger branches and trunks and the importance of these in eucalypt-dominated ecosystems is both unusual and outstanding in the global context. Eucalypt hollows are of primary importance for a significant proportion of the fauna of eucalypt-dominated vegetation which includes a large number of hollow-dependent species. Trees other than eucalypts that occur in these ecosystems seldom form hollows, placing an even greater emphasis on eucalypt hollows in the ecology of these fauna.

Other morphological and structural adaptations

In addition to the characteristics already discussed, the eucalypts possess other morphological and structural adaptations that play a significant role in the ecology of eucalypt-dominated communities, including an open canopy structure and differences between juvenile and adult leaf forms.

Canopy structure and light characteristics

The structure of the canopy of the majority of eucalypt species is much more open compared with the canopies of other similar vegetation types, such as the hardwood forests and woodlands of the northern hemisphere (Jacobs 1955). There are some dense canopied eucalypts with a predominantly horizontal leaf orientation (*Eucalyptus torelliana, E. grandis, E. botryoides, E. calophylla*) but these are relatively few in number compared with open-canopied species.

Factors that are important in contributing to this open structure of eucalypt canopies include the predominantly vertical orientation of adult leaves in most eucalypt species, described by Jacobs (1955) as a “hanging habit” (p. 96), relatively long internodes between successive leaves, and the concentration of the majority of the leaves in the last two orders of branches in the outer reaches of the crown (Jacobs 1955). In contrast, northern hemisphere trees provide dense shade associated with their more horizontal leaf orientation, the arrangement of leaves close together, short shoots and the distribution of leaves throughout the crown as well as at its periphery (Jacobs 1955).

An important effect of this hanging habit of eucalypt leaves is a decrease in light interception in the middle of the day when the sun is closer to the vertical, and increased interception of light in the early morning and late afternoon, when the sun is near the horizon. These interception characteristics allow greatly increased penetration of light to the ground below the canopy during the middle of the day. For example, Turton and Duff (1992) recorded about 45% light penetration to the understorey in *Eucalyptus intermedia* open forest in north Queensland, compared with 35% penetration for tall forest of *E.grandis* and only about 5% penetration for mature rainforest. These figures compare with averages of between 10 and 20% penetration of incident radiation to the understorey herbaceous flora for both deciduous broad-leaved forests and coniferous forests in the temperate zone of the northern hemisphere, and as little as 2% penetration below boreal birch-spruce mixed forest (see Larcher 1983).

A major ecological effect of this open canopy structure is a relatively large increase in light available to understorey plants during the day. In some situations, this has been associated with increased species richness in the understorey, possibly due to an increased presence of species that are shade intolerant (e.g. Bowman and Kirkpatrick 1984). As discussed previously, the vertical orientation of eucalypt leaves also provides a means of minimising temperature increases due to incident radiation in the middle of the day, and also of maximising light interception in the early morning when photosynthetic rates may be higher and stomatal function less influenced by plant water deficits.

Juvenile leaves

The leaves produced by most species of eucalypts in their seedling and early sapling stages tend to be markedly different from the leaves produced in the adult stage. For example, the juvenile leaves may be short, not stalked [ie sessile], opposite, largely horizontal in orientation and covered with wax, in contrast to adult leaves which may be very long, stalked [petiolate], alternate, largely vertical in orientation and glossy rather than waxy (see Jacobs 1955). Often a period of transition also occurs when leaves intermediate between juvenile and adult forms may be produced.

This unusual phenomenon of leaf difference, known as heterophylly (e.g. Bell and Williams 1997), also tends to be manifest in the juvenile leaves that develop on the first shoots from dormant buds in both the lignotuber and the trunk and main branches during vegetative regeneration (Jacobs 1955). In some species, including *Eucalyptus perriniana* and *E. pulverulenta* in southeastern Australia and *E. gamphylla*, *E. peltata* and others in northern Australia, the juvenile leaves are maintained throughout the life cycle (neoteny), with no development of adult leaves occurring (Chippendale 1988, Brooker and Kleinig 1994). In other species, a general trend of retention of juvenile leaf forms has been observed in extreme environments associated with low temperatures or drought (e.g. Potts and Jackson 1986). The reasons for and the physiological or ecological advantages associated with heterophylly in eucalypts are not fully understood (see Bell and Williams 1997). Jacobs (1955) has suggested that the phenomenon may reflect a recapitulation within the growth sequence of the individual involving leaf structures that were manifest during the evolutionary development of the eucalypts.

Diversity of invertebrate groups

Eucalypt-dominated vegetation supports high species diversities within the major groups of invertebrate fauna. There is evidence that co-evolution between invertebrates and the eucalypts has taken place over a very long time period (Matthews 1976), and this is likely to have contributed to the high diversity shown by particular groups of eucalypt specialists. Amongst the major insect groups, co-evolutionary relationships with the eucalypts have been documented in the following: bugs (Hemiptera), particularly the psyllids (Psylloidea) and leafhoppers (Cicadellidae), the beetles (Coleoptera) and especially the chrysomelid beetles (Chrysomelinae), the moths and butterflies (Lepidoptera), the ants and wasps (Hymenoptera), and the bees (Colletidae and Halictidae) (Matthews 1976, Majer *et al.* 1997). Particular invertebrate groups that have undergone evolutionary diversification in association with the eucalypts include the psyllids, coccid bugs (Eriococcidae), eurymelid bugs (Eurymelidae), cicadas (Cicadellidae and Cicadidae), squashbugs (Amorbini, Coreidae) and shieldbugs (Pentatomidae) (Carver *et al.* 1991).

An important example is the Oecophoridae or the mallee moths, a group which occurs in Australia mostly in communities dominated by the eucalypts (see Common 1990, Majer *et al.* 1997). The mallee moths currently include 2650 described species, although estimates of the number of undescribed species take this total to 5500 which represents a significant proportion (about 25%) of Australia's moth fauna (Majer *et al.* 1997). The genera of mallee moths are mostly endemic to Australia. The two largest genera (*Philobota* and *Eulechria*) occur in the central parts of the east coast (southeast Queensland and northeast New South Wales) (Common 1990) in areas which also support exceptional diversities of eucalypt species (Chippendale 1981).

The psyllid fauna or Psyllidae is another invertebrate group with a high diversity of taxa in eucalypt-dominated vegetation in Australia. An estimated 67% of the total 379 psyllid species described for Australia use eucalypts as host plants (see Majer *et al.* 1997). The subfamily Spondyliaspidinae in particular includes large numbers of psyllid species associated with the eucalypts (Matthews 1976).

<u>Outstanding universal value:</u> Unique ecology of eucalypt-dominated communities

The ecology of the eucalypts and of eucalypt-dominated vegetation has been described as "highly unusual on the global scale" (Kirkpatrick 1994). The eucalypts and the communities which they dominate encompass a range of adaptations associated with Australia's unique environments. These ecological adaptations are thought to have been important in the evolutionary development of the eucalypts in Australia as well as being pivotal to their success in dominating the woody vegetation over an exceptionally wide range of habitats, throughout the continent.

An outstanding feature of the ecology of the eucalypts is their capacity to persist in and to dominate the transitional zone between the extremes of closed forest in the wetter areas and grassland in the drier areas. Australia is distinguished by an unusually-wide expression of this transitional zone. In nearby countries, the transitional zone is often very narrow, representing a rapid change between closed forest and grassland. In Australia, the unusually low relief derived from the ancient landforms that typify most of the continent, and a relatively slow rate of change of environmental gradients across large areas have contributed to the very wide expression of this transitional zone.

The environments of the transitional zone in Australia usually include poor soils and are subject to periodic drought. Recurrent disturbance due to fire is another important feature of these environments. The transitional zone can also vary widely in terms of other environmental factors since it encompasses much of the environmental variation of the continent and extends across the entire range of latitudes.

Eucalypt-dominated vegetation is the principal vegetation type that occurs in this transitional zone in Australia. The eucalypts possess a suite of characteristics and adaptations that are fundamental to their ecology and which, in combination, provide the basis for their exceptional ability to persist in and to dominate the environments characteristic of this transitional zone.

These exceptional characteristics and adaptations of the eucalypts include:

- the production of large quantities of fuel comprising flammable litter of leaves and bark with an unusually high proportion of woody material including twigs and branches;
- the production of litter suitable for long distance propagation of fire by spotting; especially bark ribbons that can act as firebrands and be transported during a fire up to 30 kilometres ahead of the main fire front;
- the development in most species of lignotubers which, by virtue of a relatively protected position at the base of the stem and reserves of dormant buds and food, provide an important means for vegetative recovery from fire or damage;
- the capacity for vegetative regeneration from dormant buds that occur beneath the bark throughout the trunk and main branches and which provide a means of replacing part or all of the canopy following its damage by fire, insect attack or other cause;
- the cuing of mass seed release from canopy seed stores in some species of eucalypts by fire occurrence, allowing seeds to escape seed harvesters by satiating predator populations;
- post-fire release of seed into an ash bed in which environmental conditions are conducive to higher rates of germination and seedling establishment, given appropriate rainfall;

- the capacity to cope with a wide range of soil types and soil nutrient availability, including acidic soils and calcareous soils and soils of exceptionally low nutrient status, via mechanisms to overcome or cope with adverse chemical and physical soil characteristics, and by lowering plant nutrient requirements through reduced growth rates;
- the capacity to maintain high growth rates and to develop large biomass on soils of very low nutrient status via root system structures and other mechanisms that enhance nutrient acquisition, by flexible and opportunistic growth responses to periods of increased nutrient availability, by continuous internal recycling and translocation of nutrients from older tissues to sites of active growth, and by maintaining a high ratio of non-living to living biomass;
- the capacity to persist in environments subject to low rainfall, to highly variable rainfall, or to seasonal rainfall characterised particularly by summer drought in southern latitudes and winter drought in tropical latitudes;
- the ability to postpone the onset of high water deficits as a result of changes to shoot and root systems that effectively increase the ratio of water uptake to water loss tissues, by changes in leaf structure and function to reduce water losses, and by changes to tissue solute concentrations to slow water losses;
- the vertical leaf orientation of adult leaves and a relatively open canopy structure in most species that allows a high proportion of incident light to penetrate to the ground layer flora, especially during the middle of the day, and which may be important in promoting high diversity amongst understorey vegetation communities;
- the capacity to produce tree hollows which provide an important ecological resource used for shelter and nesting habitat by a wide range of vertebrate fauna and also by invertebrate fauna;
- the high diversity of particular invertebrate groups associated with the eucalypts, reflecting important co-evolutionary relationships within eucalypt-dominated communities.

These ecological characteristics and adaptations may be viewed in combination as a "package" that underpins the exceptional success of the eucalypts in dominating the vegetation of the Australian continent. The versatility and resilience of the eucalypts and their resultant wide ecological amplitude is unparalleled amongst other comparable phylogenetic groups of dominant woody taxa in the world.

Cultural significance

The traditional occupation and use of eucalypt-dominated landscapes by Aboriginal people has continued over millenia (e.g. Hope 1994). Aboriginal use of these landscapes has also been suggested as an important factor influencing eucalypt vegetation and its associated biota (Flannery 1994, Hope 1994), although the extent of the impacts of Aboriginal burning remains the subject of debate (see Norton 1997). For example, the use of fire as a management "tool" (Nicholson 1981) may have resulted in an artificial increase in ignition sources (Hill 1994). It has also been proposed that Aboriginal burning may have contributed to the eucalypts replacing other taxa such as *Allocasuarina* as the dominant vegetation type (e.g. Kershaw 1986).

Aboriginal cultural values associated with eucalypt-dominated vegetation may be related to its significance in providing living sites and a wide range of other resources, its use for hunting and gathering activities and the location of sites of religious and spiritual importance (see Thomson *et al.* 1987).

The expert workshop recognised that the cultural values of eucalypt-dominated vegetation may also have outstanding universal significance, including within the context of globally-outstanding cultural landscapes, and considered that this possible significance should be further investigated and assessed.

Aesthetic significance

The most important aesthetic qualities of eucalypt-dominated vegetation are uniquely associated with Australia (see Kirkpatrick 1994). These qualities may include an exceptional natural beauty associated with the unusual shapes and colours of the eucalypts and eucalypt-dominated vegetation, including the rounded form and characteristic blue tints that eucalypt vegetation imparts to Australian landscapes, the outstanding aesthetic qualities of the tall eucalypt forests which are dominated by the tallest flowering plants in the world, the extraordinary range of form including exceptional structural and floral qualitites associated with the understorey vegetation, and the important contribution that eucalypt-dominated vegetation has made to the visual arts.

The aesthetic significance of eucalypt-dominated vegetation was noted by the expert workshop as also requiring further investigation in relation to its possible contribution to the outstanding universal values of the sub-theme.

Economic significance

Eucalypt-dominated vegetation represents an important economic resource in Australia. For example, a large proportion of the wood harvested in Australia comes from eucalypts, with recent estimates of about 12 million cubic metres annual hardwood log production and, in 1995, a total of 6.8 million tonnes of eucalypt woodchips approved for export (see Dargavel 1995, Norton 1997). As well as wood, eucalypt-dominated vegetation provides a large range of other important products including seeds, cut flowers, honey, pollen, essential oils, tannins, medicinal plants and bark products (Resource Assessment Commission 1992).

