

## **Chapter 6.**

### **Eucalyptus (*Eucalyptus* spp.)**

*This chapter deals with the biology of eucalyptus tree (*Eucalyptus* spp.). It contains information for use during the risk/safety regulatory assessment of genetically engineered varieties intended to be grown in the environment (biosafety). It is focused on those *Eucalyptus* species and hybrids which are planted commercially and expected to be the subjects of possible genetic modification. The chapter provides elements of taxonomy; centre of origin; domestication and cultivation practices; crop improvement; morphological characters; reproductive biology including sexual/asexual reproduction; pollination and seed dispersal; genetics; abiotic interactions with nutrients, metals, temperature, water, salinity and other stresses; pests and pathogens; weediness; natural and manipulated hybridization; and health considerations.*

This chapter was prepared by the OECD Working Group on the Harmonisation of Regulatory Oversight in Biotechnology, with Australia as the lead country. It was initially issued in August 2014. Information on the main eucalypt species and their hybrids used in plantations in the world (Table 6.1) was updated in January 2016.

## Introduction

*Eucalyptus* is a diverse genus of flowering trees (and a few shrubs) that belongs to the angiosperm family Myrtaceae. The genus includes more than 700 species, most being endemic to Australia. In that continent they are found in a range of different environments, from the dry hot interiors to the cold temperate regions in the south-east, invariably constituting the dominant large plants in forests. Colloquially, many species in Australia are known as “gum trees”, a term which refers to the sticky thick sap which exudes from their stems if the bark is broken. A few species are native to Papua New Guinea and Indonesia, and one is native to the Philippines.

In the last 200 years, many of these species have been introduced as exotics in other countries around the world. Most of these are grown in large commercial plantations in the tropics and subtropics, these plantations being particularly prominent in South America, North America, southern Europe, Africa, the Middle East, the People’s Republic of China (hereafter “China”) and the Indian subcontinent. Wood from *Eucalyptus* is used for the extraction of pulp and timber for building as well as raw material for biofuel production, while some of the organic compounds derived from its leaves have medicinal and insecticidal properties.

The purpose of this chapter is to present information which may be of direct relevance to the assessment of the risks/safety of genetically engineered *Eucalyptus*. Genetically engineered plants are produced by the transformation of one or more genes into their genomes, these genes being selected to confer a desired trait upon the plant. Potentially, the inserted genes and associated traits could affect the health and safety of humans (and animals), as well as the environment. These risks need to be assessed before any such plant is released for cultivation. Information in this chapter includes the reproductive biology, genetics, hybridisation, ecology, allergens and toxins, beneficial chemical products and breeding of *Eucalyptus*.

Those *Eucalyptus* species that are planted commercially are expected to be the subjects of genetic modification. The most important of these species are *Eucalyptus grandis*, *E. urophylla*, *E. pellita*, *E. globulus*, *E. nitens*, *E. dunni*, *E. camaldulensis*, *E. tereticornis* and *E. saligna*, and the hybrids *E. urophylla* x *E. grandis*, *E. camaldulensis* x *E. grandis* and *E. globulus* x *E. nitens*. As plantations of hybrids are becoming increasingly common, it is possible that such plants will form the core of future genetically engineered *Eucalyptus*.

As the centre of *Eucalyptus* diversity, Australia produced much of the early-published research on the biology and ecology of these plants, and a corresponding emphasis on Australian material may be found in parts of this chapter. However, with the increasing commercial importance of *Eucalyptus* worldwide, there has also been considerable output by groups in South America, South Africa and Japan. The present chapter therefore draws extensively on excellent and comprehensive reviews produced by these groups. Information from other world regions has also been included where possible.

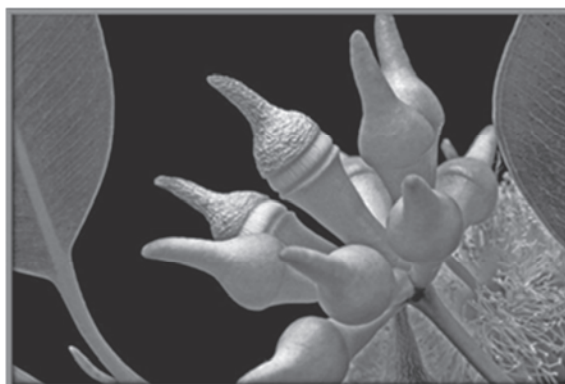
While the volume of research on *Eucalyptus* is large, it has generally focused on a limited number of species. This should be borne in mind when reading general statements relating to *Eucalyptus* biology and ecology in this document.

## Taxonomy of species

### *Classification and nomenclature*

The term *Eucalyptus* was coined by the French botanist Charles-Louis L'Héritier de Brutelle in the late 18th century while characterising a specimen brought back from Adventure Bay, Tasmania, on the third expedition of Captain Cook to Australia and the Pacific (Kantvilas, 1996). He made the word from two Greek roots, *eu* and *kalyptos*, meaning “well” and “covered” respectively, the reference being to the operculum, the cap on the flower bud which protects the plant reproductive structures prior to its displacement by the growing stamens (Figure 6.1).

Figure 6.1. **Displacement of *Eucalyptus robusta* operculum by growing stamens**



Source: Courtesy Brian Johnston, 2007.

*Eucalyptus* is a genus of the Myrtaceae family, a family which is mainly found in countries of the southern hemisphere (Rozefelds, 1996). The Myrtaceae also includes genera such as *Melaleuca*, *Callistemon*, *Psidium* (guava) and *Syzygium* (cloves).

The term “eucalypt” is sometimes used as the common name of the *Eucalyptus* genus. However, it is more accurately used as a term referring to species from a monophyletic group, broadly referred to as the “eucalypt group”, which encompasses seven genera: *Eucalyptus*, *Angophora*, *Corymbia*, *Eucalyptopsis*, *Allosyncarpia*, *Stockwellia* and *Arillastrum* (Ladiges, Udovicic and Nelson, 2003). *Eucalyptus* L'Hér. *sensu stricto* is the largest genus of the group.

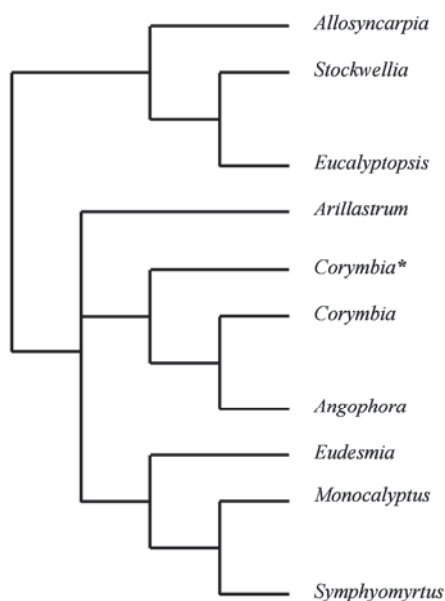
Most *Eucalyptus* species are found in Australia, where it is the dominant biota in mature forests, but species also naturally occur in Papua New Guinea and adjacent islands, Indonesia and the Philippines (one species). Members of this genus are usually long-lived evergreen hardwood plants, varying from shrubs to tall forest trees, a common distinctive feature being the aroma of their oils.

Morphological examination of *Eucalyptus* has given rise to a number of different taxonomic classifications of species. One influential study defined two genera, *Angophora* and *Eucalyptus*, the latter consisting of 7 subgenera (Pryor and Johnson, 1971), while more recently another important classification suggested a single genus (*Eucalyptus*) consisting of 13 subgenera (Brooker, 2000). Important physical characters that have been used in these classifications include the structure of the flower, the shapes of the leaves, and the shapes and sizes of the seeds. Although disagreement concerning

aspects of the taxonomic rank and number of groupings will remain, the three major lineages of *Eucalyptus* are *Symphyomyrtus*, *Monocalyptus* and *Eudesmia* (Figure 6.2). These three lineages, referred to here as subgenera, contain approximately 450, 110 and 20 species, respectively. *Symphyomyrtus* includes gums, ironbarks and mallees, *Monocalyptus* trees such as jarrah, most of the stringybarks, and the mountain ash, while Bailey's stringybark and Darwin stringybark are members of the *Eudesmia* (Boland et al., 2006). In undisturbed Australian forests it is common to find mixed stands, consisting of one species each of the *Symphyomyrtus* and *Monocalyptus* subgenera (Davidson and Reid, 1980).

Molecular techniques, involving the analysis of specified DNA sequences, have been used to establish phylogenetic relationships within *Eucalyptus*. Sequences which have been examined include the internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions of the nuclear ribosomal DNA, various chloroplast sequences, and the nuclear gene cinnamoyl CoA reductase. These studies have generally confirmed the definition of *Eucalyptus* and the other "eucalypt" genera (*Angophora*, *Corymbia*, etc.) as distinct but closely related entities, and within *Eucalyptus* the division into the subgenera *Symphyomyrtus*, *Monocalyptus* and *Eudesmia* (Ladiges, Udovicic and Drinnan, 1995; McKinnon et al., 2008; Parra-O et al., 2006; Steane et al., 2002, 1999) (Figure 6.2). These basic taxonomic classifications have also been supported by an analysis of the concentration of the metabolite quercitol amongst the eucalypts (Merchant, Ladiges and Adams, 2007).

Figure 6.2. Simplified phylogeny of the major groups of eucalypts based on both nuclear and chloroplast DNA sequence data



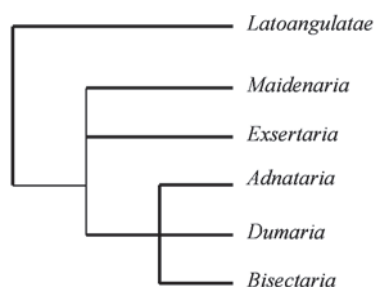
Note: \*Alternative grouping for *Corymbia* based on different data sets.

Source: Adapted from Ladiges, Udovicic and Drinnan (1995) and Ladiges, Udovicic and Nelson (2003).

The resolution of phylogenetic relationships within each of the subgenera by the use of molecular techniques has proven more difficult. Examination of variations in chloroplast DNA sequences have shown that they confirm the subgenera with *Eucalyptus*,

but within subgenera such approaches have produced data which do not always correlate with that from morphological studies (McKinnon et al., 2004; 1999). The difficulty in resolving taxonomic relationships within these subgenera is likely due to convergent evolution and hybridisation/introgression between species. At least in the *Eucalyptus* subgenus *Symphyomyrtus*, data from ITS sequences have revealed relationships between the sections of this subgenus which correlate with records of naturally occurring inter-sectional hybrids (Steane et al., 2002). Recently, amplified fragment length polymorphism (AFLP) markers have been used to resolve some of the relationships in the *Maidenaria* of the subgenus *Symphyomyrtus* (McKinnon et al., 2008). Within this section, the AFLP analysis provided both a resolution of the relationships between species for which previous molecular studies had been equivocal, as well as a set of phylogenetic relationships which strongly correlated with those based upon morphology (Figure 6.3).