Other uses and amenity values of eucalypt-dominated vegetation that are of major economic significance in Australia include in water catchments, for conservation including wilderness areas and heritage areas, recreation and tourism, mining, grazing, defence, hunting and wild foods, education and research, and as infrastructure corridors (Resource Assessment Commission 1992).

Eucalypts are also widely planted throughout the world with estimates of over 200 species having been introduced into other countries (Mabberley 1997). The eucalypts are capable of exceptionally high growth rates when planted outside of their natural Australian habitats and they have been described as the most important plantation trees worldwide (Mabberley 1997). Ten eucalypt species contribute to most overseas plantings: *Eucalyptus grandis*, *E. saligna*, *E. globulus*, *E. camaldulensis*, *E. tereticornis*, *E. urophylla*, *E. robusta*, *E. maculata*, *E. paniculata* and *E. viminalis* (Brown and Hillis 1978). An estimated several million hectares of eucalypt plantations have been established in other countries, particularly in Brazil, Chile, China and South Africa. Their principal uses in other countries include wood production for building, fibre and fuels including charcoal (Clark 1995, Eldridge *et al.* 1993) and also for lowering the water table (Brooker and Slee 1996). They are also used for a wide variety of other purposes such as a source of oils and tannins, including medicinal and industrial chemical products, as ornamentals and for cut foliage (Boland *et al.* 1991, Mabberley 1997).

The economic importance of the eucalypts was identified by the expert workshop as requiring further investigation in relation to its possible contribution to the outstanding universal values of the sub-theme.

Genetic significance

Eucalypt-dominated vegetation in Australia constitutes a major repository of genetic material. This genetic resource is important from the point of view of conservation of natural values associated with eucalypt-dominated ecosystems, including the diversity of the eucalypts and associated plants and animals in the ecosystems they dominate. Eucalypt vegetation also represents a significant genetic resource in relation to the unique properties that provide the broad range of utilitarian values and products derived from eucalypts and eucalypt-dominated vegetation both in Australia and throughout the world. Natural populations of eucalypts in Australia provide the base genetic resource for domestication programmes being undertaken for eucalypts in countries around the world (Eldridge *et al.* 1993).

The significance of eucalypt-dominated vegetation as a genetic resource in the global context was recognised by the expert workshop and identified as requiring further investigation in relation to its possible contribution to the outstanding universal values of the sub-theme.

Towards a Representative Expression of the eucalypt sub-theme

Attributes and the representation of outstanding universal values of eucalypt-dominated vegetation

The global significance of the sub-theme of eucalypt-dominated vegetation derives from the combination of particular aspects of its evolution, distribution, diversity, and ecology in Australia. The outstanding universal values of eucalypt-dominated vegetation identified by the expert workshop are summarised in the preceding sections of this report and in the publications referred to therein.

Attributes of eucalypt-dominated vegetation related to its outstanding universal values were also identified by the expert workshop. These attributes were seen as providing the basis for identifying possible places to represent the sub-theme. The attributes also provide a basis for documenting and assessing the values of places which may contribute to a best global representation of the sub-theme.

Significant attributes identified by the expert workshop in relation to eucalypt-dominated vegetation are summarised in Table 7 (see Workshop Conclusions section below).

Research Plan and Data Issues

To qualify for World Heritage listing, a natural place must meet one or more of the criteria specified in paragraph 44 (a) and fulfil the conditions of integrity specified in paragraph 44 (b) of the Operational Guidelines for Implementation of the World Heritage Convention (UNESCO 1999) (Attachment 1).

Places likely to have world heritage significance as exemplars of the sub-theme of eucalypt-dominated vegetation must include outstanding examples of globally-significant aspects of the sub-theme that meet one or more of these world heritage criteria. The conditions of integrity also require a place to have a high degree of naturalness and to be of sufficiently large size to ensure the maintenance and long term conservation of all of its relevant key elements and processes. Only places that fulfil the conditions of integrity can be eligible to contribute to a serial nomination to the World Heritage List in relation to the sub-theme. Places that fulfil the conditions of integrity may also potentially satisfy the requirements related to criterion (iii), viz:

> (iii) "*contain superlative natural phenomena or areas of exceptional natural beauty and aesthetic importance*" (paragraph 44 (a), UNESCO 1999).

Identification of large and relatively undisturbed areas of natural eucalypt-dominated vegetation is thus a pre-requisite for world heritage listing and is an essential component of the selection of places to represent the sub-theme. The selection process also needs to identify, document and assess outstanding examples of eucalypt-dominated vegetation that represent the globally-significant aspects of the sub-theme.

The expert workshop identified a research plan for the documentation of possible places to represent the sub-theme of eucalypt-dominated vegetation. The research plan embodies an approach to ensure that a minimum set of possible places is put forward for further assessment, that this minimum set provides comprehensive representation of the outstanding universal values of the sub-theme, and that the possible places in the minimum set are able to fulfil the conditions of integrity as specified in paragraph 44 (b) of the Operational Guidelines for the Implementation of the World Heritage Convention (UNESCO 1999). The research plan is summarised as a series of steps in Table 6 below.

Table 6 Steps to identify potential areas to represent the outstanding universal values of eucalypt-dominated vegetation in Australia

Step	Activity
1	Using 1:250,000 overlays, identify zones of interest in relation to the significant attributes of each outstanding universal value of eucalypt-dominated vegetation in Australia. Consider possible places identified by the World Heritage Expert Panel (see Table 1 above) as part of this process.
2	Identify separately any significant features or particular areas relevant to the outstanding universal values of eucalypt-dominated vegetation not able to be identified in step 1.
3	Identify areas of high natural integrity amongst zones and areas identified in steps 1 and 2.
4	Apply a minimum set approach to areas identified in step 3 in order to undertake steps 5, 6 and 7 below.
5	Identify any outstanding universal values of eucalypt-dominated vegetation represented in places in Australia already inscribed on the World Heritage List.
6	Identify areas of high management integrity that are designated reserves protected under legislation.
7	Identify other areas that have high management integrity.

A range of data issues related to the documentation and assessment of possible places to represent the sub-theme were also discussed by the expert workshop. These are summarised below.

Scale

It was agreed that the work specified in the research plan would require continent-wide analyses, and that the 1: 250,000 mapsheet series for the continent would be appropriate for this work. An added advantage derives from the fact that this mapsheet series forms the basis for the work of Gill *et al.* (1985) on the phytogeography of the eucalypts in Australia. Its use would therefore facilitate access to the data and analyses of Gill *et al.* (1985) as part of the assessment work for the sub-theme.

The expert workshop also noted that a large part of the work undertaken to document and assess eucalypt forests in the RFA process has been at a scale of 1:100,000. The workshop agreed that this scale would be appropriate for documenting and assessing the values of possible places to represent the sub-theme.

Vegetation maps

Broad-scale vegetation maps for Australia were discussed by the expert workshop, including those by Carnahan based on structural characteristics (Carnahan 1976, Carnahan 1986, AUSLIG 1990), by Bridgewater (1987, pp. 78-79) based on dominant genera (including the eucalypt sub-genera), by Doing (e.g. 1981, Figure 1.1, pp. 10-11) based on a combination of floristics, structure and geographical regions, and by the National Forest Inventory (National Forest Inventory 1998) based on forest types for forest and woodland areas.

It was agreed that the National Forest Inventory maps for forested and woodland areas together with the structural vegetation map of Carnahan (see AUSLIG 1990) for treeless areas would be appropriate for further work in assessing the sub-theme. The workshop also noted that it would be necessary to ensure adequate representation of the vegetation types identified in Tables 3 and 4 as well as vegetation types (e.g. marlock and mallet communities) unable to be mapped at the broader scales used for continental coverage.

Fauna

The importance of environmental variation on the distribution and diversity of fauna, including factors such as disturbance regimes, regeneration processes and nutrient regimes, and also structure and floristics of the vegetation, were discussed by the expert workshop. The workshop noted that there is a broad correspondence between variation in the vegetation and faunal distribution and variation. It considered that a representative sample of the range of the fauna of eucalypt-dominated ecosystems would be captured in samples of eucalypt-doiminated vegetation provided these were representative of the major types of environments encompassed by this vegetation, and also its major structural and floristic variation. The workshop also recognized that this approach would not necessarily capture outliers and unusual groups, and that special attention and additional work would be needed to ensure representation of these groups where they were important to the outstanding universal value of eucalypt-dominated vegetation.

Workshop Conclusions

The expert workshop was asked to advise governments concerning technical documentation of the sub-theme of eucalypt-dominated vegetation. Provision of this advice required the workshop to identify values of eucalypt-dominated vegetation that have outstanding universal significance. It also required the identification of particular attributes of the eucalypts and eucalypt ecosystems which contribute to these values and which can be used to document and assess the significance of places in relation to representing the sub-theme in the global context. In addition, the workshop was asked to advise on likely data requirements for documentation and assessment of possible places to represent the outstanding universal values of the sub-theme. Terms of Reference for the workshop are included in Attachment 5.

The conclusions of the expert workshop concerning outstanding universal values of eucalypt-dominated vegetation are summarised in Table 7 below. These conclusions are also interpreted in relation to the criteria for inclusion of natural properties on the World Heritage List specified in paragraph 44 (a) of the Operational Guidelines for the Implementation of the World Heritage Convention (UNESCO 1999) (Attachment 1) (see Table 8).

Processes for further assessment of the sub-theme of eucalypt-dominated vegetation are outlined in Attachment 3. The findings of the expert workshop (Table 7) are directly relevant to the subsequent steps embodied in these processes which involve documentation and assessment of possible places to represent the sub-theme in the global context.

Table 7 Summary of outstanding universal values and significant attributes of eucalypt-dominated vegetation in Australia

Outstanding universal value of eucalypt-dominated vegetation	**Explanatory sentence**	**Significant attributes identified in relation to eucalypt-dominated vegetation**	**Advice concerning data issues**
Ancient origins in Gondwana and evolution in Australia	Eucalypt-dominated vegetation is globally-outstanding as an example of the taxonomic radiation of a single phylogenetic group in response to environmental change following the breakup of Gondwana.	- basal taxa in eucalypt clades - taxa associated with radiation - sub-genera	- need to consider Isla Gorge, Queensland, and Walpole region, Western Australia in addition to areas identified by the World Heritage Expert Panel
	Ongoing evolutionary processes amongst the eucalypts, including introgression, hybridisation and divergence, <u>contribute to</u> the globally-outstanding value of eucalypt-dominated vegetation in terms of its evolution in Australia.	- peaks of richness within subgenera [surrogate] - peaks of total eucalypt species richness - relicts - spatially-restricted species (ie less than 100 x 100 km) - rare taxa	- use Leigh & Briggs (1988) - data of A.M Gill *et al.* 1985 - data of A.M. Gill *et al.* (in progress)
	The high taxonomic diversity of the eucalypts <u>contributes to</u> the globally-outstanding value of eucalypt-dominated vegetation in terms of its evolution in Australia.	- peaks of richness within subgenera [surrogate] - peaks of total eucalypt species richness - relicts - spatially-restricted species - rare taxa	- use Leigh & Briggs (1988) - data of A.M Gill *et al.* 1985 - data of A.M. Gill *et al.* (in progress)
Domination of an entire continent	Eucalypt-dominated vegetation is a globally-outstanding and unique example of the domination of an entire continent by a single phylogenetic lineage.	- norms of environmental classes - extremes of environmental classes	- total number of classes flexible, (but within 10-25) - 8-12 climatic zones (Belbin & Margules - Bioclim) - 3 nutrient classes (based on lithology) - need to capture catenas in broad classes (e.g. sea to alps, laterite cap to sandy plain)
Diverse range of growth forms	Eucalypt-dominated vegetation is globally-outstanding for the unusual diversity of growth forms amongst the eucalypts which range from the world's tallest hardwood trees to low or even prostrate shrubs.	- structural classes [surrogate] - representation of extreme types (e.g. marlocks, mallets)	- use Carnahan structural mapping for treeless areas, - use NFI maps for tree areas - ensure representation of unmappable types (e.g. mallets, marlocks, creepers etc)
Wide diversity of eucalypt-dominated communities	Eucalypt-dominated vegetation is globally-outstanding for its wide diversity of communities, reflecting its exceptional range of structural, physiognomic and floristic diversity	- vegetation types - floristic regions	as for "diverse range of growth forms" (see above) - ensure specified vegetation types included (Tables 3 & 4)
Unique ecology of eucalypt dominated communities	Eucalypt-dominated vegetation is globally-outstanding for its unique ecology <u>which includes</u>: - a globally-outstanding range of fire regimes.	- environmental classes - vegetation maps including structural classes vegetation types floristic regions	- as for "domination of an entire continent" (see above) - as for "wide diversity of eucalypt-dominated communities" (see above) - ensure specified vegetation types included (Tables 3 & 4)
	- a wide range of characteristics that facilitate survival and reproduction under different fire regimes.	as above	as above
	-exceptional lignotuber and epicormic shoot responses to defoliation.	as above	as above

Table 7 (cont)

Outstanding universal value of eucalypt-dominated vegetation	Explanatory sentence	Significant attributes identified in relation to eucalypt-dominated vegetation	Advice concerning data issues
Unique ecology of eucalypt dominated communities(cont)	Eucalypt-dominated vegetation is globally-outstanding for its unique ecology which includes: - unusual types of fuels with a high woody component.	- environmental classes - vegetation maps including structural classes vegetation types floristic regions	- as for "domination of an entire continent" (see above) - as for "wide diversity of eucalypt-dominated communities" (see above) - ensure specified vegetation types included (Tables 3 & 4)
	- characteristics that facilitate long-distance propagation of fire.	as above	as above
	- the capacity to maintain high growth rates under a wide range of soil nutrient conditions.	as above	as above
	- adaptations to a-wide range of soils and moisture regimes.	as above	as above
	- the capacity to produce hollows utilised by fauna, including a large proportion of vertebrate fauna.	- structural vegetation - floristic survey data	as above
	-an exceptional diversity of groups of invertebrate fauna, including the mallee moths and the psyllids.	environmental classes - vegetation maps including structural classes vegetation types floristic regions	- as for "domination of an entire continent" (see above) - as for "wide diversity of eucalypt-dominated communities" (see above) - ensure specified vegetation types included (Tables 3 & 4) - ensure unusual groups included
Cultural significance of eucalypt-dominated vegetation	Eucalypt-dominated vegetation requires further investigation for possible global significance for cultural values, including as a cultural landscape.	*[expert opinion required]*	
Aesthetic significance of eucalypt-dominated vegetation	Eucalypt-dominated vegetation requires further investigation for possible global significance for aesthetic values associated with landscapes, tall trees, understoreys and contribution to the visual arts.	*[expert opinion required]*	
Economic significance of eucalypt-dominated vegetation	Eucalypt-dominated vegetation requires further investigation for possible global significance for economic values associated with wood production, fuel and other commodities and uses in many countries of the world.	*[expert opinion required]*	
Genetic significance of eucalypt-dominated vegetation	Eucalypt-dominated vegetation requires further investigation for possible global significance as a genetic repository in relation to the natural values of eucalypt ecosystems in Australia and also for the utility values of eucalypts which are exceptionally-widely planted throughout the world.	*[expert opinion required]*	

Table 8 Outstanding universal values of eucalypt-dominated vegetation in Australia interpreted in relation to the criteria for inclusion of natural properties on the World Heritage List (UNESCO 1999)

Outstanding universal value of eucalypt-dominated vegetation	**Explanatory sentence**	**World Heritage criteria for natural properties (see Attachment 1)**
Ancient origins in Gondwana and evolution in Australia	Eucalypt-dominated vegetation is globally-outstanding as an example of the taxonomic radiation of a single phylogenetic group in response to environmental change following the breakup of Gondwana.	criterion (ii) criterion (iv)
	Ongoing evolutionary processes amongst the eucalypts, including introgression, hybridisation and divergence, <u>contribute to</u> the globally-outstanding value of eucalypt-dominated vegetation in terms of its evolution in Australia.	not “best of the best” in own right; supportive to above value only
	The high taxonomic diversity of the eucalypts <u>contributes to</u> the globally-outstanding value of eucalypt-dominated vegetation in terms of its evolution in Australia.	not “best of the best” in own right; supportive to above value only
Domination of an entire continent	Eucalypt-dominated vegetation is a globally-outstanding and unique example of the domination of an entire continent by a single phylogenetic lineage.	criterion (ii) criterion (iii) criterion (iv)
Diverse range of growth forms	Eucalypt-dominated vegetation is globally-outstanding for the unusual diversity of growth forms amongst the eucalypts which range from the world’s tallest hardwood trees to low or even prostrate shrubs.	criterion (ii) criterion (iii) criterion (iv)
Wide diversity of eucalypt-dominated communities	Eucalypt-dominated vegetation is globally-outstanding for its wide diversity of communities, reflecting its exceptional range of structural, physiognomic and floristic diversity	criterion (ii) criterion (iii) criterion (iv)
Unique ecology of eucalypt dominated communities	Eucalypt-dominated vegetation is globally-outstanding for its unique ecology <u>which includes</u>: - a globally-outstanding range of fire regimes.	criterion (ii) criterion (iv)
	- a wide range of characteristics that facilitate survival and reproduction under different fire regimes.	criterion (ii)
	-exceptional lignotuber and epicormic shoot responses to defoliation.	criterion (ii)
	- unusual types of fuels with a high woody component.	criterion (ii)
	- characteristics that facilitate long-distance propagation of fire.	criterion (ii)
	- the capacity to maintain high growth rates under a wide range of soil nutrient conditions.	criterion (ii)
	- adaptations to a-wide range of soils and moisture regimes.	criterion (ii) criterion (iv)
	- the capacity to produce hollows utilised by fauna, including a large proportion of vertebrate fauna.	criterion (ii) criterion (iv)
	-an exceptional diversity of groups of invertebrate fauna, including the mallee moths and the psyllids.	criterion (ii) criterion (iv)

Bibliography

Abbott I. (1992) Ecological implications of insect pests in jarrah and karri forests. Western Australia Department of Conservation and Land Management Occasional Paper 2/92, 77-97.

Abbott I., Bell D. and Loneragan O. (1989) The jarrah plant. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 41-51.

Abbott I. and Loneragan O. (1986) Ecology of Jarrah *(Eucalyptus marginata)* in the Northern Jarrah Forest of Western Australia. Bulletin No. 1, Department of Conservation and Land Management, Perth.

Ambrose G.J., Callen R.A., Flint R.B. and Lange R.T. (1979) *Eucalyptus* fruits in stratigraphic context in Australia. *Nature*, 280, 387-9.

Andersen A.N. (1982) Seed removal by ants in the mallee of northwestern Victoria. In: Buckley R.C. (ed) *Ant-Plant Interactions in Australia*. Dr. W Junk, The Hague, pp. 31-43.

Andrews E.C. (1913) The development of the natural Order Myrtaceae. *Proceedings of the Linnean Society of New South Wales*, 38, 529-69.

Andrews E.C. (1916) The geological history of the Australian flowering plants. *American Journal of Science*, 42, 171-232.

Ashton D.H. (1975) Studies of litter in Eucalyptus regnans forests. *Australian Journal of Botany*, 23, 413-33.

Ashton D.H. (1976) The development of even-aged stands of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Botany*, 24, 397-414.

Ashton D.H. (1979) Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Ecology*, 4, 265-77.

Ashton D.H. (1981a) Tall open-forests. In: Groves R.H. (ed) *Australian Vegetation*. Cambridge University Press, Melbourne, pp. 121-51.

Ashton D.H. (1981b) Fire in tall open-forests (wet sclerophyll forests). In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, pp. 339-66.

Ashton D.H. and Attiwill P.M. (1994) Tall open-forests. In: Groves R.H. (ed) *Australian Vegetation*. Second Edition, Cambridge University Press, Cambridge, pp. 157-96.

AUSLIG (1990) *Atlas of Australian Resources, Vegetation, Volume 6*. Third Series, Australian Surveying and Land Information Group, Department of Administrative Services, Canberra.

Austin M.P, Pausas J.G. and Noble I.R. (1997) Modelling environmental and temporal niches of eucalypts. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 129-150.

Barlow B.A. (1981) The Australian Flora: Its Origin and Evolution. In: *Flora of Australia, Volume 1, Introduction*. Australian Government Publishing Service, Canberra, pp. 25-76.

Barlow B.A. (1985) A revised natural regions map for Australia. *Brunonia*, 8, 387-92.

Barlow B.A. (1994) Phytogeography of the Australian region. In: Groves R.H. (ed) *Australian Vegetation*. Second Edition, Cambridge University Press, Cambridge, pp. 3-35.

Barrow N.J. (1977) Phosphorus uptake and utilization by tree seedlings. *Australian Journal of Botany*, 25, 571-84.

Beadle N.C.W. (1966) Soil phosphate and its role in moulding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. *Ecology*, 47, 992-1007.

Beadle N.C.W. (1981) *The Vegetation of Australia*. Cambridge University Press, Cambridge.

Beadle N.C.W. and Costin A.B. (1952) Ecological classification and nomenclature. *Proceedings of the Linnean Society of New South Wales*, 77, 61-82.

Beard J.S. (1980) A new Phytogeographic map of Western Australia. *Western Australian Herbarium Research Notes*, 3, 37-58.

Bell D.T. and Heddle E.M. (1989) Floristic, morphologic and vegetational diversity. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 53-66.

Bell D.T., McCaw W.L. and Burrows N.D. (1989) Influence of fire on jarrah forest vegetation. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 203-15.

Bell D.T. and Williams J.E. (1997) Eucalypt ecophysiology. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 168-96.

Bentham G. (1867) *Flora Australiensis*. *Volume 3.* L. Reeve & Co., London.

Bishop P. and Bamber R.K. (1985) Silicified wood of Early Miocene *Nothofagus*, *Acacia* and Myrtaceae (aff. *Eucalyptus* B) from the Upper Lachlan Valley, New South Wales. *Alcheringa*, 9, 221-8.

Blakely W.F. (1934) *A Key to the Eucalypts*. Third Edition, Forestry and Timber Bureau, Canberra.

Blakers M. (1987) *Australia's Eucalypt Forests: World Heritage Values. A Preliminary Study of Eucalypt Forests in South Eastern Australia*. Australian Conservation Foundation, The Wilderness Society, South East Forests Alliance, Melbourne.

Blazey J. (1994) *A Late Miocene flora from Bacchus Marsh*. Unpublished Honours Thesis, School of Botany, University of Melbourne (quoted in Ladiges 1997).

Boland D.J., Brophy J.J. and House A.P.N. (1991) Eucalyptus *Leaf Oils*. Inkata Press, Melbourne.

Bowen G.D. (1981) Coping with low nutrients. In: Pate J.S. and McComb A.J. (eds) *The Biology of Australian Plants*. University of Western Australia Press, Nedlands, WA, pp. 33-64.

Bowler J.M. (1982) Aridity in the late tertiary and quaternary of Australia. In: Barker W.R. and Greenslade P.J.M. (eds) *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications, Frewville, pp. 35-45.

Braithwaite R.W. and Estbergs J.A. (1985) Fire patterns and woody vegetation trends in the Alligator Rivers region of Northern Australia. In: Tothill J.C. and Mott J.J. (eds) *Ecology and Management of the World's Savannas*. Australian Academy of Science, Canberra, pp. 359-64.

Bridgewater P.B. (1987) The present Australian environment - terrestrial and freshwater. In: Dyne G.R. and Walton D.W. (eds) *Fauna of Australia*, *Volume 1A*, *General Articles*.

Bureau of Flora and Fauna, Australian Government Publishing Service, Canberra, pp. 69-100.

Brooker M.I.H. and Kleinig D.A. (1994) *Field Guide to Eucalypts, Volume 3, Northern Australia*. Inkata Press, Sydney.

Brooker M.I.H. and Slee A.V. (1996) Chapter 4, Eucalyptus. In: Walsh N.G. and Entwistle T.J. (eds) *Flora of Victoria, Volume 3, Dicotyledons: Winteraceae to Myrtaceae*. Reed International Books Australia, trading as Inkata Press, Melbourne.

Brown A.G. and Hillis W.E. (1978) General introduction. In: Hillis W.E. and Brown A.G. (eds) *Eucalypts for wood production*. CSIRO, Australia.

Burbidge N.T. (1952) The significance of the mallee habit in *Eucalyptus*. *Proceedings of the Royal Society of Queensland*, 62, 73-8.

Burbidge N.T. (1960) The phytogeography of the Australian region. *Australian Journal of Botany*, 8, 75-212.

Burrows N.D., Gardiner G., Ward, B. and Robinson A. (1990) Regeneration of *Eucalyptus wandoo* following fire. *Australian Forestry*, 53, 248-58.

Busby J.R. (1992) The National and International Scientific Significance of National Parks in Eastern Victoria. Occasional Paper Series, NPPL No. 8. Department of Conservation and Environment, Victoria.

Carey G. (1930) The leaf buds of some woody perennials in the NSW flora. *Proceedings of the Linnean Society of New South Wales*, LV, 708-37.

Carnahan J.A. (1976) Natural Vegetation, Map with accompanying booklet commentary. In: *Atlas of Australian Resources*. Second Series, Department of National Resources, Canberra.

Carnahan J.A. (1986) Vegetation. In: Jeans D.N. (ed) *Australia, a Geography: Volume 1, The Natural Environment*. Sydney University Press, Sydney.

Carr S.G.M. and Carr D.J. (1962) Natural groups within the genus *Eucalyptus*. In: Leeper G.W. (ed) *The Evolution of Living Organisms*. Melbourne University Press, Melbourne, pp. 426-45.

Carver M., Gross G.F. and Woodward T.E. (1991) Hemiptera (Bugs, leafhoppers, cicadas, aphids, scale insects, etc.). In: Naumann I.D. (ed) *Insects of Australia*. Second Edition, Melbourne University Press, Melbourne, pp. 429-509.

Chattaway M.M. (1958) Bud development and lignotuber formation in eucalypts. *Australian Journal of Botany*, 6, 103-5.

Cheney N.P. (1981) Fire behaviour. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, pp. 151-75.