Figure 6.3. **Phylogeny of the sections within the *Eucalyptus* subgenus *Symphyomyrtus***



Source: Adapted from Ladiges (1997).

The *Eucalyptus* species that have become the focus of major commercial enterprises and biotechnology belong mainly to the subgenus *Symphyomyrtus*. The major morphological identifying features of this lineage are seeds possessing coats consisting of one integument, and flowers with two opercula, the latter being sometimes fused. More specifically, these commercially important species belong to 3 of the 15 taxonomic sections of *Symphyomyrtus*. These sections, and their principle species, are:

- Section *Latoangulatae*: *E. grandis*, *E. urophylla*, *E. pellita* and *E. saligna*
- Section *Maidenaria*: *E. globulus*, *E. nitens* and *E. dunni*
- Section *Exsertaria*: *E. camaldulensis* and *E. tereticornis*

*Latoangulatae* (or *Transversaria* under the informal classification of Pryor and Johnson, 1971) are characterised by discolourous dorsiventral adult leaves (Boland et al., 2006; Brooker, 2000). Most of the species in this section are native to the mountain ranges of eastern Australia and the adjacent coasts, although a small number are found in the islands to the north of Australia. Plants in the section *Maidenaria* usually have sessile juvenile leaves and oil glands in their bark. They are mainly native to south-eastern Australia. The red gums, native to south-eastern and north-eastern Australia, constitute the section *Exsertaria*, one of their defining features being the petiolate nature of their juvenile leaves.

## Origin and cultivation

### *Centre of diversity and domestication*

The earliest fossils of Myrtaceae pollen, dating to the late Cretaceous period (85 million years ago), have been identified in deposits from Colombia, Gabon and Borneo (Muller, 1981). In Australia, the earliest occurrences of pollen fossils from this family date to the Palaeocene (65-55 million years ago), but identifying specimens as belonging to *Eucalyptus* (as opposed to other eucalypt genera such as *Angophora*) has proven more difficult (Martin, 1994). However, pollen from *E. spathulata* has been described from three sites dating to the end of the Tertiary period (Martin, 1988). Fossils of leaves and fruit from plants identified as belonging to the Myrtaceae family have been unearthed from a number of sites in Australia, and dated to various epochs within the Tertiary (Christophel and Lys, 1986; Lange, 1978). Other fossils have been more specifically identified as originating from *Eucalyptus* species. These include the Miocene fossils of leaves and fruit from species which have features similar to extant members of the subgenus *Symphyomyrtus* (Holmes, Holmes and Martin, 1982; Pole et al., 1993).

Fossils identified as coming from plants that may be members of *Eucalyptus* have been described from both Argentina and New Zealand (Frenguelli, 1953; Pole, 1993). At least in the case of the fossils from New Zealand, it has been suggested that they reflect a trans-Tasman migration of species. Although it may not be possible to determine with certainty the place of origin of the first plant that can be defined as *Eucalyptus*, the predominant native distribution of this genus in Australia (together with its modern absence from regions such as New Zealand and South America) has led to Australia being accepted as the likely region of its evolution.

As noted above, *Eucalyptus* is native not only to Australia, but some species are also endemic to the neighbouring islands to the north. These include *E. urophylla* and *E. deglupta* and a small number which occur in both Australia and Papua New Guinea (e.g. *E. alba* and *E. tereticornis*). Within Australia, *Eucalyptus* species are found in nearly all vegetation zones, the only exceptions being the rainforests in the north-east of the continent, the arid interior and the high alpine areas of the south-east. The subgenus *Symphyomyrtus*, which contains the most species, is also the most widespread. As large areas of Australia are prone to drought with infrequent floods, *Eucalyptus* species that come from these areas are adapted to surviving in soils with little available moisture (Morton et al., 2011).

The history of eucalypt introductions and subsequent domestication in exotic environments has been reviewed by Eldridge et al. (1994). Following the first record in Australia in the late 18th century, eucalypts were spread rapidly around the world into countries such as India (c. 1790), France (c. 1804), Chile (1823), Brazil (1825), South Africa (1828) and Portugal (1829) (Iglesias-Trabado and Wisterman, 2008; Potts, 2004) (Figure 6.4). They were initially introduced as botanical curiosities, but the potential for some species to grow fast was quickly recognised and they became widely planted for fuel wood and timber production. Eucalypts are now found in more than 90 countries (Iglesias-Trabado and Wisterman, 2008), having expanded rapidly in recent decades to total over 20 millions hectares in 2013 (Harwood, 2014)<sup>1</sup>.

The majority of plantations consist of only a few eucalypt species and hybrids. Based on visits to the major grower countries and discussions with grower agencies, Harwood (2011) estimated that nine eucalypt species in the subgenus *Symphyomyrtus* (Brooker,

2000), and clonal plantations of various interspecific hybrids among these species, account for 90-95% of the world's planted eucalypts (Table 6.1).

Figure 6.4. *Eucalyptus globulus* in Hawaii



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### ***Cultivation and commercial uses***

*Eucalyptus*, together with *Pinus*, are the most important commercially grown tree taxa (Richardson, 1998). Brazil and India have the largest areas of *Eucalyptus* plantations, but significant areas are found in Angola, China, Portugal, South Africa, Spain and Viet Nam.

The wood from *Eucalyptus* can be used for the production of poles and timber boards and beams for building, pallets, crates and furniture. Wood chips and bark particles from trees can be used for mulch, as well as serving as a fuel. More processed products include plywood, chipboards and fibreboards. Australian aboriginals have traditionally used *Eucalyptus* as a source of wood for making didgeridoos and many other artefacts.

Especially in Australia, Brazil, Chile, Portugal and South Africa, the wood from plantation-grown *Eucalyptus* species is used for the production of paper pulp, especially bright photocopy paper (Turnbull, 1999). *Eucalyptus* is the largest single global source of market pulp; it has been estimated that, by the end of 2011, global market pulp production would reach about 65 million tonnes, with about 33 million coming from hardwoods, and 55% of this coming from eucalypts (ICEP, 2011). Brazil also uses significant amounts of *Eucalyptus* wood to produce charcoal for its iron and steel industries (Figure 6.5).

*Eucalyptus* is renowned for the wide range of organic compounds that it produces. Climatic factors in Australia have likely played a significant role in the evolution of this feature. Originating in environments that are usually rich in sunshine and exposed to periodic rainfall, *Eucalyptus* species frequently conduct photosynthesis year-round, enabling the production of an abundant quantity and variety of carbohydrates and other carbon-based compounds (Orians and Milewski, 2007). From a chemical perspective, these compounds are often low in their nitrogen content, almost certainly a reflection of the poor available nitrogen content of many Australian soils. *Eucalyptus* oils are used in flavourings, fragrances, cosmetics and mouthwash.

Table 6.1. Nine eucalypt species and their hybrid combinations dominate the world's eucalypt plantations

Country	Most important species	Approximate range of mean annual temperature (°C) for good growth in plantations	Area in plantations 2012 (M ha)	% of clonal plantations	Rotation length (years)	Coppicing
Argentina, Australia, Chile, China (People's Republic of), Ethiopia, Portugal, Spain	<i>E. globulus</i>	9-18	3.0	10	12	Yes
Australia, Chile	<i>E. nitens</i>	9-18	0.4	0	12	No
Brazil	<i>E. urophylla</i> x <i>grandis</i>		4.0		6-7	Yes
China (People's Republic of)	<i>E. dunnii</i>	14-22	0.1	0	7	No
	<i>E. grandis</i>	14-25	0.1	80	7	Yes
	<i>E. urophylla</i> x <i>grandis</i>		2.0	100	5	Yes
	<i>E. camaldulensis</i> and <i>E. tereticornis</i>	18-28 (northern provenances) 13-22 (southern provenances) 17-27 (northern provenances)	2.0	30	4-7	Yes
India					4-7	Yes
Indonesia	<i>E. pellita</i>	20-27	0.3	90	5	Yes
South Africa	<i>E. grandis</i>	14-25	0.6	60	7	Yes
	<i>E. dunnii</i>	14-22				
	<i>E. urophylla</i> x <i>grandis</i>					
Thailand	<i>E. camaldulensis</i> and hybrids	18-28 (northern provenances) 13-22 (southern provenances)	0.3	90	4	Yes
Viet Nam	<i>E. urophylla</i> <i>E. camaldulensis</i>	18-28 18-28 (northern provenances) 13-22 (southern provenances)	0.4	10	6-8	Yes
Uruguay	<i>E. grandis</i> <i>E. dunnii</i>	14-25 14-22	0.7	20	8	Yes No
Other countries	Various, including <i>E. saligna</i>	Various 14-23	7	Various	Various	Various
<b>TOTAL</b>			<b>20</b>			

Source: Adapted from Harwood (2014; 2011).



Figure 6.5. *Eucalyptus* plantation in Brazil

Source: Cássio Abreu, licenced under CC-BY-2.0.

Worldwide, the most important plantation species are the pure species *E. camaldulensis*, *E. grandis*, *E. saligna*, *E. nitens* and *E. globulus*, and the hybrids *E. urophylla* x *E. grandis*, *E. camaldulensis* x *E. grandis* and *E. globulus* x *E. nitens* (Martin, 2003). In Australia, *Eucalyptus* species make up approximately 95% of broadleaf plantation species, over half of the *Eucalyptus* estate being composed of *E. globulus* (540 000 ha) and one-quarter by *E. nitens* (236 000 ha) (Gavran, 2012). Due to its adaptations to soils with low fertility, the hybrid *E. urophylla* x *E. grandis* has become the most common tree in Brazilian plantations, whereas in drier regions, hybrids of *E. camaldulensis* are favoured (Goncalves et al., 2008). In Brazil, the yield of wood products, mainly pulp, from *Eucalyptus* plantations has increased from 12 m<sup>3</sup>/ha/year to 40 m<sup>3</sup>/ha/year in 30 years (Campinhos, 1999), while in India, eucalypt plantations may be able to meet that country's demand for paper and pulp (Lal, 2010). Probably over 25% of the world's eucalypt plantation area involves interspecific hybrids, because these dominate the plantations of two of the biggest growing nations, Brazil and China, and are important in several other countries such as South Africa (Harwood, 2014)<sup>2</sup>.