Chippendale G.M. (1981) Distribution density of *Eucalyptus* species in Australia. *Search*, 12, 131-3.

Chippendale G.M. (1988) *Eucalyptus, Angophora* (Myrtaceae). *Flora of Australia, Volume 19*. Australian Government Publishing Service, Canberra.

Christensen P. (1971) Stimulation of seedfall in karri. *Australian Forestry*, 35, 182-90.

Christensen P, Recher H. and Hoare J. (1981) Responses of Open Forest to Fire Regimes. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, pp. 367-94.

Clark J. (1995) *Prospects for Australia's Forest Plantations*. Environment Victoria, Melbourne.

Common I.F.B. (1990) *Moths of Australia*. Melbourne University Press, Melbourne.

Commonwealth of Australia (1992) *National Forest Policy Statement, A New Focus for Australia's Forests*. Commonwealth of Australia, Canberra.

Costin A.B. (1989) The Alps in a global perspective. In: Good R. (ed) *The Scientific Significance of the Australian Alps*. Proceedings of the First Fenner Conference on the Environment, Canberra, September 1988. The Australian Alps Liaison Committee, Canberra, pp. 7-19.

Cremer K.W. (1965) How eucalypt fruits release their seed. *Australian Journal of Botany*, 13, 11-16.

Crisp M.D. (1988) *Eucalyptus recurva* (Myrtaceae), a new species from the Southern Tablelands of New South Wales. *Telopea*, 3, 223-30.

Dargavel J. (1995) *Fashioning Australia's Forests*, Oxford University Press, Melbourne.

Dell B. and Havel J.J. (1989) The jarrah forest, an introduction. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 1-10.

DEST (1994) Australia's Biodiversity. An overview of selected significant components. Biodiversity Series, Paper No. 2, Biodiversity Unit, Department of Environment, Sport and Territories, Canberra.

Doing H. (1981) Phytogeography of the Australian floristic kingdom. In: Groves R.H. (ed) *Australian Vegetation*. Cambridge University Press, Cambridge, pp. 3-25.

Domicelj J., Halliday H., James P. (1992) Australia's Cultural Estate. Framework for assessment of Australia's cultural properties against the World Heritage Criteria. Commonwealth Department of the Arts, Sport, Environment and Territories, Canberra.

Eldridge K., Davidson J., Harwood C. and van Wyk, G. (1993) *Eucalypt Domestication and Breeding*. Oxford Science Publications, New York.

Fitzpatrick E.A. and Nix H.A. (1970) The climatic factor in Australian Grassland Ecology. In: Moore R.M. (ed) *Australian Grasslands*. Australian National University Press, Canberra, pp. 3-26.

Flannery T. (1994) *The Future Eaters*. Reed Books, Melbourne.

Florence R.G. (1981) The Biology of the Eucalypt Forest. In: Pate J.S. and McComb A.J. (eds) *The Biology of Australian Plants*. University of Western Australia Press, Perth, pp. 147-80.

Florence R.G. and Crocker R.L. (1962) Analysis of blackbutt (*Eucalyptus pilularis* Sm.) seedling growth in a blackbutt forest soil. *Ecology*, 43, 670-9.

Frenguelli J. (1953) Restos del genero *Eucalyptus* en el Mioceno del Neuquen. *Paleontologia*, 97, 208-13.

Gardner C.A. (1957) The fire factor in relation to the vegetation of Western Australia. *Western Australian Naturalist*, 5, 166-73.

Gibbons P. (1994) Sustaining key old-growth characteristics in native forests used for wood production: retention of trees with hollows. In: Norton T.W. and Dovers S.R. (eds) *Ecology and Sustainability of Southern Temperate Ecosystems*. CSIRO, Melbourne, pp. 59-84.

Gibson A., Bachelard E.P. and Hubick K.T. (1994) Growth strategies of *Eucalyptus camaldulensis* Dehnh. at three sites in northern Australia. *Australian Journal of Plant Physiology*, 21, 653-62.

Gill A.M. (1975) Fire and the Australian flora: a review. *Australian Forestry*, 39, 4-25.

Gill A.M. (1978) Crown recovery of *Eucalyptus dives* following wildfire. *Australian Forestry*, 41, 207-14.

Gill A.M. (1981) Adaptive responses of Australian vascular plant species to fires. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, pp. 243-72.

Gill A.M. (1994) Patterns and processes in open-forests of *Eucalyptus* in southern Australia. In: Groves R.H. (ed) *Australian Vegetation*. Second edition, Cambridge University Press, Cambridge, pp. 197-226.

Gill A.M. (1997) Eucalypts and fires: interdependent or independent? In: Williams J.E. and Woinarski J.C.Z. (eds) (1997) *Eucalypt ecology: individuals to ecosystems*, Cambridge University Press, Cambridge, pp. 151-67.

Gill A.M., Belbin L. and Chippendale G.M. (1985) Phytogeography of *Eucalyptus* in Australia. Australian Flora and Fauna Series Number 3, Bureau of Flora and Fauna, Australian Government Publishing Service, Canberra.

Gill E.D. (1975) Evolution of Australia's unique flora and fauna in relation to the plate tectonics theory. *Proceedings of the Royal Society of Victoria*, 87, 215-34.

Gillison A.N. (1994) Woodlands. In: Groves R.H. (ed) *Australian Vegetation*. Second Edition, Cambridge University Press, Cambridge, pp. 227-56.

Griffin A.R., Burgess I.P. and Wolf L. (1988) Patterns of natural and manipulated hybridisation in the genus *Eucalyptus* L'Herit. - a review. *Australian Journal of Botany*, 36, 41-66.

Groombridge E. (ed) (1992) *Global Biodiversity: Status of the Earth's Living Resources*. World Conservation Monitoring Centre, in collaboration with the Natural History Museum, London, IUCN, UNEP, WWF and WRI, Chapman and Hall, London.

Grose R.J. (1960) Effective seed supply for the natural regeneration of *Eucalyptus delegatensis* R.T. Baker, syn. *Eucalyptus gigantea* Hook.F. *Journal of the Australian Pulp and Paper Industry Association*, 13, 131-47.

Grove T.S. (1988) Growth responses of trees and understorey to applied N and P in karri (*Eucalyptus diversicolor*) forest. *Forest Ecology and Management*, 23, 87-103.

Groves R.H. (ed) (1981) *Australian Vegetation*. Cambridge University Press, Cambridge.

Groves R.H. (ed) (1994) *Australian Vegetation*. Second Edition. Cambridge University Press, Cambridge.

Gullan P.K. and Robinson A.C. (1980) Vegetation and small mammals of a Victorian forest. *Australian Mammalogy*, 3, 87-95.

Hardy A.D. (1935) Australia's great trees. *Victorian Naturalist*, 51, 231-41.

Heatwole H. (1987) Major components and distributions of the terrestrial fauna. In: Walton D.W. and Dyne G.R. (eds) *Fauna of Australia, Volume 1A, General Articles*. Bureau of Flora and Fauna, Australian Government Publishing Service, Canberra, pp. 101-35.

Hill K.D. and Johnson L.A.S. (1995) Systematic studies in the eucalypts. 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). *Telopea*, 6, 185-504.

Hill R.S. (1994) The Australian fossil plant record: an introduction. In: Hill R.S. (ed) *History of Australian Vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge. pp. 1-4.

Hingston F.J., O'Connell A.M. and Grove T.S.. (1989) Nutrient cycling in jarrah forest. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 155-77.

Holmes W.B.K., Holmes F.M. and Martin H.A. (1982) Fossil *Eucalyptus* remains from the Middle Miocene Chalk Mountain Formation, Warrambungle Mountains, New South Wales. *Proceedings of the Linnean Society of New South Wales*, 106, 299-310.

Hope. G.S. (1994) Quaternary Vegetation. In: Hill R.S. (ed) *History of the Australian vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge, pp. 368-89.

Horak M. (1994) New Koala scat moth. *Australian National Insect Collection News*, 4, 5-6.

Humphries F.R. and Criag F.G. (1981) Effects of fire on soil chemical, structural and hydrological properties. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra. pp. 177-200.

Inions G.B., Tanton M.T. and Davey S.M. (1989) The effect of fire on the availability of hollows in trees used by the Common Brushtail Possum, *Trichosurus vulpecula* Kerr 1872, and Ringtail Possum, *Pseudocheirus peregrinus* Boddarts 1785. *Australian Wildlife Research*, 16, 449-58.

Jacobs M.R. (1936) The Primary and Secondary Leaf Bearing Systems of the Eucalypts. Commonwealth Forestry and Timber Bureau, Bulletin No. 22.

Jacobs M.R. (1955) *Growth Habits of the Eucalypts*. Commonwealth Government Printer, Canberra.

Janzen D. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics*, 2, 465-92.

Johnson C.N. (1994) Distribution of feeding activity of the Tasmanian Bettong (*Bettongia gaimardi*) in relation to vegetation patterns. *Wildlife Research*, 21, 249-56.

Johnson L.A.S. and Briggs B.G. (1981) Three old southern families - Myrtaceae, Proteaceae and Restionaceae. In Keast A. (ed) *Ecological Biogeography of Australia*. Dr W. Junk bv Publishers, the Hague, pp. 427-70.

Kavanagh R.P. (1984) Seasonal changes in habitat use by gliders and possums in southeastern New South Wales. In: Smith A. and Hume I. (eds) *Possums and Gliders*. Surrey Beatty, Chipping Norton, pp. 527-43.

Keast A. (1981) The evolutionary biogeography of Australian birds. In Keast A. (ed) *Ecological Biogeography of Australia*. Dr W. Junk bv Publishers, the Hague, pp. 1585-636.

Keith H. (1997) Nutrient cycling in eucalypt ecosystems In: Williams J.E. and Woinarski J.C.Z. (eds) (1997) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 197-226.

Kelly A.E., Napier A.C. and Hopper S.D. (1995) Survey of rare and poorly known eucalypts of Western Australia. *CALMScience Supplement* 2, 1-207.

Kelly R. and Robson M. (1993) Towards a systematic approach for identifying gaps in the Australian system of protected areas. Draft Technical Appendix to the report *Establishment of a National Reserve System in Australia*, prepared for the October 1993 meeting of ANZECC. Environmental Resources Information Network and Australian Nature Conservation Agency, Canberra.

Kerr L.R. (1925) The lignotubers of eucalypt seedlings. *Proceedings of the Royal Society of Victoria*, 37, 79-97.

Kershaw A.P. (1986) Climatic change and aboriginal burning in north-east Australia during the last two glacial/interglacial cycles. *Nature*, 322, 47-9.

Kershaw A.P., Martin H.A. and McEwen Mason J.R.C. (1994) The Neogene: a period of transition. In: Hill R.S. (ed) *History of the Australian vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge, pp. 299-327.

Kikkawa J. (1986) Complexity, diversity and stability. In: Kikkawa J. and Anderson D.J. (eds) *Community Ecology: Pattern and Process*. Blackwell Scientific Publications, Melbourne, pp. 41-62.

Kirkpatrick J.B. (1994) The International Significance of the Natural Values of the Australian Alps. A Report to the Australian Alps Liaison Committee, May 1994.

Kirkpatrick J.B. (1997) Vascular plant - eucalypt interactions. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 227-45.

Kirkpatrick, J.B., Gilfedder L. and Fensham R.J. (1988) *City Parks and Cemeteries: Tasmania's Remnant Grassland and Grassy Woodlands*. Tasmanian Conservation Trust Inc., Hobart.

Lacey C.J. (1974) Rhizomes in tropical eucalypts and their role in recovery from fire damage. *Australian Journal of Botany*, 22, 29-38.

Lacey C.J. and Whelan P.I. (1976) Observations on the ecological significance of vegetative reproduction in the Katherine-Darwin region of the Northern Territory. *Australian Forestry*, 39, 131-39.

Ladiges P.Y. (1997) Phylogenetic history and classification of eucalypts. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 16-29.

Ladiges P.Y., Udovicic F. and Drinnan A.N. (1995) Eucalypt phylogeny - molecules and morphology. *Australian Systematic Botany*, 8, 483-97.

Landsberg J.J. and Cork S.J. (1997) Herbivory: interactions between eucalypts and the vertebrates and invertebrates that feed on them. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge. pp. 342-72.

Lange R.T. (1978) Carpological evidence for fossil *Eucalyptus* and other Leptospermae (subfamily Leptospermoidae of Myrtaceae) from a Tertiary deposit in the South Australian arid zone. *Australian Journal of Botany*, 26, 221-3.

Lange R.T. (1980) Evidence for lid-cells and host specific microfungi in the search for Tertiary *Eucalyptus*. *Review of Palaeobotany and Palynology*, 29, 29-33.

Larcher W. *Physiological Plant Ecology*. Translated by M.A. Biederman-Thorson, Springer-Verlag, Berlin.

Lee A.K. and Martin R. (1988) *The Koala: A Natural History*. University of New South Wales Press, Sydney.

Leigh J.H. and Briggs J.D. (1988) *Rare or Threatened Australian Plants*, Australian National Parks and Wildlife Service, Canberra.

Lindenmayer D.B., Cunningham R.B., Donnelly C.F., Tanton M.T. and Nix H.A. (1993) The abundance and development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management*, 60, 77-104.

Loyn R. (1985) Bird populations in successional forests of Mountain Ash *Eucalyptus regnans* in central Victoria. *Emu*, 85, 213-30.

Lunt I.D. (1990) Species-area curves and growth-form spectra for some herb-rich woodlands in western Victoria, Australia. *Australian Journal of Ecology*, 15, 155-63.

Mabberley D.J. (1997) *The Plant-book. A Portable Dictionary of the Vascular Plants*. Second Edition, Cambridge University Press, Cambridge.

Macphail M.K., Alley N.F., Truswell E.M. and Sluiter I.R.K. (1994) Early Tertiary vegetation: evidence from spores and pollen. In: Hill R.S. (ed) *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 189-261.

Majer J.D., Recher H.F. and Ganeshasasdam S. (1992) Variation in foliar nutrients in *Eucalyptus* trees in eastern and western Australia. *Australian Journal of Ecology*, 17, 383-93.

Majer J.D., Recher H.F., Wellington A.B., Woinarski J.C.Z. and Yen A.L. (1997) Invertebrates of eucalypt formations. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems, Cambridge University Press*. Cambridge, pp. 278-302.

Martin H.A. (1981) The Tertiary flora. In: Keast, A. (ed) *Ecological Biogeography of Australia*. Dr W. Junk bv Publishers, the Hague. pp. 391-406.

Martin H.A. (1989) Vegetation and climate of the late Cainozoic in the Murray Basin and their bearing on the salinity problem. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics*, 11, 291-9.

Martin H.A. (1994) Australian Tertiary phytogeography: evidence from palynology. In: Hill R.S. (ed) *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 104-42.

Martin H.A. and Gadek P.A. (1988) Identification of *Eucalyptus spathulata* pollen and its presence in the fossil record. *Memoirs of the Association of Australasian Palaeontologists*, 5, 313-27.

Matthews E.G. (1976) *Insect Ecology*. University of Queensland Press, St. Lucia.

May F.E. and Ash J.E. (1990) An assessment of the allelopathic potential of *Eucalyptus*. *Australian Journal of Botany*, 38, 245-54.

McArthur W.M. and Clifton A.L. (1975) Forestry and agriculture in relation to soils in the Pemberton area of WA. CSIRO Soils and Land Use Series No 54, CSIRO, Melbourne.

Mildenhall D.C. (1980) New Zealand late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 31, 197-233.

Milewski A.V. (1986) A comparison of bird-plant relationships in southern Australia and southern Africa. In: Ford H.A. and Paton D.C. (eds) *The Dynamic Partnership: Birds and Plants in Southern Australia*. Government Printer, Adelaide, pp. 111-8.

Moran G.F. (1992) Patterns of genetic diversity in Australian tree species. *New Forests*, 6, 49-66.

Mosley G. and Costin A.B. (1992) World Heritage Values and their Protection in Far South East New South Wales. Report to the Earth Foundation, Australia, July 1992.

Mott J.J. and Groves R.H. (1981) Germination strategies. In: Pate J.S. and McComb A.J. (eds) *The Biology of Australian Plants*. University of Western Australia Press, Nedlands, WA, pp. 307-41.

Mullette K.J., Hannon N. and Elliott A.G.L. (1974) Insoluble phosphorus usage by *Eucalyptus*. *Plant and Soil*, 41, 199-205.

Mulligan D.R. and Patrick J.W. (1985) Growth of and phosphorus partitioning in *Eucalyptus pilularis* Smith seedlings raised in a phosphorus deficient soil. *Australian Journal of Botany*, 33, 245-59.

Mulligan D.R. and Sands R. (1988) Dry matter, phosphorus and nitrogen partioning in three *Eucalyptus* species grown under a nutrient deficit. *New Phytologist*, 109, 21-8.

National Forest Inventory (1998) *Australia's State of Forests Report 1998*. Bureau of Rural Sciences, Canberra, December 1998.

Naumann I.D., van Achterberg, K., Houston T.F., Michener C.D. and Taylor R.W. (1991) Hymenoptera. In: *The Insects of Australia, Volume 2*. Second Edition, CSIRO & Melbourne University Press, Melbourne.

Nichols O.G. and Muir B. (1989) Vertebrates of the jarrah forest. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 133-53.

Nicholson P.H. (1981) Fire and the Australian Aborigine - an enigma. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, pp. 55-76.

Norton T.W. (1997) Conservation and management of eucalypt ecosystems. In: Williams J.E. and Woinarski J.C.Z. (eds) (1997) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 373-401.

O'Brien T.P., Forbes C. and Jobe L. (1986) The impact of severe frost on Mallee eucalypts, *Banksia ornata*, and *Leptospermum coriaceum* at Wyperfeld National Park. *Proceedings of the Royal Society of Victoria*, 98, 121-31.

O'Dowd D.J. and Gill A.M. (1984) Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology*, 65, 1052-66.

Pahl L. (1984) Diet preference, diet composition and population density of the Ringtail Possum (*Pseudocheirus peregrinus cooki*) in several plant communities in southern Victoria. In: Smith A. and Hume I.D. (eds) *Possums and Gliders*. Surrey Beatty, Chipping Norton, pp. 253-60.

Parsons R.F. (1981) *Eucalyptus* scrubs and shrublands. In: Groves R.H. (ed) *Australian Vegetation*. Cambridge University Press, Cambridge, pp 227-52.

Parsons R.F. (1994) *Eucalyptus* scrubs and shrublands. In: Groves R.H. (ed) *Australian Vegetation*. Second Edition, Cambridge University Press, Cambridge, pp. 291-320.

Penfold A.R. and Willis J.L. (1961) *The Eucalypts*. World Crop Books, London.

Pereira J.S. and Kozlowski T.T. (1976) Leaf anatomy and water relations of *Eucalyptus camaldulensis* and *E. globulus* seedlings. *Canadian Journal of Botany*, 54, 2868-80.

Pole M.S. (1989) Early Miocene floras from central Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 19, 121-5.

Pole M.S. (1993) Early flora of the Manuherikia Group, New Zealand. 7. Myrtaceae, including *Eucalyptus*. *Journal of the Royal Society of New Zealand*, 23, 313-28.

Pole M.S., Hill R.S., Green N. and Macphail M.K. (1993) The Oligocene Berwick quarry flora - rainforest in a drying environment. *Australian Systematic Botany*, 6, 399-427.

Pook E.W. (1967) The effects of the 1965 drought on eucalypts in the Canberra district. *Victoria's Resources*, 9, 43-6.

Potts B.M. and Jackson W.D. (1986) Evolutionary processes in the Tasmanian high altitude eucalypts. In: Barlow B. (ed) *Flora and Fauna of Alpine Australasia: Ages and Origins*. CSIRO, Melbourne, pp. 511-27.

Potts B.M. and Wiltshire R.J.E. (1997) Eucalypt genetics and genecology. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 56-91.

Prider R.T. (1966) The laterized surface of Western Australia. *Australian Journal of Soil Science*, 28, 443-51.

Pryor L.D. (1976) *The Biology of the Eucalypts*. Edward Arnold, Southampton.

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: Keast A. (ed) *Ecological Biogeography of Australia*. Dr W Junk bv Publishers, The Hague, pp. 499-536.

Pryor L.D., Williams, E.R. and Gunn B.V. (1995) A morphometric analysis of *Eucalyptus urophylla* and related taxa with descriptions of two new species. *Australian Systematic Botany,* 8, 57-70.

Quilty P.G. (1994) The background: 144 million years of Australian palaeoclimate and palaeogeography. In: Hill R.S. (ed) *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 14-43.

Raison R.J., Woods P.V., Jakobsen B.F. and Bary G.A.V. (1986) Soil temperatures during and following low intensity prescribed burning in a *Eucalyptus pauciflora* forest. *Australian Journal of Soil Research*, 24, 33-47.

Recher H.F., Majer J.D. and Ganesh S. (1996) Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. *Forest Ecology and Management*, 85, 177-96.

Renbuss M.A., Chilvers G.A. and Pryor L.D. (1973) Microbiology of an ashbed. *Proceedings of the Linnean Society of New South Wales*, 97, 302-10.

Resource Assessment Commission (1992) *Forest and Timber Inquiry Final Report, Volume 1*. Commonwealth of Australia, Australian Government Publishing Service, Canberra.

Saunders D.A., Smith G.T. and Rowley I. (1982) The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Australian Wildlife Research*, 9, 541-56.

Schodde R. and Calaby J.H. (1972) The biogeography of Australo-Papuan bird and mammal faunas in relation to the Torres Strait. In: Walker D. (ed) *Bridge and Barrier: the Natural and Cultural History of Torres Strait*. Australian National University Press, Australian National University, Canberra, pp. 257-306.

Schofield N.J., Stoneman G.L. and Loh I.C. (1989) Hydrology of the jarrah forest. In: Bell D, Havel J.J. and Malajczuk N. (eds) *The Jarrah Forest: a complex Mediterranean ecosystem*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 179-201.

Setterfield S.A. and Williams R.J. (1996) Patterns of flowering and seed production in *Eucalyptus miniata* and *E. tetrodonta* in a tropical savanna woodland, Northern Australia. *Australian Journal of Botany*, 44, 107-22.

Singh. G., Kershaw A.P. and Clark R. (1981) Quaternary vegetation and fire history in Australia. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra. pp. 23-54.

Specht R.L. (1970) Vegetation. In: Leeper G.W. (ed) *The Australian Environment*. Fourth Edition (revised), CSIRO and Melbourne University Press, Melbourne, pp. 44-67.

Specht R.L. (1981) Ecophysiological principles determining the biogeography of major vegetation formations in Australia. In Keast A. (ed) *Ecological Biogeography of Australia*. Dr W. Junk bv Publishers, the Hague, pp. 299-334.

Specht R.L., Roe E.M. and Boughton V.H. (1974) Conservation of major plant communities in Australia and Papua New Guinea. *Australian Journal of Botany Supplementary Series*, 7, 1-667.

Specht R.L., Specht A., Whelan M.B. and Hegarty E.E. (1995) *Conservation Atlas of Plant Communities in Australia*. Centre for Coastal Management, Lismore, in association with Southern Cross University Press, Lismore.

Stace H.C.T., Hubble G.D., Brewer R., Northcote K.H., Sleeman J.R., Mulcahy M.J. and Hallsworth E.G. (1968) *A Handbook of Australian Soils*. Rellim Technical Publications, Glenside, South Australia.

Stewart G.A. (1959) Some aspects of soil ecology. In: *Biogeography and Ecology in Australia*. Junk, The Hague, pp. 303-14.

Stoneman G.L. (1994) Ecology and physiology of establishment of eucalypt seedlings from seed: a review. *Australian Forestry*, 57, 11-29.

Stoneman G.L. and Dell B. (1994) Emergence of *Eucalyptus marginata* (jarrah) from seed in Mediterranean-climate forest in response to overstorey, site, seedbed and harvesting. *Australian Journal of Ecology*, 19, 96-102.

Taylor G. (1994) Landscapes of Australia: their nature and evolution. In: Hill R.S. (ed) *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 60-79.

Thackway R. and Cresswell I.D. (1995) An interim biogeographic regionalisation for Australia: a framework for establishing the national system of reserves. Version 4.0, Australian Nature Conservation Agency, Canberra.

Thomson J.M., Long J.L. and Horton D.R. (1987) Human exploitation of and introductions to the Australian fauna. In: Dyne G.R. and Walton D.W. (eds) *Fauna of Australia. Volume 1A. General Articles*. Bureau of Flora and Fauna, Australian Government Publishing Service, Canberra, pp. 227-49.

Truswell E.M. (1990) Australian rainforests: the 100 million year record. In: Webb L.J. and Kikkawa J. (eds) *Australian Tropical Rainforests: Science, Value, Meaning*. CSIRO, Melbourne, pp. 7-22.

Turton S.M. and Duff G.A. (1992) Light environments and floristic composition across an open forest-rainforest boundary in northeastern Queensland. *Australian Journal of Ecology*, 17, 415-23.

Udovicic F., McFadden G. and Ladiges P.Y. (1995) Phylogeny of *Eucalyptus* and *Angophora* based on 5S rDNA spacer sequence data. *Molecular Phylogenetics and Evolution*, 4, 247-56.

Udvardy M.D.F. (1975) A Classification of the biogeographical provinces of the World. IUCN Occasional Paper No. 18, International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Udvardy M.D.F. (1984) A biogeographical classification system for terrestrial environments. In: McNeely J.A. and Miller K.R. (eds) *National Parks, Conservation and Development*:

The Role of Protected Areas in Sustaining Society. Smithsonian Institution Press, Washington.

UNESCO (1973) International Classification and Mapping of Vegetation. UNESCO, Paris.

UNESCO (1999) Operational Guidelines for the Implementation of the World Heritage Convention. Intergovernmental Committee for the Protection of the World Cultural and Natural Heritage, United Nations Educational, Scientific and Cultural Organisation (revision adopted December 1998), March 1999.

Unwin G.L., Applegate G.B., Stocker G.C. and Nicholson D.I. (1988) Initial effects of tropical cyclone 'Winifred' on forests in North Queensland. *Proceedings of the Ecological Society of Australia*, 15, 283-96.