Generally, the rotation period in *Eucalyptus* plantations is 6-14 years, with the density ranging from 400 trees to 1 100 trees per hectare (Martin, 2003). Rotation periods are even lower for some hybrids: from four to seven years (Harwood, 2014)<sup>3</sup>. These rotation times are significantly less than for other plantation species, especially species of *Pinus*, *Betula* and *Picea* (Campinhos, 1999). The ability to coppice plants (cut back to their stumps to allow fresh regeneration) in a plantation is advantageous because the costs of re-establishment are substantially reduced. Moreover, at least the first stages of regrowth are usually faster than growth from seed, and the resulting trunks straighter. *Eucalyptus* is readily amenable to coppicing, and most *Eucalyptus* plantations around the world are managed by this method (Matthews, 1991). In Brazil, *E. grandis* plantations are usually grown on coppice rotations of between five and ten years (Turnbull, 1999), and six to seven years for *E. urophylla* x *E. grandis* plantations (Table 6.1). It is normally possible to coppice *Eucalyptus* many times, but, while the yield from the first regrowth is occasionally greater than that of the original plant, the yields from subsequent such treatments are lower. Typically, the forest will be replanted with new seedlings of a genetically improved clone or seed crop newly derived from the breeding programme.

*Eucalyptus* plantation management has benefited from the application of the 3-PG model, a generalised forest carbon allocation model. Studies in Brazil and Portugal have demonstrated the usefulness of the model in predicting the growth patterns of stands, including characters such as height (Almeida, Landsberg and Sands, 2004; Rodriguez-Suarez et al., 2010).

The narrow genetic base of *Eucalyptus* plantations with clonally propagated elite trees (see below) has raised concerns about increasing vulnerability to insect or pathogen attack. After more than 30 years of clonal plantations in Brazil, however, this concern has proven largely overestimated and no documented cases exist of increased pest or pathogen attack to eucalypt clonal forests. Reasons that in practice mitigate this risk include: 1) every company recommends 2-5 new clones every 3-4 years so that a complete replacement of the clone portfolio will take place every 10-15 years; 2) each company plants 8-15 clones at any time so that the contribution of a single clone to the total planted area will be relatively small, and problematic clones, if they occur, can be rapidly removed with small relative damage; 3) clonal plantations are established in clonal blocks of 5-50 hectares with a single clone per block in a mosaic format so as to avoid a neighbourhood of blocks with the same clone; 4) breeding programmes exploit large amounts of genetic diversity so that output clones have very diverse genetic backgrounds; 5) clonal trials prior to final recommendation for commercial use adopt rigorous screening procedures for the common pathogens, since one of the major advantages of clonal deployment is the large-scale plantation of highly resistant trees (Grattapaglia et al., 2012). Additionally, in most plantations in Brazil, the maintenance of extensive areas of native vegetation contiguous to the *Eucalyptus* forests has proven an effective measure for the control of insects, as this vegetation is preferred by native birds which feed on insects. It has been recommended that plantations have a range of clones to both diminish the risk of low genetic variability and enable adaptation to changed environmental conditions (Campinhos, 1999). Percentages of clonal plantations estimated for some countries in 2012 are reported in Table 6.1.<sup>4</sup>

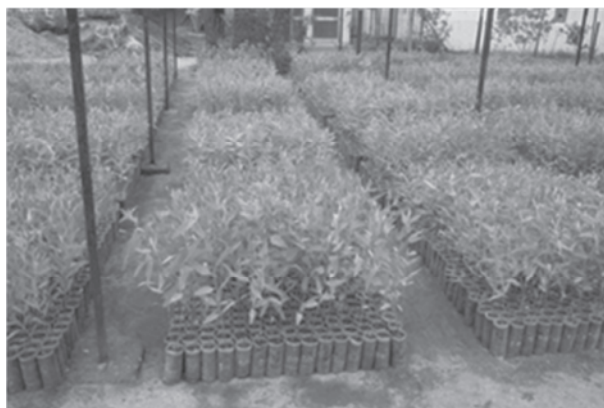
## ***Crop improvement***

### ***Breeding***

Breeding programmes in *Eucalyptus*, as with most common crop plants, have focused on the crossing of relevant elite lines containing desirable traits. The open pollination of flowers (i.e. pollination through natural mechanisms) is often used to produce hybrid seed, but controlled (hand) pollination is also practised (Horsley, Johnson and Myburg, 2010; Suitor et al., 2008). Open pollination is obviously easy, but suffers from the disadvantage that it will usually result in the presence of undesired self-pollinated individuals. Controlled pollinations have traditionally involved multiple visits to flowers, emasculation, and wounding or cutting of the stigma or style to enhance its receptivity to germination of pollen and the formation of pollen tubes. Such techniques are both time-consuming and costly, but so-called one-stop pollination, involving a single visit to a flower, has been developed for some species (Harbard, Griffin and Espejo, 1999). At least for *E. globulus*, it is possible to obtain successful fertilisation by the pollination of immature styles prior to flower dehiscence (Trindale et al., 2001), and also by cutting the style but not concurrently utilising emasculation (Patterson et al., 2004). This technique has now been optimised for several eucalypt species and given the term artificially induced protogyny; it has led to a significant advance in the ability to generate large quantities of seed from controlled crosses (de Assis, Warburton and Harwood, 2005).

The development of techniques for the clonal (asexual) propagation of plants has meant that plantations in countries such as Brazil and India now consist largely of clonal plantations, the sowing of seeds having been largely abandoned (Eldridge et al., 1994; Lal, 2010). Clonal propagation can be conducted by the use of rooted stem cuttings, but this technique has proven unsuitable for a number of commercially important species, either because of the difficulty in obtaining roots or of the large number of rooted plants which have developmental problems. However, cuttings taken from cotyledons, shoot apices and axillary sprouts are much easier to manage (de Assis, Fett-Neto and Alfenas, 2004; Le Roux and Van Staden, 1991). The mini-cutting technique, now widely adopted in Brazil and some other countries, currently represents the most efficient way to clonally propagate eucalypts (de Assis, 2011) (Figure 6.6). Experiments in Africa with terminal shoots of *E. urophylla* x *E. grandis* have demonstrated that root development is superior if they come from juvenile trees (at least during the dry season), but shoots derived from the regrowth of coppiced trees root equally well regardless of the age of the felled tree (Mankessi et al., 2011).

Figure 6.6. Mass propagation of *Eucalyptus* seedlings



Source: Balaji Kasirajan, licenced under CC BY-SA 3.0.

Clones of *Eucalyptus* can also be generated by somatic embryogenesis, a technique which allows the formation of embryos from somatic or haploid cells, avoiding the need for gamete fusion. Somatic embryogenesis has been used to propagate *E. citriodora*, *E. dunnii*, *E. grandis*, *E. nitens* and *E. globulus* (Pinto et al., 2002) at the experimental level. For *E. globulus*, a protocol for somatic embryogenesis has been developed that may enable the industrial production of such tissue (Pinto et al., 2010), although no operationally viable protocol exists. In that plant, it is apparent that induction of somatic embryogenesis is under additive genetic effects, in particular the so-called general combining ability effect (Pinto et al., 2008). Importantly, micro-propagated tissues and embryos are amenable to protocols for the transformation of genes, such as those using *Agrobacterium tumefaciens*.

In Brazil, trees with desirable traits, such as above-average rates of growth, are selected in screenings of individuals and cloned by using one of these techniques. However, at least in some cases, further enhancement of populations through the selection of individuals from already improved trees is proving difficult, and techniques such as artificial hybridisation may be useful (Fonseca et al., 2010). This latter technique involves the controlled crossing of individuals and the field evaluation of the progeny.

Modern molecular techniques, such as measuring the expression levels of genes known to influence a trait, may prove useful in selecting the individual trees for clonal propagation. Even for trees which are the product of natural or traditional breeding, such techniques can be employed to measure the success and/or levels of outcrossing (Gaiotto, Bramucci and Grattapaglia, 1997). In order to compare the expression of genes between species, especially when employing the polymerase chain reaction (PCR), a reference gene is needed for normalisation. Genes suitable for this role have been identified for *E. globulus*, and should prove useful in other species (Almeida et al., 2010b).

Genetic linkage maps, based on RFLP, RAPD and AFLP molecular markers, have been constructed for species such as *E. grandis*, *E. urophylla* and *E. globulus* (Gan et al., 2003; Grattapaglia and Kirst, 2008; Grattapaglia and Sederoff, 1994; Myburg et al., 2003). A microsatellite map, covering at least 90% of the genome of *Eucalyptus* and containing over 230 mapped loci, has also been published (Brondani et al., 2006), which was recently significantly expanded by using much higher throughput marker technologies (Hudson et al., 2012b). Microsatellite markers have been widely used for genotyping species of *Eucalyptus*, especially those in the subgenus *Symphomyrtus* (Faria et al., 2011; Kirst et al., 2005). These latter markers were based on the sequences of existing expressed sequence tags (ESTs), and it is expected that they will be useful in differentiating individuals and become part of work which necessitates clone fingerprinting and the testing of parentage. Future marker-assisted breeding programmes will likely use a range of different molecular markers, including those arising from high throughput techniques such as diversity arrays technology (Sansaloni et al., 2010) or genotyping by sequencing (Faria et al., 2012).

### *Genetic modification*

The success of *Eucalyptus* as a plantation crop has meant that it has been the subject of research aimed at improving some of its associated traits by the use of genetic engineering. In particular, the role of *Eucalyptus* in the paper industry has focused attention on improving traits of productivity and wood quality, for which the sensitivity of many commercial species and hybrids to cold temperatures has been a major target. Constitutive overexpression and controlled stress induction of C-repeat binding factor (*CBF*) genes in *E. grandis* x *E. urophylla* has resulted in the isolation of “freeze-tolerant” plants (Hinchee et al., 2009; Navarro et al., 2011). The US Department of Agriculture, Animal and Plant Health Inspection Service (USDA-APHIS) has issued a number of permits for the field testing of *Eucalyptus* trees engineered with the *CBF* gene, this process involving the preparation of environmental assessments (APHIS, 2012a; 2012b).

These plants have demonstrated tolerance to temperatures of -9°C. The products of the *CBF* genes are transcription factors which activate a stress responsive pathway by binding to specific *cis*-acting regulatory sequences. In a different approach, cold stress tolerance in *E. saligna* has been addressed by the transformation into plants of the  $\Delta^1$ -pyrroline-5-carboxylate synthetase gene (*P5CS*, coding for a key enzyme in proline biosynthesis) from *Vigna aconitifolia* (Dibax et al., 2010).

Other traits of *Eucalyptus* that have been subject to modification by genetic engineering include responses to a range of biotic and abiotic stresses, constitution of the endogenous essential oils and the biosynthesis of lignin. Table 6.2 summarises the major genetic modifications of *Eucalyptus* in published literature.

Table 6.2. Genetic modifications of *Eucalyptus*

Plant	Gene inserted	Trait	Reference
<i>E. urophylla</i>	RS-AFP2 from radish	Disease resistance	Ouyang et al. (2012)
<i>E. globulus</i>	Choline oxidase ( <i>codA</i> ) from <i>Arthrobacter globiformis</i>	Salt stress and/or drought tolerance	Matsunaga et al. (2012); Yu et al. (2009; 2012a)
<i>E. globulus</i>	<i>des9</i> from cyanobacteria	Low temperature	Japan Biosafety Clearing-House (2011)
<i>E. globulus</i>	Antisense LIM domain transcription factor	Decrease in lignin content	Shimazaki et al. (2009)
<i>E. grandis</i> x <i>E. urophylla</i>	CBF from <i>Arabidopsis</i> and <i>E. gunnii</i>	Cold tolerance	Hinchee et al. (2009); Navarro et al. (2011)
<i>E. saligna</i>	P5CS from <i>Vigna aconitifolia</i>	Cold tolerance	Dibax et al. (2010)
<i>E. camaldulensis</i>	Mangrin from the mangrove plant <i>Bruguiera sexangula</i>	Salt tolerance	Lelmen et al. (2010)
<i>E. camaldulensis</i>	Limonene synthase from <i>Perilla frutescens</i>	Monoterpene composition	Ohara et al. (2010)
<i>E. camaldulensis</i>	Antisense LIM domain transcription factor	Decrease in lignin content	Kawaoka et al. (2006)
<i>E. camaldulensis</i>	choline oxidase ( <i>codA</i> ) from <i>Arthrobacter globiformis</i>	Salt stress and drought tolerances	Kikuchi et al. (2009)
<i>E. camaldulensis</i>	DREB1A from <i>Arabidopsis</i>	Salt stress and drought tolerances	Hibino (2009)
<i>E. camaldulensis</i>	Mangrin from the mangrove plant <i>Bruguiera sexangula</i>	Salt stress and drought tolerances	Lelmen et al. (2010); Yu et al. (2012b)
<i>E. grandis</i> x <i>E. urophylla</i>	Radish plasma membrane aquaporin gene	Drought tolerance and water use efficiency	Tsuchihira et al. (2010)
<i>E. grandis</i> x <i>E. urophylla</i>	Antisense cinnamyl alcohol dehydrogenase (CAD)	Decrease in lignin content	Tournier et al. (2003); Valerio et al. (2003)

Transformation of *Eucalyptus* has been achieved both through biolistics and the use of *Agrobacterium tumefaciens*. In regard to biolistics, for example, zygotic embryos of *E. globulus* have been stably transformed after biolistic delivery with linear DNA constructs (Serrano et al., 1996). However, *Agrobacterium* mediated transformation was used to generate all of the genetically modified plants in Table 6.2. Other reports pertaining more generally to *Agrobacterium* transformation relate to *E. camaldulensis* (Mullins et al., 1997), *E. globulus* (Moralejo et al., 1998), *E. grandis* x *E. urophylla* (Gonzalez et al., 2002; Machado et al., 1997), *E. occidentalis* (Southerton, 2007) and *E. tereticornis* (Prakash and Gurumurthi, 2009). Usually explants of shoots, leaves and cotyledons are used for *Agrobacterium* transformation.

The isolation and characterisation of genes associated with a specific trait is instrumental in the understanding of the molecular basis of that trait, as well as providing a pool of clones from which promising members can be selected for transformation (Harakava, 2005). For *Eucalyptus*, many endogenous genes for transformation are likely to come from the screening of EST and cDNA libraries for genes involved in fundamental (and commercially important) developmental processes, such as the biosynthesis of lignin. Genes can be expressed with their endogenous promoters, engineered to be expressed with tissue-specific, temporal-specific or constitutive promoters, or appropriately manipulated and inserted in transformation vectors for the silencing of their expression.

## Morphology

### *Plant morphology*

*Eucalyptus* species are almost all broad-leaved evergreens, but in northern Australia there are a small number of deciduous or semi-deciduous species which will lose their leaves if severely water stressed by the end of the dry season. Most prominent among these latter plants is *E. platyphylla*, commonly known as the poplar gum or cabbage gum.

Species of *Eucalyptus* vary greatly in height, from less than 1 m to over 90 m. In Australia, the larger species constitute the dominant visual flora of most landscapes (Williams and Brooker, 1997). *E. diversifolia*, one of the smaller species, may grow to only 40 cm in the windy environments along the southern coast of Australia, while *E. regnans* (mountain ash), which is native to the south-eastern Australian mainland and Tasmania, reaches at least 90 m, with reports of individuals of over 100 m (<http://gianttrees.com.au>; Hickey, Kostoglou and Sargison, 2000). The diameters of trees of this latter species can reach well over 5 m (Figure 6.7).

Figure 6.7. Diversity of form amongst eucalypt species

A. A tall forest tree, *E. grandis* can grow to 45-50 m in height



B. *E. macrocarpa*, a small mallee grows up to 4 m in height



Source: Courtesy Alison Wardrop, OGTR.

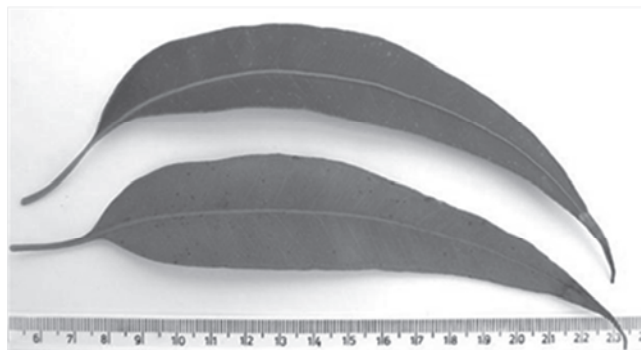
The leaves of *Eucalyptus* are usually asymmetrical about the central midrib, a feature common in many tree genera (Figure 6.8). In most species, the leaves of adult trees hang vertically, while those of juvenile trees are near horizontal. This feature of adult trees is responsible for the large amount of light which reaches the floor of *Eucalyptus* forests, especially in comparison to broad-leaf and conifer forests.

The developmental stage at which the shift in leaf angle from horizontal to vertical occurs varies between species. Generally, leaves that are vertical have almost the same colour and morphology on both sides; conversely, these traits are much less common in species with horizontal leaves (King, 1997). Vertical leaves have the advantage of decreasing the interception of light in the middle of the day, thus decreasing the loss of water by transpiration when the day is hottest. In the case of the vertical hanging leaves of *E. globulus*, there is no preference for either side of the leaves receiving most of the incident radiation. On the other hand, the horizontal leaves of young plants intercept



greater amounts of radiation than vertical leaves, and as such their leaves are almost certainly exposed to greater transpirational water loss (James and Bell, 2000). Nevertheless, the horizontal nature of these leaves may be beneficial in increasing photosynthesis and promoting the growth of young plants and the formation of a mature canopy.

Figure 6.8. Leaves of *E. grandis*



Source: SelecTree (2016). This citation has been added for update in January 2016.

In Australia, as might be expected, species with adult vertical leaves predominate in the dry interior, but surprisingly they are also very common in the wetter forests of the south-eastern part of the mainland and in Tasmania. The explanation for this latter phenomenon may be related to advantages in accessing radiation in winter when the sun is lower in the skies (especially at higher latitudes), and in reducing the effects of cold night temperature induced photoinhibition (Ball, Hodges and Laughlin, 1991; King, 1997).

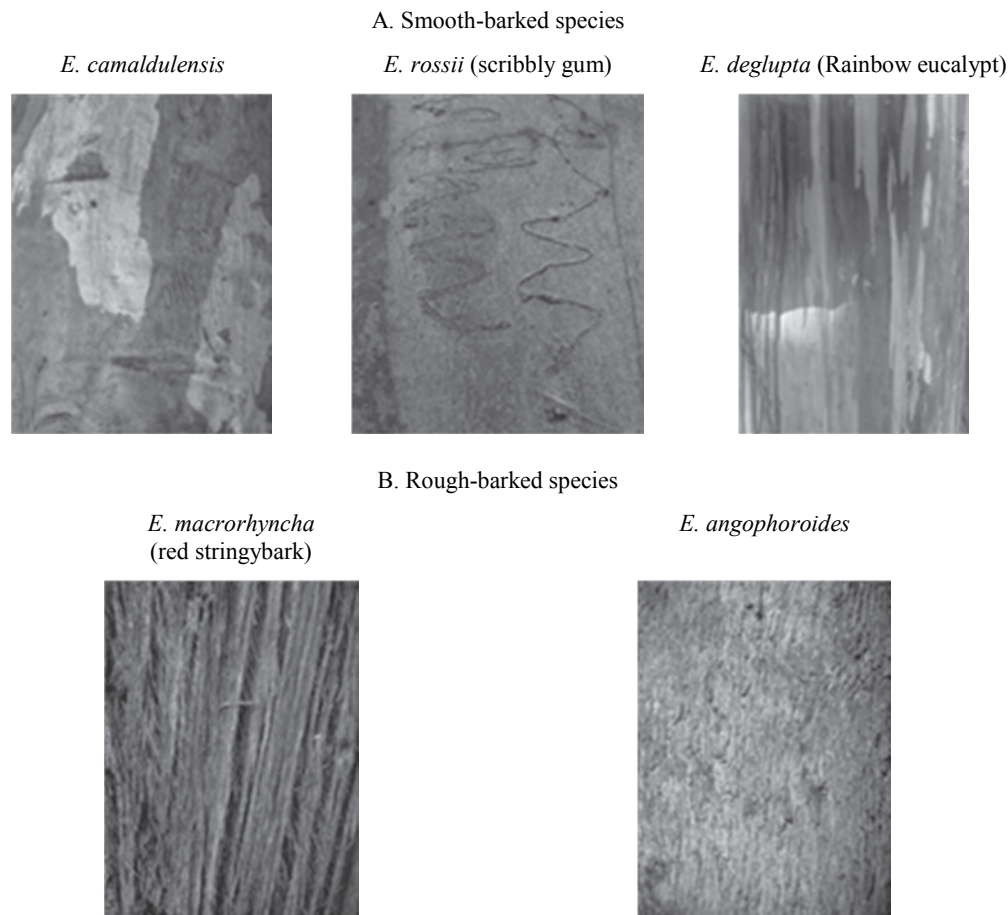
The barks of *Eucalyptus* species are usually classified as either “rough” or “smooth”. Rough-barked species (invariably large trees) have thick barks which break and are lost all year round, the surface beneath being essentially bark identical to that which is lost. The bark of smooth-barked species seasonally sheds, partially detaching and then finally falling off trunks in long strips. The exposed surface of the trunk is often characterised by the scribbles left by insects, leading to the term “scribbly gums” being loosely applied to such species. *E. deglupta*, a native of Papua New Guinea, the adjacent islands, and Mindanao in the Philippines, has brightly coloured smooth bark of shades of yellow, orange, red, green and brown; it is commonly known as the Rainbow *Eucalyptus* (Figure 6.9).