Usher G. (1979) *A Dictionary of Botany*. Constable & Co. Ltd., London.

Walker J. (1981) Fuel dynamics in Australian vegetation. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, pp. 101-27.

Warcup J.H. (1981) Effect of fire on the soil microflora and other non-vascular plants. In: Gill A.M., Groves R.H. and Noble I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra. pp. 202-214.

Wardell-Johnson G.W. and Nichols O. (1991) Forest wildlife and habitat management in southwestern Australia: knowledge, research and direction. In: Lunney D. (ed) *Conservation of Australia's Forest Fauna*. Royal Zoological Society of New South Wales, Sydney, pp. 161-92.

Wardell-Johnson G.W., Williams J.E., Hill K.D. and Cumming R. (1997) Evolutionary biogeography and contemporary distribution of eucalypts. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 92-128.

Wasson R.J. (1982) Landform development in Australia. In: Barker W.R. and Greenslade P.J.M. (eds) *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications, Frewville, South Australia, pp. 23-33.

Wellington A.B. (1981) *A study of the population dynamics of the mallee* Eucalyptus incrassata. Unpublished Ph.D. Thesis, The Australian National University, July 1981.

Wellington A.B. (1984) Leaf water potentials, fire and the regeneration of eucalypts in semi-arid, south-eastern Australia. *Oecologia*, 64, 360-2.

Wellington A.B. (1989) Seedling regeneration and the population dynamics of eucalypts. In: Noble J.C. and Bradstock R.A. (eds) *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management*. CSIRO, Melbourne, pp. 155-67.

Wellington A.B. and Noble I.R. (1985) Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *Journal of Ecology*, 73, 657-66.

Whittaker R.H. (1975) *Communities and Ecosystems*. Second Edition, Macmillan, London.

Wild A. (1958) The phosphate content of Australia soils. *Australian Journal of Agricultural Research*, 9, 193-204.

Wilford G.E. and Brown P.J. (1994) Maps of late Mesozoic-Cenozoic Gondwana break-up: some palaeogeographical implications. In: Hill R.S. (ed) *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 5-13.

Williams R.J. and Costin A.B. (1994) Alpine and subalpine vegetation. In: Groves R.H. (ed) *Australian Vegetation*. Second Edition, Cambridge University Press, Cambridge, pp. 467-500.

Winterhalder E.K. (1963) Differential resistance of two species of *Eucalyptus* to toxic soil manganese levels. *Australian Journal of Science*, 25, 363-4.

Withers J.R. (1978) Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II. The differential seedling establishment of *Eucalyptus ovata* Labill. and *Casuarina littoralis* Salisb. *Australian Journal of Botany*, 26, 465-83.

Woinarski J.C.Z., Recher H.F. and Majer J.D. (1997) Vertebrates of eucalypt formations. In: Williams J.E. and Woinarski J.C.Z. (eds) *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge, pp. 303-41.

World Heritage Report (1996) Chapter 6. World Heritage. In: Comprehensive Regional Assessment East Gippsland Environment and Heritage Report, Joint Commonwealth and Victorian Regional Forest Agreement (RFA) Steering Committee, Melbourne, July 1996.

World Heritage Report (1997a) Tasmania-Commonwealth Regional Forest Agreement Background Report Part I. World Heritage Report: Record of the Tasmanian World Heritage Expert Panel meeting and a Preliminary analysis of the forest and mineral resources in areas identified by the Panel, Tasmanian Public Land Use Commission in conjunction with Commonwealth Forests Taskforce, Hobart, June 1997.

World Heritage Report (1997b) World Heritage Report. Record of the World Heritage Expert Panel meeting: Western Australia, New South Wales and Queensland, State/Commonwealth Regional Forest Agreement Process, Commonwealth of Australia, Canberra, January 1998.

Zimmer W.J. and Grose R.J. (1958) Root systems and root/shoot ratios of seedlings of some Victorian eucalypts. *Australian Forestry*, 22, 13-18.

Attachment 1 World Heritage Convention: Criteria and Operational Guidelines (natural properties)

D. <u>Criteria for the inclusion of natural properties in the World Heritage List</u>

43. In accordance with Article 2 of the Convention, the following is considered as "natural heritage":

> "natural features consisting of physical and biological formations or groups of such formations, which are of outstanding universal value from the aesthetic or scientific point of view;
>
> geological and physiographical formations and precisely delineated areas which constitute the habitat of threatened species of animals and plants of outstanding universal value from the point of view of science or conservation;
>
> natural sites or precisely delineated natural areas of outstanding universal value from the point of view of science, conservation or natural beauty."

44. A natural heritage property - as defined above - which is submitted for inclusion in the World Heritage List will be considered to be of outstanding universal value for the purposes of the Convention when the Committee finds that it meets one or more of the following criteria and fulfils the conditions of integrity set out below. Sites nominated should therefore:

(a)(i) be outstanding examples representing major stages of earth's history, including the record of life, significant on-going geological processes in the development of land forms, or significant geomorphic or physiographic features; or

(ii) be outstanding examples representing significant on-going ecological and biological processes in the evolution and development of terrestrial, fresh water, coastal and marine ecosystems and communities of plants and animals; or

(iii) contain superlative natural phenomena or areas of exceptional natural beauty and aesthetic importance; or

(iv) contain the most important and significant natural habitats for in-situ conservation of biological diversity, including those containing threatened species of outstanding universal value from the point of view of science or conservation;

<u>and</u>

(b) also <u>fulfil the following conditions of integrity:</u>

(i) The sites described in 44(a)(i) should contain all or most of the key interrelated and interdependent elements in their natural relationships; for example, an "ice age" area should include the snow field, the glacier itself and samples of cutting patterns, deposition and colonization (e.g. striations, moraines, pioneer stages of plant succession, etc.); in the case of volcanoes, the magmatic series should be complete and all or most of the varieties of effusive rocks and types of eruptions be represented.

(ii) The sites described in 44(a)(ii) should have sufficient size and contain the necessary elements to demonstrate the key aspects of processes that are essential for the long-term conservation of the ecosystems and the biological diversity they contain; for example, an area of tropical rain forest should include a certain amount of variation in elevation above sea-level, changes in topography and soil types, patch systems and naturally regenerating patches; similarly a coral reef should include, for example, seagrass, mangrove or other adjacent ecosystems that regulate nutrient and sediment inputs into the reef.

(iii) The sites described in 44(a)(iii) should be of outstanding aesthetic value and include areas that are essential for maintaining the beauty of the site; for example, a site whose scenic values depend on a waterfall, should include adjacent catchment and downstream areas that are integrally linked to the maintenance of the aesthetic qualities of the site.

(iv) The sites described in paragraph 44(a)(iv) should contain habitats for maintaining the most diverse fauna and flora characteristic of the biogeographic province and ecosystems under consideration; for example, a tropical savannah should include a complete assemblage of co-evolved herbivores and plants; an island ecosystem should include habitats for maintaining endemic biota; a site containing wide-ranging species should be large enough to include the most critical habitats essential to ensure the survival of viable populations of those species; for an area containing migratory species, seasonal breeding and nesting sites, and migratory routes, wherever they are located, should be adequately protected; international conventions, e.g. the Convention of Wetlands of International Importance Especially as Waterfowl Habitat (Ramsar Convention), for ensuring the protection of habitats of migratory species of waterfowl, and other multi- and bilateral agreements could provide this assurance.

(v) The sites described in paragraph 44(a) should have a management plan. When a site does not have a management plan at the time when it is nominated for the consideration of the World Heritage Committee, the State Party concerned should indicate when such a plan will become available and how it proposes to mobilize the resources required for the preparation and implementation of the plan. The State Party should also provide other document(s) (e.g. operational plans) which will guide the management of the site until such time when a management plan is finalized.

(vi) A site described in paragraph 44(a) should have adequate long-term legislative, regulatory, institutional or traditional protection. The boundaries of that site should reflect the spatial requirements of habitats, species, processes or phenomena that provide the basis for its nomination for inscription on the World Heritage List. The boundaries should include sufficient areas immediately adjacent to the area of outstanding universal value in order to protect the site's heritage values from direct effects of human encroachment and impacts of resource use outside of the nominated area. The boundaries of the nominated site may coincide with one or more existing or proposed protected areas, such as national parks or biosphere reserves. While an existing or proposed protected area may contain several management zones, only some of those zones may satisfy criteria described in paragraph 44(a); other zones, although they may not meet the criteria set out in paragraph 44(a), may be essential for the management to ensure the integrity of the nominated site; for example, in the case of a biosphere reserve, only the core zone may meet the criteria and the conditions of integrity, although other zones, i.e. buffer and transitional zones, would be important for the conservation of the biosphere reserve in its totality.

(vii) Sites described in paragraph 44(a) should be the most important sites for the conservation of biological diversity. Biological diversity, according to the new global Convention on Biological Diversity, means the variability among living organisms in terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part and includes diversity within species, between species and of ecosystems. Only those sites which are the most biologically diverse are likely to meet criterion (iv) of paragraph 44 (a).

45. In principle, a site could be inscribed on the World Heritage List as long as it satisfies one of the four criteria and the relevant conditions of integrity. However, most inscribed sites have met two or more criteria. Nomination dossiers, IUCN evaluations and the final recommendations of the Committee on each inscribed site are available for consultation by States Parties which may wish to use such information as guides for identifying and elaborating nomination of sites within their own territories.

(UNESCO (1999) Operational Guidelines for the Implementation of the World Heritage Convention, pp. 10-12).

Attachment 2 Thematic approach to World Heritage Assessment

Step A: Identify, on expert advice, significant themes relating to natural and cultural values relevant to all biomes in Australia. By consideration of their global context, sort the themes into:

(a) outstanding universal value
(b) important universal value
(c) outstanding national/regional value
(d) important national/regional value.

Identify those themes of (a) outstanding universal value relevant to forest biomes in Australia.

Outcome: *Only forest themes of (a) outstanding universal value proceed*

Step B: Identify, on expert advice, and with reference to the World Heritage criteria, those places where further work is needed to determine whether they represent the forest themes of outstanding universal values.

Step C: Determine, with reference to the World Heritage criteria, which of those places identified in Step B have integrity and authenticity, and identify existing legal protection and management mechanisms.

Outcome *(i) Only places with integrity and authenticity proceed.*
(ii) Current management status and any further management requirements are identified.

Step D: Evaluate the significant places selected in Step C by consideration of their global context, into those:

(a) essential to a theme of outstanding universal value
(b) integral to a theme of outstanding universal value
(c) peripheral to a theme of outstanding universal value
(d) no relevance to a theme of outstanding universal value

Outcome: *Only places (a) essential and (b) integral to a theme of outstanding universal value proceed*

Step E: Undertake final assessment of the places selected in Step D against the definitions in Articles 1 and 2 of the World Heritage Convention and the criteria in paragraphs 24 (a) and 44 (a) of the Operational Guidelines

Outcome: *Only places which satisfy one or more of the criteria as well as the test of integrity and authenticity to proceed.*

Note: The Attorney's General's Department has advised the World Heritage Unit in correspondence of 7 June 1996 that: "the mere application of any or all stages of the methodology to a place will not make that place 'identified property' for the purposes of the *World Heritage Properties Conservation Act* 1983. The Act will not be capable of applying to a place solely by reason of the application of the above steps of the methodology."

(from *World Heritage Report. Record of the World Heritage Expert Panel meeting: Western Australia, New South Wales and Queensland,* State/Commonwealth Regional Forest Agreement Process, Commonwealth of Australia, Canberra, January 1998, Attachment 1, p. 88.)

Attachment 3 Further assessment of the sub-theme of eucalypt-dominated vegetation

Methodology for documentation and assessment of potential places to represent the sub-theme

Documentation of the sub-theme

1. Prepare a technical report which identifies aspects of eucalypt-dominated vegetation related to its outstanding universal value based on current understanding of its evolutionary history, distribution, diversity and ecology.
2. Finalise the report as part of a joint State/Commonwealth Expert Workshop on the sub-theme. The Expert Workshop will be attended by selected, invited experts and representatives of participating governments.
3. The Expert Workshop will advise governments concerning both the technical documentation of the sub-theme, and likely data requirements for further assessment of identified forest places.

Documentation of potential places

1. Document the identified forest places in terms of their representation of the sub-theme.

For each forest place identified in relation to the sub-theme:

2. Describe and map (at appropriate scales) the occurrence of existing eucalypt-dominated vegetation with high integrity of natural values using available data relevant to eucalypt species distributions, biophysical naturalness, and disturbance.
3. Describe and map (at appropriate scales) the distribution of the characteristics of each place related to eucalypt-dominated vegetation and likely to contribute to its outstanding universal value in representing the sub-theme.

Data compiled for RFA regions as part of the CRA/RFA process will need to be used for documentation of identified forest places located within the regions.

The adequacy of these data in describing all relevant aspects of the sub-theme will need to be evaluated for each place. Additional data may also be required.