Some species of *Eucalyptus* produce a single stem from the time of germination, while others are characterised in their juvenile stage by several horizontal and/or oblique shoots, one of which will later become the major vertical stem. In the growing crown, the major branches seemingly compete with each other for prominence, eventually establishing the structure of the mature crown. A tree can remain in this mature phase for decades, and even more than a century (Florence, 1996).

Morphological characters that are used to differentiate *Eucalyptus* species, and the subspecies within a species, include the structure of the flower (number of capsules per umbel, size of the capsule, number of ribs per capsule), and the size and shapes of leaves (both in seedlings and adult plants). Leaf characteristics have proven particularly useful in differentiating two or more species that are nearly identical in other visible traits. Not

only do leaves show variation between species, but often show both intraspecific and interspecific clinal variation<sup>5</sup> (Phillips and Reid, 1980; Potts and Reid, 1985). At least in some cases, if not most, this clinal variation is under genetic control.

Figure 6.9. **Barks of *Eucalyptus* species**



Sources: (A): left: courtesy Paul Venter, July 2006, [http://en.wikipedia.org/wiki/Image:Euc\\_cam03.jpg](http://en.wikipedia.org/wiki/Image:Euc_cam03.jpg); centre: courtesy Alison Wardrop, OGTR; right: Mann Jess, licenced under CC BY-SA 3.0. (B): left: courtesy Alison Wardrop, OGTR; right: benjamint444, licenced under CC BY-SA 3.0.

Traditionally, observation of the existence of hybrid plants, and the frequency of hybridisation, has depended on the examination of morphological characters, the expectation being that hybrid individuals will possess a mixture of characters and/or characters intermediate between those of the pure bred progenitors. Usually hybrid plants are found where two closely related *Eucalyptus* species overlap in their respective habitats, the presence of these plants indicating the plasticity of the reproductive barriers between the species. However, it is now generally accepted that relying on morphological characters alone will invariably underestimate the number of hybrid plants, and molecular markers give a more accurate estimate of the levels of hybridisation (Field et al., 2009). As with other plants, the ability of *Eucalyptus* species to hybridise depends upon the flowering times of the potential parents (Barbour et al., 2002). Generalised flowering times in Australia of the major plantation species have been compiled and summarised by Potts, Barbour and Hingston (2001; also see Eldridge et al., 1994).



Some species show distinct intraspecific variation. For instance, there are four subspecies of *E. globulus*, each defined not only by their distinct morphology but, in their native Australia, by separate yet overlapping geographical locations (Jones et al., 2002). Likewise, *E. diversifolia* can be divided into three morphologically separate subspecies (Wright and Ladiges, 1997). In many cases, intraspecific variation is at least partly due to the definite isolation of populations, these often being separated by large distances (Shaw, Potts and Reid, 1984). Such variation is also reflected in traits such as pest and pathogen resistance (Guimaraes et al., 2010; O'Reilly-Wapstra, McArthur and Potts, 2002).

### ***Reproductive morphology***

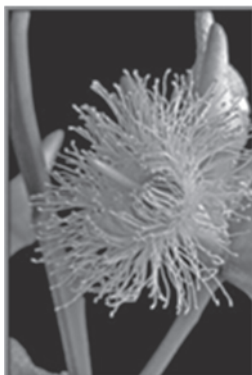
The inflorescences of *Eucalyptus* species are formed in the axils of leaves. Most species have a simple inflorescence, but some possess a compound inflorescence which may be either lateral or terminal. Initially, the inflorescence is surrounded by bracts, which are shed to reveal the juvenile bud or buds. Each bud, the progenitor of a flower, develops into a cup-shaped structure, with this process often occurring over at least a two-year period prior to the actual commencement of flowering. Although some species, such as *E. globulus*, have a single bud per inflorescence, most species have higher odd numbers of buds arranged in a cyme, the most common numbers being three and seven. In cymes with only a small number of buds, the pattern of branching is dichasial, but with increasing numbers of buds, an initial dichasial system is usually replaced by a monochasial system (Carr and Carr, 1959). Some species, such as *E. pauciflora*, can have inflorescences with over 50 buds. For many species, a single tree branch will concurrently contain inflorescences still surrounded by bracts, immature buds, flowers and seed pods, thus representing the entire range of developmental stages in flowering (Florence, 1996) (Figure 6.10).

Figure 6.10. *Eucalyptus tereticornis* buds, capsules, flowers and foliage



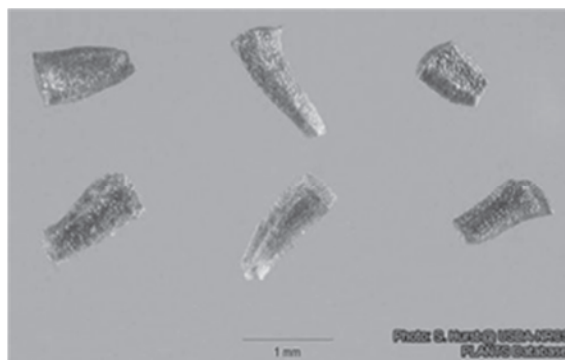
Source: Ethel Aardvark, licenced under CC BY-SA 3.0.

The flowers of most *Eucalyptus* species have functional male and female structures. The stamens and style are covered by a cap termed the operculum, which is forced off the cup-shaped base of a bud by the growing stamens. There are no true petals in the flowers, the cap representing a fusion of these organs alone or with the sepals, although sometimes the mature structures are almost indistinguishable (Carr and Carr, 1968). Depending on the species, the stamens are brightly coloured white, yellow, pink or red, this colour giving the visual showy effect to *Eucalyptus* flowers (Figure 6.11).

Figure 6.11. *Eucalyptus* flowersA. *E. robusta* flower showing displacement of cap (operculum)B. *E. robusta* flower showing central green style and stigma and surrounding anthersC. Bright pink stamens of *E. leucoxylon* flowers

Source: (A) and (B) courtesy Brian Johnston, 2007; (C) Jean Tosti, licenced under CC BY-SA 3.0.

After flowering and fertilisation, most species develop hard, woody seed capsules (fruits) (Figure 6.12). Each capsule usually contains fertile seeds alongside unfertilised ovules termed “chaff”. Examination of the capsules from 21 species of *Eucalyptus* from south-western Australia showed that the largest seeds were 9 times wider than the smallest and 200 times heavier, while the number of fertile seeds per capsule varied from 1 to over a 100. These differences were somewhat associated with subgenera, species from *Monocalyptus* usually having fewer fertile seeds than *Symphyomyrtus* species (Gill, Brooker and Moore, 1992). Species that are subject to frequent fires produce smaller seeds, which are likely to provide superior abilities to germinate and colonise ash beds. Conversely, species that are less prone to fires produce larger seeds, the resulting larger seedlings being able to grow and establish over the periods between fires (Murray and Gill, 2001). Seeds are reported to be very small in the fast-growing plantation species (100 000-600 000 seeds per kg) (Eldridge et al., 1994).

Figure 6.12. Seeds of *E. camaldulensis*

Source: Courtesy Steve Hurst, hosted by the USDA-NRCS Plants Database.

Nectar is produced from the base of the style, and attracts a wide range of insects, birds, possums and bats, which facilitate pollination. The few studies of nectar production

suggest that for *Eucalyptus* there is greater secretion at night, but at least one species of *Corymbia*, *C. gummifera*, appears to have no diurnal or nocturnal cycle (Goldingay, 2005; Horskins and Turner, 1999).

## Development

### *Reproductive biology*

#### *Sexual reproduction*

*Eucalyptus* species are usually capable of self-fertilisation, but in most cases breed by a combination of self-pollination and outcrossing, with the latter being more common. Outbreeding rates are relatively high (0.69-0.84; Moran and Bell, 1983) and are maintained by protandry.<sup>6</sup> Self-fertilisation frequently results in a reduction in the production of capsules, the number of seeds and in the vigour of the seedlings themselves (Eldridge et al., 1994; Potts and Wiltshire, 1997). However, although outcrossing may be favoured in *Eucalyptus*, its rate is dependent upon the number and density of trees, and even within a species, individual trees may be either fully self-fertile or almost incapable of self-fertilisation.

Extensive research supports the above conclusions. For example, in comparison to the analogous self-pollinations, cross-pollination of *E. nitens* resulted in greater numbers of healthy, developing ovules (Pound et al., 2003b) and cross-pollination of hybrids of *E. platypus* and *E. spathulata* resulted in more seeds per capsule (Wallwork and Sedgley, 2005). Experiments involving pollination of *E. grandis* with self and donor pollen demonstrated that the latter pollen results in the set of a greater number of seed, and in the case of pollinations with mixtures of self and donor pollen, the progeny were all the result of outcrossing (Horsley and Johnson, 2010). This is likely due to differential rates of pollen tube growth, a phenomenon which has been observed for self- versus donor-pollen tubes in *E. urophylla* and *E. grandis* (Horsley and Johnson, 2007). However, in other cases, the progeny of self-fertilisations may be selected against by mechanisms which operate after the formation of the zygote (James and Kennington, 1993). Regardless of the type of fertilisation, it is generally believed that the germination of pollen on the stigma is rapid, its viability on the stigma not exceeding a few days (Eldridge et al., 1994).

The reproductive success of any tree is linked to a range of factors. These include its age, location, health, and the number and size of its flowers. In *E. globulus* (Figure 6.13), the reproduction of individuals is associated with the size of flowers and features of the female reproductive organs, such as the size of the style and number of ovules (Suitor et al., 2009).

#### *Asexual reproduction*

Most eucalypt species can be artificially propagated by rooted cuttings provided the cuttings are taken from young seedlings (Eldridge et al., 1994). However, natural asexual means of reproduction such by the use of rhizomes and stolons, and the ability of tissues to give rise to small plantlets (natural vegetative propagation), is extremely rare. Only in isolated instances, amongst tropical woody species such as *E. porrecta*, *E. ptychocarpa*, and *E. jacobiana*, as well as *E. moluccana* and *E. stellulata* which are found in more temperate climates, have rhizomes and/or stolons been observed (Gillison, Lacey and Bennett, 1980; Lacey, 1974).

Figure 6.13. *Eucalyptus globulus*

Source: Rezerga, licenced under CC BY-SA 3.0.

Many species, especially the mallee eucalypts that are more tolerant to fire, drought and defoliation, can form lignotubers; these are woody swellings at the base of the stem from which a number of stems sprout forth to form multi-stemmed trees. Similarly, other species are capable of sprouting from epicormic buds (buds protected under the outer bark), following the destruction of their crowns by fire (Nicolle, 2006) (Figure 6.14). Some species are able to sprout from both lignotubers and stems (combination sprouters). Nutrient-rich structures such as lignotubers and sprouts from stems both promote the survival of plants in times of stress such as severe cold, and contribute to natural regeneration after fires. However, they do not contribute to the widespread dispersal of any species.

Regenerative strategies in the eucalypts have been collated by Nicolle (2006) and Rejmanek and Richardson (2011); based on these sources, information for the major plantation eucalypts is summarised in Table 6.3.

### ***Pollen dispersal and pollination***

The distribution of pollen from a source plant, whether by wind or animal, is usually described as being leptokurtic, being greatest a few metres from the source and then gradually decreasing with increasing distance (Levin, 1981). A pollinator will also likely carry pollen to a number of flowers. Although most will be deposited on the first few flowers, pollen can remain on the pollinator's body over extended visitations, leading to it being deposited on a flower long after it was collected.

Figure 6.14. Shoots springing from *Eucalyptus* epicormic bud after bushfire

Source: John O'Neill, Wikimedia, licensed under GNU FDL 1.2.

Table 6.3. Regenerative strategies in *Eucalyptus* species

Species	Lignotuber	Habit	Regenerative strategy	Source <sup>†</sup>
<i>E. saligna</i>	Variable	Tree	Lignotuber sprouter	s,c,f,r
<i>E. grandis</i>	Variable	Tree	Possible sprouter or obligate seeder	s,c,f,r
<i>E. urophylla</i>	Yes	Tree	Combination sprouter	s,c,f,r
<i>E. pellita</i>	Yes	Tree	Combination sprouter	s,c,f,r
<i>E. tereticornis</i>	Yes	Tree	Combination sprouter	s,c,f
<i>E. camaldulensis</i>	Variable	Tree	Sprouter (variable)	s,c,f,r
<i>E. dunnii</i>	Yes	Tree or facultative mallee	Combination sprouter	s,c,f,r
<i>E. globulus</i>	No	Tree	Combination sprouter	s,c,f,r
<i>E. nitens</i>	No	Tree	Stem sprouter	s,c,f,r

<sup>†</sup>Source of data: s: seedling examination (live and/or herbarium specimens); c: examination of late juvenile-stage individuals (saplings); f: field examination of mature individuals; and r: observation of response to fire in natural stands and/or cultivated individuals.

Source: Adapted from Appendix, Nicolle (2006) and Table 1, Rejmanek and Richardson (2011).

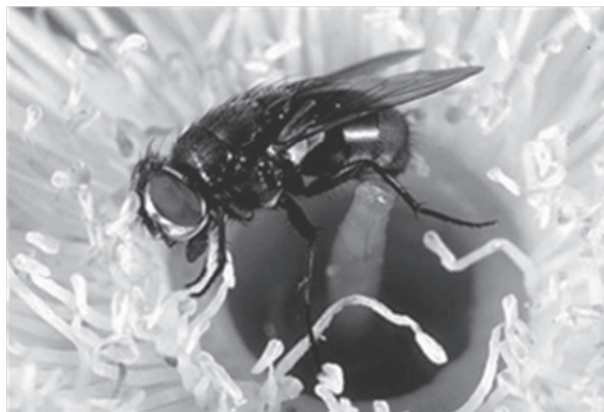
*Eucalyptus* species are mainly pollinated by vectors such as birds, insects and mammals, and reports of wind pollination are rare (House, 1997; Potts and Gore, 1995; Pryor, 1976). Wind pollination has been reported for *E. tereticornis* (Pryor, 1976) which has loose, non-sticky pollen, but this has not been verified (Potts and Gore, 1995). In Australia, it has been suggested that species with small flowers are predominantly pollinated by insects, while those with larger flowers are mainly pollinated by birds. However, the flowers of species are usually capable of being pollinated by all the above-listed vectors, a characteristic which may be of advantage in the often dry and unpredictable Australian climate (Ford, Paton and Forde, 1979). The major vector associated with any species is likely to be attracted by factors such as the type of nectar reward, the season and the weather at the time of flowering. For example, one localised study in Western Australia identified a number of birds as the major pollinators of *Eucalyptus* and other native Australian plants in winter (Hopper, 1981).

Nectar-feeding birds, of which honeyeaters are a representative, are a major feature of Australia and other southern hemisphere countries, but are extremely rare in the northern

hemisphere (Ford, Paton and Forde, 1979). As such, it is not surprising that in Australia the main birds that effect pollination of *Eucalyptus* are nectar-feeding ones. Honeyeaters, in particular, are likely the major pollinators of at least 200 species of *Eucalyptus*. Potentially, due to their visitations to greater numbers of flowers compared to insects, birds can lead to more cross-pollinations.

The principal insect pollinators of *Eucalyptus* are bees, flies and beetles. As with birds, their major interest in the flowers of this genus is the nectar. In Australia, both native bees and the introduced honey bee (*Apis mellifera*) act as pollinators, the latter being the major bee associated with the production of honey. Other insects, such as ants, butterflies and moths, probably play only a marginal role in pollination (Figure 6.15). Similarly, in Brazil, both *Apis mellifera* and other species of bees are probably the most important insect vectors of pollination (Barth, 2004; D'Apolito et al., 2010). Pollen can also be transferred between individuals, thus further enabling its dispersal.

Figure 6.15. Pollinator (sheep blowfly) on eucalypt flower



Source: CSIRO, licenced under CC BY 3.0.

Mammals that feed upon nectar and/or pollen are all potential vectors of pollen. In Australia, the most important are the arboreal marsupials, such as possums and gliders (gliding possums). For example, the yellow bellied glider (*Petaurus australis*) and the feathertail glider (*Acrobates pygmaeus*) are both known to feed on the nectar and pollen of *Eucalyptus*, likely inadvertently depositing pollen between flowers and trees (Goldingay, 1990; Turner, 1984). Fruit bats are also probably involved in pollination. The morphology of the tongues of some species is very similar to that of nectar-feeding birds and mammals, implying a diet high in nectar and the concurrent ability to pick up and transfer pollen (Birt, Hall and Smith, 1997).

In general, pollen dispersal in *Eucalyptus* is largely restricted to the immediate vicinity of its source, but patterns of pollen dispersal may change with spatial and temporal variation in the flowering resource and the pollinator community (Potts, Barbour and Hingston, 2001). For predominantly bird- (and flying fox-)pollinated eucalypts, pollen dispersal distance is likely to be greater than for those predominantly pollinated by insects.

Some cases of potential long-distance dispersal over several kilometres have been reported. For example, natural F<sub>1</sub> hybrids between *E. regnans* and *E. macrorhyncha* have been observed in forests of the latter, located over 5 km away from the closest stands of



*E. regnans* (Ashton and Sandiford, 1988). The occurrence of hybrids of *E. risodnii* in the range of *E. amygdalina* has suggested that, although pollen dispersal is largely confined to within a few metres of trees, it can occur several hundred metres from its source (Potts and Reid, 1988). Similarly, a study of pollen dispersal from *E. nitens* into a natural *E. ovata* population showed hybrid seed occurring at 200-300 m, though occasional hybrids were still found at 1.6 km from its source (Barbour, Potts and Vaillancourt, 2005). Examination of the trees of *Eucalyptus* plantations in Brazil by the use of isozyme electrophoresis has likewise demonstrated that pollen can travel several hundred metres across isolation belts of natural forest. In one study, it was demonstrated that 14.2% of seedlings in *E. grandis*/*E. urophylla* orchards showed evidence of crossing with plants 400 m distant (Campinhos et al., 1998), while in a second it was shown that pollen could travel over 800 m to fertilise plants (Junghans et al., 1998). In a seed orchard of *E. grandis* in Madagascar, 40% pollen immigration was observed over 100 m (Chaix et al., 2003). Long-distance pollen dispersal has also been observed for remnant populations of *E. wandoo*, where over 65% of pollen was found to be sourced from outside the populations at distances of at least 1 km (Byrne et al., 2008).

### ***Fruit/seed development and dispersal***

After pollination and fertilisation, the development of seed capsules usually takes several months before they are mature for harvest or release of seed. Species that originate in the northern regions of Australia and the islands to the north will usually shed their seeds after the capsules reach maturity. However, under natural circumstances, for species originating in temperate climates, the capsules invariably remain closed for a further 12-24 months, after which the valves open and release the seeds. Such trees are often characterised by a slow release of seeds throughout the year. In most cases, capsules release seed prior to any dissociation from a tree, but after exposure to fire and dropping to the ground they may soon open. Capsule abortion is associated with the level of fertilisation. Those capsules that have a low level of fertilised ovules are more likely to abort, but abortion is also influenced by the levels of nutrients available to the plant (Suitor et al., 2008). If seed capsules have been collected, placing them in a warm dry environment for several days will usually induce them to open and release seed. If seed is not to be sown, its viability is best retained by cold storage, seeds stored in this manner often remaining viable for at least 20 years.