Assessment of potential places

1. Assess the representation of the sub-theme by the identified forest places.

For each forest place identified in relation to the sub-theme:

2. Assess the relative contribution of each of the agreed characteristics related to eucalypt-dominated vegetation at each place in representing the outstanding universal value of the sub-theme;
3. Assess the overall significance of each place in representing the outstanding universal sub-theme, in terms of the composite suite of its characteristics related to eucalypt-dominated vegetation;

For forest places identified in relation to the sub-theme:

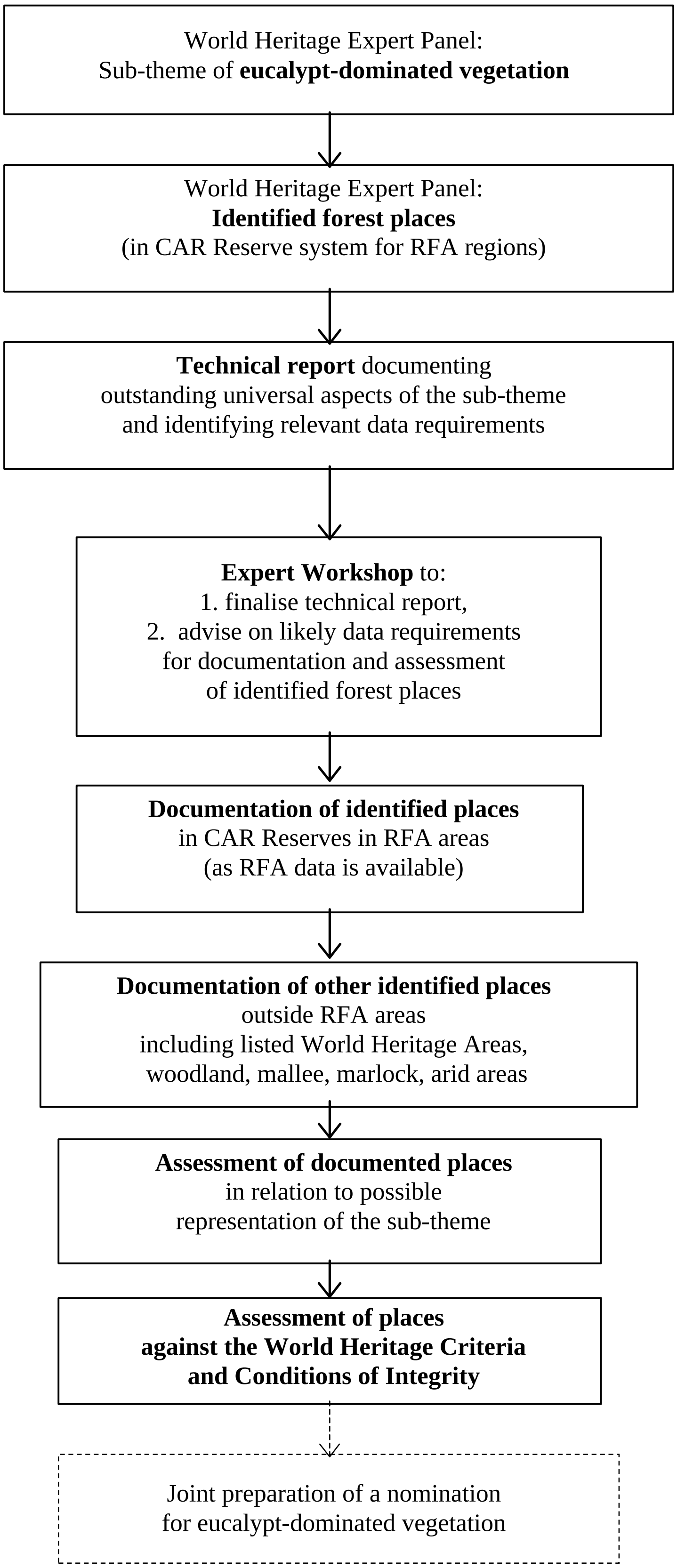
4. Assess their significance in terms of their representation of the outstanding universal sub-theme of eucalypt-dominated vegetation in Australia.
5. Assess their outstanding universal value against the definitions in Articles 1 and 2 of the World Heritage Convention and the criteria in paragraph 44 (a) and the conditions of integrity in paragraph 44 (b) of the Operational Guidelines.

Assessment of potential places outside RFA regions

The Expert Panel advised that forest places outside of RFA regions, and non-forest places, would also be required to represent the outstanding universal aspects of the sub-theme of eucalypt-dominated vegetation.

Documentation and assessment of these non-RFA places would need to be undertaken to represent the sub-theme of eucalypt-dominated vegetation. This work would need to be undertaken separately to CRA/RFA processes.

Figure 1. Diagrammatic summary of the assessment process



Attachment 4 Terms of Reference - Expert Workshop

TERMS OF REFERENCE

1. Develop an agreed list of significant characteristics of eucalypts and eucalypt-dominated vegetation that contribute to the outstanding universal value of the sub-theme of "eucalypt-dominated vegetation".

2. Revise the draft technical report on the sub-theme of eucalypt-dominated vegetation so that it provides an appropriate summary of the significant characteristics of eucalypts and eucalypt-dominated vegetation that contribute to their outstanding universal value.

3. Provide advice where appropriate on likely data requirements for future assessment of areas identified by the World Heritage Expert Panel as having potential World Heritage significance in representing the eucalypt sub-theme.

4. Provide comments on drafts and assist where necessary with the development of the final report of the workshop.

Attachment 5 Workshop participants

Experts

Professor Jamie Kirkpatrick (Chairman)
Department of Geography and Environmental Studies
University of Tasmania, Hobart, Tas.

Dr Mike Austin
CSIRO Wildlife and Ecology, Canberra, ACT.

Dr Bryan Barlow
Centre for Plant Diversity Research
CSIRO Plant Industry, Canberra, ACT.

Dr Ian Brooker
Centre for Plant Diversity Research
CSIRO Plant Industry, Canberra, ACT.

Dr Mick Brown
Forestry Tasmania, Hobart, Tas.

Dr Malcolm Gill
Centre for Plant Diversity Research
CSIRO Plant Industry, Canberra, ACT.

Dr Gordon Guymer
Queensland Herbarium, Toowong, Qld.

Mr Joe Havel
Havel Land Consultants, Wanneroo, WA.

Professor Pauline Ladiges *(Day 1 only)*
Department of Botany
University of Melbourne, Parkville, Vic.

State Observers

New South Wales

Mr Ashley Love
New South Wales National Parks and Wildlife Service, Coffs Harbour, NSW.

Queensland

Dr Gordon Guymer
Queensland Herbarium, Toowong, Qld.

Tasmania

Dr Mick Brown
Forestry Tasmania, Hobart, Tas.

Victoria

Mr Doug Hooley *(Day 2 only)*
Department of Natural Resources and Environment, East Melbourne, Vic.

Western Australia

Dr Geoff Stoneman
Department of Conservation and Land Management, Crawley, WA.

Commonwealth Observers

Environment Forest Taskforce

Ms Anne-Marie Delahunt
Assistant Secretary
Forest Assessment Branch 1

Dr Rhondda Dickson
Assistant Secretary
Forest Assessment Branch 2

Ms Bronwen Wicks
Senior Project Officer

Ms Tara Harris
Heritage Advice and Listing

World Heritage Unit

Mr Daryl King
Director

Mr Mike Preece
Assistant Director

Scribe

Dr Bruce Wellington
Freelance Ecology

Attachment 6 Summaries of biogeographic pattern amongst eucalypt-dominated vegetation at the continental scale

Vegetation pattern according to Beadle (1981)

In his discussion of the distribution of vegetation communities in Australia, Beadle (1981, pp. 130-135) identified eight broad biogeographic regions. These included:

1. the Wetter Tropics, which extends across large parts of the tropical north of the continent;
2. the Eastern Coastal Lowlands, which extends the length of the east coast;
3. the Eastern Inland Lowlands, which includes the inland slopes of the Great Divide together with the northern parts of the Divide;
4. the Eastern Highlands, comprising the southern parts Great Divide in New South Wales and Victoria;
5. Tasmania, which is separate due to its island status;
6. the Mallee, which extends across the southern part of the continent and is divided by the Nullarbor Plain;
7. South-western Australia, which includes higher rainfall areas in the south-west of the continent; and
8. the Semi-arid and Arid Areas, which comprise a large part of the centre of the continent, extending to the coast in some areas.

Within this regional context, eight broad eucalypt-dominated vegetation types were recognised by Beadle (1981). He noted that eucalypt species dominate most of the regions with higher rainfall. The species generally differ from region to region, except for a few which occur in two contiguous regions. A brief summary, derived from Beadle (1981), of each of the major eucalypt-dominated vegetation types classified at the continental scale follows.

1. Eucalypt Communities of the Tropics

The northern tropical regions are characterised by summer rainfall and winter drought. Much of the area supports eucalypt forests and woodlands, broadly divided into two regional components by the Gulf of Carpentaria and its associated grassland areas. All subgenera are represented in these tropical regions. A high proportion of eucalypt taxa are from three subgenera *Blakella*, *Corymbia* and *Eudesmia*, and many of these are community dominants.

2. Tall Eucalypt Forests of the Eastern Coastal Lowlands on soils of higher fertility

The tall eucalypt forests on fertile soils occur mainly in the temperate areas of northern New South Wales extending into southern and central Queensland. Relict stands also occur north of the Tropic. These tall forests typically occur at warmer coastal lowlands sites, but also extend up onto the cooler tablelands of the Divide. They often share a common boundary with rainforest vegetation and rainforest species are common in the understorey. *Eucalyptus robusta* forests with a predominantly grassy or halophytic understorey located adjacent to the littoral zone are included amongst these forests.

3. Eucalypt Forests and Woodlands of the Eastern Coastal Lowlands on soils of lower fertility

The forest and woodland communities on less fertile soils extend down the east coast, from near the Tropic into Victoria. They give way to heath vegetation on the poorest soils or where drainage is poor, and also intergrade with the tall forests on more fertile soils. The understorey vegetation includes a major scleromorphic component, which generally increases in species diversity from north to south, and reaches its maximum expression on the sandstones of the Sydney region. Some of the eucalypt dominants have a broad latitudinal range, whereas others are restricted in their distribution, generally either to the northern or southern part of the region.

4. Eucalypt Communities of the cooler climates of the Eastern Highlands, Lowland Victoria and Tasmania

Cold-adapted eucalypt forests and woodlands dominate the higher parts (above 1000 metres) of the Great Divide, extending to treeline. The higher parts of the Divide broadly include the Northern, Central and Southern Tablelands regions of New South Wales, and the Southern Alps region in the south-east of the continent, which extends from the Koscuiszko plateau into Victoria. High altitude areas also occur in parts of Tasmania. In these regions, the higher parts of the Divide separate the wetter, eastern flora from the drier, western flora. In general, the species assemblage of the northern parts of the Divide differs from that of the southern parts. Species with a wide latitudinal range also occur, extending to progressively lower altitudes from north to south. Some species have wide altitudinal ranges and several display pronounced ecotypic variation with altitude.

5. The Ironbark Forests and Woodlands

Ironbark forests and woodlands typically occur on lower fertility soils, extending from Cape York Peninsula to Victoria. In the north, they occur from the coast across the Great Divide to semi-arid, inland areas. In the south, they are confined to drier areas adjacent to and west of the Divide, although some taxa also occur in rainshadow areas in the lowlands to the east of the Divide. Two broad species groups can be distinguished. One, which mostly includes taxa in Series *Pruinosae*, occurs mainly in northern regions with summer rainfall. The other, which comprises *Eucalyptus sideroxylon*, Series *Melliodorae*, and taxa in Series *Paniculatae*, occurs predominantly in southern areas with winter rainfall. Ironbark forests and woodlands adjoin all of the other eastern eucalypt communities, except for the higher altitude communities. They also co-occur with other species of *Eucalyptus* and *Angophora*, and include a large number of ecotonal associations.

6. The Box Woodlands of the East and South-east

The box woodlands occur in drier areas in the eastern and southern parts of the continent, extending from Cape York Peninsula to South Australia. They effectively separate the forests of wetter coastal and montane areas from the arid interior of the continent, although they also extend into coastal regions associated with areas of rainshadow. The box woodlands are dominated by species in the subgenus *Symphyomyrtus*. The species tend to be stratified latitudinally, but also display areas of overlapping distribution and ecotonal interaction.

7. The Mallee and Marlock Communities

Mallee communities are dominated by multi-stemmed, shrub forms of *Eucalyptus*. They typically extend across the southern half of the continent in areas of between 220 and 375 mm mean annual rainfall. The southern area of mallee fringes the arid zone, and is broadly divided into eastern and western components by the Nullarbor Plain and Great Australian Bight. Some mallee species are widely distributed, but many are restricted in their distribution to the east or the west. Mallee communities occur as isolated patches scattered throughout the arid interior of the continent, and extend as far north as the Tropic. Some mallee outliers also occur in wetter areas; these are apparently relictual and may reflect a former, wider distribution of this vegetation type. Marlock communities are structurally similar to mallee, but are dominated by single-stemmed, shrub forms of *Eucalyptus*. They are found in drier parts of the south-west of the continent. The composition of the understorey of mallee vegetation varies widely, depending on soil factors.