*Eucalyptus* seeds are mainly dispersed by gravity and wind. Dispersal by animals (e.g. in fur of larger animals or intentionally by ants [House, 1997]) is unimportant, and dispersal by water dependent on either proximity to water courses or infrequent flooding. However, seed dispersal by water can be over long distances, and if this is seen as a problem, plants should not be grown near water courses (Rejmanek and Richardson, 2011). The distance of dispersal of seed from a tree is largely a function of the height of release, wind velocity and weight (Cremer, 1977). Generally, seeds have no adaptation for dispersal (wings or fleshy tissues), and wind or gravity will carry seeds no further from the base of the tree than the height of the tree (Cremer, 1977). Terminal velocities of seeds of all tested eucalypt species are between 2.0 and 5.5 metres per second. Although ants are considered the only invertebrate which can move plant seeds, they are not known to play a significant role in the dispersal of *Eucalyptus* seeds. However, in Australia, seeds of *E. torelliana* can be transported distances of over 300 m from their source by the bee *Trigona carbonaria*, which collects a resin to which the seeds adhere (Wallace and Trueman, 1995). Similarly, seeds of *Corymbia torelliana* are dispersed by related species of bees (Wallace and Lee, 2010).

The number of seeds produced is much lower than the number of flowers and ovules available for fertilisation. Possible reasons for this include the outlay of resources specifically to attract pollinators, production of excess pollen to increase the chances of fertilisation of the available ovules and the reduction of the impact of predators which target seed prior to dispersal (House, 1997). However, a model has been developed and successfully used for the estimation of the seed quantity for stands of *Eucalyptus*. This model factors in the number of branches in the crowns of trees, the number of capsules per branch and the average number of viable seeds per capsule (Bassett, White and Dacy, 2006).

### ***Seed dormancy and germination***

In general, eucalypt seeds do not display innate dormancy, i.e. inhibition of germination on a year-to-year scale (Gill, 1997). However, seeds may have an after-ripening period following dispersal, and short-lived dormancy may be induced by exposure to high temperatures (see Grose, 1960; Wellington, 1989). Seed storage in the soil is usually less than a year (Grose, 1960). Any substantial store of eucalypt seed is in the canopy of the plant: in temperate eucalypts such as *E. grandis*, seeds are retained in the woody capsules until hot, dry conditions or fire cause their release, while in forest trees and mallees there is a continuous, low level of seed release throughout the year (House, 1997). Therefore, if seedling establishment is to be successful in any eucalypt species, it is likely to take place within a year of seed dispersal (Gill, 1997).

Under both natural and artificial conditions, the germination of seed from *Eucalyptus* is dependent on a range of factors, including temperature, moisture, light and the mineral constituents of the soil. For example, germination of seeds of *E. globulus* in controlled environment chambers was found to be optimal at 28°C, and to be sensitive to water potential and the size of the seeds (Lopez et al., 2000). In the case of *E. delegatensis*, which grows in cooler temperate regions, the germination optimum was between 15°C and 20°C, and was found to be sensitive to both water potential and the soil matric potential (Battaglia, 1993). These, and other studies, underline a correlation between the optimal temperature for germination and the climate where *Eucalyptus* trees originate. Boland, Brooker and Turnbull (1980) have established temperature optima for germination of more than 400 species of *Eucalyptus*. South Australian species have germination optima between 15°C and 25°C whereas Northern Australian species have optima closer to 30°C. Further, comparison of seed-lots of one species taken from different areas can sometimes show significant differences in the rate of germination, underlying regional differences in populations (Humara et al., 2000).

The presence of moisture is an essential pre-requisite for successful germination and subsequent establishment of seedlings. In Australia, germination in the wild is usually linked to the season of rainfall in a particular region. Often, controlled seed germination can also be promoted by exposure to heat, cold, smoke, scarification and/or the use of specific light-darkness regimes (Bell, 1994; Close and Wilson, 2002). Plants native to regions with Mediterranean climates, such as Australia, are frequently dependent upon either heat or smoke from fires to help stimulate germination (Moreira et al., 2010; Read et al., 2000). Under controlled conditions, the germination of some species, such as *E. blakelyi*, is increased significantly by the use of light (Li et al., 2003), while that of other species, such as *E. globulus*, is enhanced by constant darkness, as opposed to a constant light or a mixed light-dark regime (Nair, Wilson and Spurr, 2009). Although cold may help seeds of some species germinate, there is likely to be an increase in the



mortality of germinating seed of most species exposed to surface frost (Cremer and Mucha, 1985).

Seed stratification, a technique that involves placing the seed in a moist environment for defined time periods, can also enhance germination (Donald and Jacobs, 1993), as can the use of osmotic solutions of polyethylene glycol, which are used to control water potential (Donald and Lundquist, 1988). Often, the consecutive use of more than one of these methods will lead to a greater level of seed germination.

In general, it appears that species from the subgenus *Symphyomyrtus* have a higher root-to-shoot ratio and can establish themselves faster than those from *Monocalyptus* (Davidson and Reid, 1980). However, the successful establishment of seedlings is largely dependent upon the surrounding environment. Usually the growth of seedlings is slow, and mortality high, in areas of established forest. In some circumstances this may be due to the release of allelopathic chemicals which result in a general suppression of understorey growth in *Eucalyptus* forests (May and Ash, 1990). Fires, which in natural circumstances have been part of the Australian environment and to which its flora is adapted, present opportunities for the establishment of new seedlings (Jurskis, 2005). For some species, such as *E. regnans*, the creation of both large forest gaps and destruction of understorey plants by fires may be essential for regeneration (Ashton and Chinner, 1999; Van der Meer and Dignan, 2007). From an industrial perspective, larger gaps would be expected to result in increased timber yields.

## Genetics

As with most other plants of commercial significance, there have been recent rapid advances in research concentrating on the genetics and genomics of *Eucalyptus* species in particular, as well as other species in the Myrtaceae (Grattapaglia et al., 2012).

Although there are some reports of varying chromosome numbers among species of *Eucalyptus*, it is likely that all species are characterised by a diploid ( $2n$ ) number of 22, corresponding to that observed among virtually all examined plants in the Myrtaceae family (Bachir and Abdellah, 2006; Rye, 1979). Reports of higher chromosome numbers in some species may be the result of the fragmentation of certain chromosomes while they were being prepared for counting. There are no reports of the occurrence of natural polyploids in the genus, but occasionally in counting chromosomes from individual plants, cells with a tetraploid number ( $4n = 44$ ) are encountered.

In one study, the nuclear ( $2C$ ) DNA content of 12 *Eucalyptus* species and 5 hybrids, including some of the species most widely grown around the world, was estimated to range from 0.77 pg/ $2C$  to 1.47 pg/ $2C$ , equivalent to haploid genome sizes of 370-700 megabase pairs (Grattapaglia and Bradshaw, 1994). A more recent investigation of the genomes of *E. globulus*, *E. grandis* and *E. urophylla* suggested that the sizes of their nuclear DNAs were between 1.05 pg/ $2C$  and 1.41 pg/ $2C$ , corresponding to approximately 500-600 megabase pairs per haploid genome (Praca, Carvalho and Novaes, 2009). For comparison, the nuclear DNA content of *Arabidopsis thaliana* (selected as a “model” plant species partly on the grounds of its small genome size) is 0.32 pg/ $2C$ , while those of banana, *Brassica rapa*, cotton and wheat are 1.26, 1.6, 4.8 and 34.66 pg/ $2C$ , respectively (Bennett and Leitch, 2012).

Maps of molecular markers have been constructed for a range of *Eucalyptus* species, including *E. grandis*, *E. globulus*, *E. nitens* and *E. urophylla*, as well as a number of commercial hybrids (Grattapaglia et al., 2012). These maps represent AFLP, RAPD, RFLP

and SNP markers, most covering over 90% of the respective genomes. A DArT genome array has been developed that has approximately 1 000-2 000 polymorphic markers that can be used for population studies and linkage mapping in most *Eucalyptus* mapping populations (Sansaloni et al., 2010). The sequencing of the clones on the array will enable the integration of the sequence of any *Eucalyptus* genome with the location of QTLs and other markers. By using over 4 000 DArT and microsatellite markers, a high-density marker map for *Eucalyptus* has also been produced, the average interval between adjacent markers being 0.31 cM (Hudson et al., 2012a).

Recent studies have used next generation sequencing to produce *Eucalyptus* expressed sequence tags (ESTs) and develop single-nucleotide polymorphisms (SNPs). Using a pool of cDNAs from different tissues and genotypes of *E. grandis*, nearly 150 Mbp of expressed sequences could be assembled. Further, alignment of the sequences from the different genotypes allowed the detection of over 23 000 SNPs (Novaes et al., 2008). In another study, 23 genes from individuals of *E. globulus*, *E. nitens*, *E. camaldulensis* and *E. loxophleba* were sequenced, identifying over 8 500 SNPs, with *E. camaldulensis* averaging one SNP every 16 bp for the sequenced genes (Kulheim et al., 2009). Lastly, by using a 1.2 million EST dataset, consisting of both Sanger and Next Generation sequences from six *Eucalyptus* sequences (representing three sections of the subgenus *Symphyomyrtus*), it was possible to develop a set of 768 genome-wide SNPs (Grattapaglia et al., 2011). These were assayed in *Eucalyptus* using the Golden Gate genotyping technology, their reliability as SNPs being extremely high.

Rapid advances in genomics and the techniques of recombinant DNA technology have led to the characterisation and sequencing of the genomes of an ever-increasing number of plants. Data from such research can then be applied in programmes aimed at both understanding the fundamental developmental process of plants and genetically engineering plants with desired traits. The ~600 Mbp genome of *E. grandis* is being sequenced by the US Department of Energy, Joint Genome Institute (DOE-JGI). An assembly sequence is available.<sup>7</sup> The DOE-JGI has also conducted sequencing of a clone (X46) of *E. globulus*, while the Japanese Kazusa DNA Research Institute has produced a draft sequence for *E. camaldulensis*, showing that the genome is approximately 650 Mbp and consists of over 77 000 (complete or partial) genes (Hirakawa et al., 2011). To facilitate the map-based cloning of genes in *Eucalyptus*, BAC libraries have been constructed from the species *E. grandis* (Paiva et al., 2011).

Quantitative traits within *Eucalyptus* have been the subject of much research. Recent studies include those on cold hardiness and growth in *E. urophylla* x *E. tereticornis* hybrids (He et al., 2012), lignin composition and growth traits in *E. urophylla* (Mandrou et al., 2012), and resistance to the rust fungus *Puccinia psidii* in *Eucalyptus* species (Alves et al., 2012). The understanding and evaluation of QTLs is further enhanced by the use of genomic selection, a technique that may enable breeding times in *Eucalyptus* to be drastically reduced (Resende et al., 2012).