8. Eucalypt Forests and Woodlands in the South-West

Eucalypt forests and woodlands dominate higher rainfall areas in the south-west of the continent. The forest communities are restricted to the wetter areas in the far south-west, whereas woodland vegetation extends into the drier regions to the east. Rainfall and soil type are major determinants of eucalypt species distribution. The tallest forests of karri (*Eucalyptus diversicolor*) and red tingle (*Eucalyptus jacksonii*) occur in the few wetter areas with fertile soils. Extensive lateritic soils support forests of jarrah (*Eucalyptus marginata*) and marri (*Eucalyptus calophylla*), and the tuart forests (*Eucalyptus gomphocephala*) are associated with coastal limestones. In response to decreasing rainfall, some of these forest dominants may exhibit decreasing stature, but all are eventually replaced by other eucalypt species. Areas of forest and woodland are frequently interspersed with extensive areas of mallee and marlock, or with non-eucalypt heath communities, in response to low nutrient soils or impeded drainage.

Vegetation pattern according to Groves (1981, 1994)

Groves (1994) provided a recent overview of vegetation in Australia at a continental-scale, based primarily on structural characteristics including canopy density and height. The eucalypt-dominated component of the vegetation is divided into tall open forests (Ashton and Attiwill 1994), open forests (Gill 1994), woodlands (Gillison 1994, Williams and Costin 1994) and scrubs and shrublands (Parsons 1994). A brief summary of aspects of biogeographic pattern amongst each of these vegetation types, derived primarily from respective chapters of Groves 1994, is included below.

Tall open-forests

The tall open forests are characterised by a height exceeding 30 metres, and a canopy cover of between 30 and 70 percent (Specht 1970). These are predominantly eucalypt forests which include examples of the tallest hardwood trees in the world. Occasionally, other genera may form tall open-forests, but these are now very restricted in distribution; they include *Melaleuca*, *Acacia* and *Lophostemon* (Ashton and Attiwill 1994).

Two main types of tall open-forests were identified by Ashton and Attiwill (1994). These included "wet sclerophyll forests" (Beadle and Costin 1952) which occur in high rainfall areas (1000 to 1500 mm per annum) with deep, fertile soils on both the east and the west sides of the continent, and river red gum forests which occur as occasional stands limited to optimal sites associated with the Murray River system (Ashton and Attiwill 1994).

In the east, the wet sclerophyll forests form a discontinuous arc extending from northern Queensland to Tasmania. In the west, they are confined to small areas in the far south-west of corner of Western Australia. Wet sclerophyll forests exhibit wide variation of both understorey and overstorey species, both across their latitudinal range in the east, and also between the east and west of the continent, where there is a marked discontinuity in species composition. In the east a gradual replacement of canopy dominant species occurs with latitude, and species with a primarily southern distribution may also extend further into northern regions associated with areas of higher altitude (Ashton and Attiwill 1994).

Ashton and Attiwill (1994) identified three broad species groups within wet sclerophyll forest. These include a northeast group primarily associated with central New South Wales and Southern Queensland (including *Eucalyptus cloeziana*, *E. microcorys*, *E. pilularis*, *E. saligna* and *E. grandis*), a south-east group primarily in Victoria and Tasmania (*Eucalyptus regnans, E. viminalis, E. obliqua, E. globulus, E. fastigata, E. delegatensis, E. cypellocarpa*, *E. dalrympleana*, and *E. nitens*), and a far south-west group in Western Australia (including *Eucalyptus diversicolor*, *E. calophylla*, *E. guilfoylei*, and *E. jacksonii*) (Ashton and Attiwill 1994).

Open-forests of southern Australia

Open-forests are defined as having a height of between 10 and 30 metres and canopy cover of between 30 and 70 percent (Specht 1970). They are dominated almost exclusively by eucalypts, including species of *Eucalyptus* and *Angophora*. Open forests typically occur in areas with moderate rainfall and temperature and intermediate levels of available soil nutrients. They extend broadly from the margins of tall open-forest at the wetter end of their range, to woodland vegetation at the drier end of their range (Gill 1994).

In the south-east of the continent, open-forests are found throughout coastal and sub-coastal regions, extending from Brisbane to Adelaide, as well as in Tasmania. In the west, they occur predominantly in the south-west of Western Australia. Open-forests in the east tend to be dominated by mixtures of co-occurring species, whereas in the west, monospecific (pure) stands are more common. Co-occurring species are often, but not always, from different eucalypt subgenera. The understorey of open-forests varies considerably across its range, and includes many species with disjunct distributions. Many understorey genera are common to open-forest in both the south-eastern and south-western parts of the continent. The south-west region also includes a large number of endemic understorey taxa (species and genera) (Gill 1994).

Woodlands

Woodlands are an intermediate structural form between the open-forest of wetter areas and the shrubland vegetation typical of extreme environments associated with low rainfall, high altitude, low soil fertility, etc. Most eucalypt woodlands are evergreen, although deciduous woodlands with some eucalypt species occur in parts of northern Australia. More than 400 eucalypt species have been recorded in woodland formations. These are mostly from the subgenera *Blakella*, *Corymbia*, *Eudesmia*, *Idiogenes* and *Symphyomyrtus*, although some *Monocalyptus* species occur in high altitude woodlands (Gillison 1994).

Eucalypt woodland vegetation varies considerably in structure, depending on environmental factors that influence plant growth. The canopy dominants are predominantly single-stemmed. Gillison (1994) described several broad woodland types based primarily on height. These included: very tall woodland, tall woodland, medium-height woodland, low woodland and very low woodland. Woodland vegetation also varies widely in species diversity (Gillison 1994)

Very tall woodland occurs on deeper, weathered sandy soils in the tropical northern regions. The understorey vegetation includes both shrub and grass components. Tall woodlands extend eastwards from the semi-arid regions of eastern Australia. *Eucalyptus microcarpa* is a common canopy dominant in the drier areas whereas *Eucalyptus moluccana* dominates in wetter areas, sometimes extending into open-forest formations. Overstorey taxa of tall woodlands in eastern Australia also include the ironbarks *Eucalyptus crebra*, *E. drepanophylla*, *E. melanophloia* and *E. sideroxylon* and the bloodwoods *Eucalyptus intermedia* and *E. polycarpa*. In northern areas, the dominants also include species of woollybuts and stringybarks. The understorey of the tall woodlands is highly variable, with grassy understoreys being more common in northern regions (Gillison 1994).

Woodlands of medium height are the most widespread of all woodland vegetation. They include a wide range of dominant canopy species. In the north, canopy dominants include species of bloodwoods, ironbarks and gum-barked eucalypts. In eastern Australia, the dominants largely comprise boxes, including poplar box (*Eucalyptus populnea*), and ironbarks. In the west, the canopy dominants include *Eucalyptus ptychocarpa* and *Eucalyptus salmonophloia*. The understoreys are variable, and may include varying proportions of grasses and shrubs depending on a range of factors including soil type (Gillison 1994).

Low eucalypt woodlands typically occur in the semi-arid areas of northern Australia characterised by summer rainfall and winter drought. The formation also includes the paperbark (*Melaleuca*) woodlands typical of the extensive swamp areas of far north-eastern Australia (Gillison 1994).

Low woodlands are also characteristic of the sub-alpine regions of eastern Australia where snow gum (*Eucalyptus pauciflora*) constitutes the main canopy dominant. The understorey of these high altitude woodlands may be grassy or heathy or include shrubs up to 5 metres in height (Williams and Costin 1994).

Very low woodlands typically occur in extreme environments characterised by periods of severe drought in northern Australia. The canopy is low (from 2 to 4 metres in height) and usually sparse (2 to 60 percent crown cover). The understorey comprises predominantly grasses, including hummock grasses (Gillison 1994).

Scrubs and shrublands

Eucalypt scrubs and shrublands are characteristically dominated by multi-stemmed shrub forms of *Eucalyptus*. Canopy height varies between 2 and 10 metres. Scrubs have a denser canopy cover (>30%) compared to shrublands. The dominant eucalypts include lignotuberous mallee growth forms, and non-lignotuberous marlocks (Parsons 1994).

Marlock vegetation occurs in the south-west of Western Australia where it has a relatively restricted distribution. In contrast, mallee vegetation is widespread, particularly in semi-arid areas (200 to 550 mm mean annual rainfall) in the south of the continent where it extends from New South Wales to Western Australia. Isolated patches of mallee also occur scattered throughout the arid areas of the continent (Parsons 1994).

Mallee represents the most arid of the eucalypt-dominated vegetation types in Australia. In wetter areas, it is replaced by woodland, and in more arid areas, by *Acacia*-dominated shrubland. As discussed previously, mallee vegetation also occurs in other areas in response to extremes of temperature, soil infertility, salt exposure etc (Parsons 1994).

An estimated 200-210 eucalypt taxa occur as canopy dominants in mallee vegetation. All eucalypt subgenera are represented amongst these. Some species such as *Eucalyptus diversifolia*, *E. incrassata* and *E. eremophila* exhibit widespread distributions in both eastern and western areas of the continent. Many others have restricted distributions. Up to 75 percent of mallee eucalypt species are endemic to Western Australia. Mallee areas of greatest species diversity also occur in south-west Western Australia. Marlock vegetation occurs in this region as well, with canopy dominants including *Eucalyptus annulata*, *E. platypus*, and *E. spathulata* (Parsons 1994).

Mallee communities include a wide diversity of understorey vegetation. The main types of understorey comprise scleromorphic shrubs, semi-succulent shrubs, and hummock grasses. A large complement of annual species is also present in some communities. The distribution of understorey types is broadly correlated with climate and soil factors. Infertile soils in areas with high and intermediate rainfall tend to support dense, rich understoreys dominated by scleromorphic shrubs. In the drier areas, infertile soils tend to support understoreys of hummock grasses, with varying complements of shrubs. Fertile soils display a variety of understorey types with varying proportions of grasses and shrubs. Generally, semi-succulent shrubs form an increasingly dominant component of mallee understoreys on fertile soils with decreasing rainfall (Parsons 1994).

Vegetation pattern according to Bridgewater (1987)

Another interpretation of vegetation pattern in Australia has been put forward by Bridgewater (1987). He used a combination of the natural regions defined by Barlow (1985), broad climate types based on those of UNESCO (1973), structural characteristics of the vegetation and the distribution of a few key taxa, including the eucalypt subgenera, to delineate major patterns in the distribution of vegetation at the continental scale.

Bridgewater (1987) used three broad classes of mapping units for the vegetation, including: Tropical/Subtropical evergreen wooded vegetation; Semi-arid grassland and shrublands; and Temperate forests, grasslands and shrubland. Within these classes, 34 vegetation types were recognised, including 16 eucalypt-dominated vegetation types. A map of these may be found in Bridgewater (1987, pp 78, 79). The eucalypt vegetation types described by Bridgewater (1987) and their mapping unit numbers are listed below:

Tropical/Subtropical evergreen wooded vegetation

1. *Eudesmia - Corymbia - Blakella - Symphyomyrtus* forest or woodland
2. *Corymbia - Blakella - Symphyomyrtus* woodland
5. *Corymbia - Symphyomyrtus* woodland
6. *Symphyomyrtus - Monocalyptus* forest
7. *Angophora - Eudesmia - Corymbia - Blakella - Symphyomyrtus* woodland
8. *Monocalyptus - Symphyomyrtus - Idiogenes* forest
9. *Corymbia - Symphyomyrtus - Gaubea* forest

Semi-arid grassland and shrublands

18. *Eudesmia - Monocalyptus - Symphyomyrtus* sclerophyllous shrubland (Mallee)

Temperate forests, grasslands and shrubland

21. *Corymbia - Monocalyptus - Symphyomyrtus* forest
22. *Symphyomyrtus* woodland, with scattered shrubs understorey
23. *Symphyomyrtus* woodland, with shrub or grass understorey
24. *Symphyomyrtus* woodland, with *Bothriochloa*/*Heteropogon* understorey
26. *Monocalyptus* woodland
28. *Symphyomyrtus - Monocalyptus* forest
29. *Corymbia - Symphyomyrtus - Monocalyptus* winter-rain forest
30. *Symphyomyrtus* winter-rain sclerophyllous forest

These mapping units for eucalypt vegetation can be interpreted within the eight broad biogeographic regions of Beadle (1981, Figure 6.2, p. 125) as follows. Mapping units are included in square brackets.

1. **Wetter Tropics**, which extends across large parts of the tropical north of the continent [1, 2, 5];
2. **Eastern Coastal Lowlands**, which extends the length of the east coast [6, 8, 9, 21];
3. **Eastern Inland Lowlands**, which includes the inland slopes of the Great Divide together with the northern parts of the Divide [1, 7, 9, 23, 24, 28];
4. **Eastern Highlands**, comprising the southern parts Great Divide in New South Wales and Victoria [26, 28];
5. **Tasmania** [27, 28];

6. the **Mallee**, which extends across the southern part of the continent and is divided by the Nullarbor Plain [18, 22, 28];
7. **South-western Australia**, which includes higher rainfall areas in the south-west of the continent [18, 22, 29, 30]; and
8. the **Semi-arid and Arid Areas**, which comprise a large part of the centre of the continent, extending to the coast in some areas [5, 8, 18].