Collections of ESTs for several species, representing a number of organs and growth conditions, have been generated in Australia, Brazil, France and the United States (Teulieres and Marque, 2007). Some of these collections are publicly available while others belong to private companies. Published EST isolations include a collection of those preferentially expressed in the xylem tissue of *E. gunnii* (Paux et al., 2004) and from a cold acclimatised line of the same species (Keller et al., 2009). Bioinformatic (BLAST) searching of the Brazilian FOREST EST database has identified sequences from genes

that, in other species, are known to be involved in both abiotic and biotic stresses (Rosa et al., 2010).

Both chloroplasts and mitochondria are usually maternally inherited in angiosperms, and *Eucalyptus* appears to be no exception (Byrne, Moran and Tibbits, 1993; Vaillancourt, Petty and McKinnon, 2004). Not only does this form of inheritance occur in individual species, but at least in the case of chloroplast DNA, the barriers which prevent pollen mediated transmission appear to operate identically in hybrids between species (McKinnon et al., 2001). The chloroplast genomes of *E. globulus* and *E. grandis* have been sequenced, establishing that they share over 99% sequence identity, together with identical gene orders (Paiva et al., 2011; Steane, 2005). The genes found on these organelle genomes are not significantly different from those established for other angiosperms.

From the perspectives of ecology and silviculture, genetic variation within a *Eucalyptus* plantation species reduces the competition between individual plants and promotes coexistence with other species (Boyden, Binkley and Stape, 2008). However, where competition between individual trees is low (as may be the case when they are widely spaced), trees of identical genetic (clonal) origin are likely to outperform those with genetic diversity.

## Abiotic interactions

As with other plants, abnormal growth in *Eucalyptus* is almost always a symptom of an abiotic or biotic stress. Abiotic stresses include nutrient deficiencies, metal toxicities, the effects of extremes of temperature, excess or deficiency in water, and even the presence of pollutants in the air.

### *Nutrient stress*

The supply of nutrients is important not only to *Eucalyptus* trees in their native Australasian habitats, but in all areas around the world where *Eucalyptus* species are grown as plantation crops. Australia is renowned for its high proportion of nutrient poor soils, even when compared to the arid or semi-arid zone soils in other continents; in particular, many Australian soils are deficient in phosphorus (Orians and Milewski, 2007). However, although *Eucalyptus* species are thus adapted to growing in environments where nutrients may be deficient, they can nonetheless show distinct symptoms of stress when one nutrient (or more) becomes limiting.

Nutrient in plants can be broadly classified into three groups: those that are phloem mobile from leaves (nitrogen, phosphorus, potassium), those that are immobile from leaves (boron, calcium, iron, manganese) and those that are mobile only under only certain conditions (copper, magnesium, sulphur, zinc) (Dell et al., 2002). Indicative symptoms of stress are the colour and shape of leaves (e.g. chlorosis and/or necrosis of leaf tissue), the shape and the presence of leaves in the canopy, and the thickness of the stem compared to healthy plants (Snowdon, 2000).

Nitrogen and phosphorus feature prominently as essential elements, the former being part of nucleic acids and proteins while the latter occurs in nucleic acids and important cellular molecules such as ATP. The availability of phosphorus and nitrogen in soils is often linked, and a balanced supply of both nutrients is needed for ideal growth. Deficiency in nitrogen is frequently characterised by the yellowing of leaves in

*Eucalyptus*, while that of phosphorus by the formation of purple patches and necrosis on leaves (Dell et al., 2002).

Symptoms of deficiencies in other nutrients include the scorching of leaves, sickle-shaped leaves, impairment of the growth of the shoot tip and loosely hanging branches. Sometimes the visible signs of stress relating to the deficiency of one element are virtually identical to those of another, making it difficult to ascertain the cause of the problem. For example, uniformly yellow leaves on a plant may be indicative of either nitrogen or sulphur deficiency.

In soils where the level of nitrogen and phosphorus is so low that it is restricting the growth of trees, the use of fertilisers is common. The application of a nitrogen- and phosphorus-based fertiliser for three years to trees of *E. grandis* in Queensland, Australia, demonstrated that it significantly increased both tree heights and basal areas as compared to non-fertilised controls, the growth of the latter in fact being severely inhibited by a low supply of nutrients (Cromer et al., 1993a; 1993b). In the southern Australian state of Tasmania, where low levels of nitrogen in soils can limit the growth of *E. nitens*, the application of a nitrogen fertiliser was found to increase growth, the availability of nitrogen in treated soils remaining elevated for one to two years after treatment (Smethurst et al., 2004).

Other studies, in Argentina and China, have demonstrated that the application of phosphorus increases the growth of trees, and is able to concurrently elevate the extraction of nitrogen from soils, plants accumulating more nitrogen than those fertilised with nitrogen alone (Graciano et al., 2006; Xu et al., 2002). The application of fertilisers is common in the large plantations in Brazil, substantially increasing productivity, most often by accelerating the growth of trees (Goncalves et al., 2008).

### ***Toxicity of metals***

The discharge into the environment of metals, especially cadmium, chromium and aluminium, can be a problem in areas where industry is located. These metals can find their way into all biological organisms, affecting their health and ability to reproduce.

Approximately 30% of the world's soils are acidic, such soils being particularly common in the humid temperate and humid tropical regions of Australia, Asia, Africa, India, and Central and South America. These soils can restrict, if not inhibit, the growth of plants, in turn leading to the failure of crops and the impoverishment of people. Aluminium toxicity is often associated with acidic soils, reducing the growth of roots and their efficient uptake of water and nutrients (Eswaran, Reich and Beinroth, 1997). Growth of seedlings of six *Eucalyptus* species in liquid media with varying concentrations of aluminium showed that they had different degrees of tolerance to high aluminium levels, but the elongation of their roots was actually promoted by low levels (Silva et al., 2004).

It is possible to reduce the effects of aluminium toxicity by the addition of lime to soils, but often this is not economically or physically possible. In addition to the use of *Eucalyptus* cultivars that are inherently resistant to aluminium toxicity, it has also been reported that certain fungi can prove beneficial in such soils. Concurrent inoculation of both saprobe and arbuscular mycorrhizal fungi was observed to increase the resistance of *E. globulus* to aluminium (Arriagada et al., 2007), whereas inoculation with a mycorrhizal fungus was associated with lower aluminium accumulation in shoots of *E. tereticornis* (Khosla and Reddy, 2008). Plants can also respond to aluminium toxicity by the excretion of organic acids. In the case of *E. camaldulensis*, a number of membrane

proteins involved with the excretion of citrate have been isolated and characterised (Sawaki et al., 2013).

Cadmium is a by-product of the refining of zinc, being used in nickel/cadmium batteries and as a corrosion-resistant coating, while chromium figures prominently in the pigments of paints and other commodities. Both metals accumulate in organisms, have been demonstrated to be both toxic to *E. camaldulensis* (Shah et al., 2011) and, at least in the case of chromium, to inhibit the growth and colonisation of *E. urophylla* by the mycorrhizal fungus *Pisolithus* (Aggangan, Dell and Malajczuk, 1998).

### ***Temperature stress***

Many species of *Eucalyptus* are sensitive to frost, with species of *Monocalyptus* being generally less resistant to frost than those of *Symphyomyrtus* (Noble, 1989). As might be expected, there is usually increased tolerance to frost in the species that grow at higher altitudes and/or are more often exposed to colder temperatures. Within a given species, individuals may demonstrate a range of responses to frost, indicating that the selection and breeding of populations with tolerance is possible (Doran et al., 2005). Further, continual exposure to low non-freezing temperatures, a process called hardening, can acclimatise plants to freezing temperatures, enabling them to resist frosts. This process may be accompanied by an elevation in the level of soluble sugars, and at least in the case of cell suspension cultures, incubation with soluble sugars increases the frost-hardiness of these cells (Travert et al., 1997).

At the other extreme, many *Eucalyptus* species native to the dry areas of Australia are well able to withstand high temperatures and the associated frequent drought conditions. However, seedlings are prone in particular to heat stress and mortality from high temperatures. To cope with heat, seedlings develop roots with deep and wide penetration, while it is not uncommon for adult plants to continually shed leaves during dry conditions to reduce the loss of water. At a fundamental level, there appears to be a direct relationship between the distribution of *Eucalyptus* species and their optimum temperature for growth and ability to withstand extreme conditions (Paton, 1980).

### ***Water stress***

The response of plants to drought is usually linked to changing the balance between an investment in the growth and maintenance of shoots (including the leaves), as opposed to that of roots. As shoots, and leaves in particular, are more prone to water loss than roots, it is ideal for a plant that is adapted to drought conditions to have a large root system, or if a plant is experiencing drought to expand its root system at the expense of the aerial organs. Often linked to this is the ability to control the loss of water through stomata. Any plant exposed to drought must also be able to maintain the efficient conduct of water through its xylem.

Eucalypts use extensive and deep root systems to access water and close their stomata for longer periods in the day to prevent loss of water (Costa e Silva et al., 2004; Eldridge et al., 1994). Osmotic adjustment as a means of enhancing turgor maintenance, and even the intercellular storage of water, are used by some species of *Eucalyptus* to cope with drought (Ladiges, 1974; Myers and Neales, 1986). As in the case of frost tolerance, the ability of *Eucalyptus* seedlings to withstand drought can be enhanced by a process of hardening. For example, seedlings of *E. pilularis* were drought hardened by reducing irrigation, and after transplantation to a glasshouse drought regime were seen to have increased survival (Thomas, 2009).

Conversely, exposure to excess water can drastically reduce the growth and development of plants. Waterlogged soils invariably restrict the uptake of oxygen by roots, in turn reducing aerobic respiration and inducing reliance upon anaerobic respiration, the latter being accompanied by the production of toxic organic and inorganic molecules. *Eucalyptus* species that grow waterlogged soils have evolved a number of adaptations, including adventitious roots, aerenchyma (pores to allow diffusion of oxygen from the shoot to root) and hypertrophy (swelling) of the stem. The ability of *E. camaldulensis* to withstand flooding has been attributed to its ability to produce ethylene, which results in hypertrophy (Blake and Reid, 1981; Van der Moezel et al., 1988). In one study of the three *Eucalyptus* species – *E. grandis*, *E. robusta* and *E. saligna* – the first was found to be the most resistant to waterlogging, this phenotype being dependent upon the formation of adventitious roots (Clemens, Kirk and Mills, 1978).

### ***Salinity stress***

Many areas of Australia, both along both the coast and inland, including those with a tendency for waterlogging, are characterised by saline soils. Some species such as *E. camaldulensis*, *E. tereticornis* and *E. occidentalis*, all in the subgenus *Symphyomyrtus*, have a high resistance to saline conditions, while species in the subgenus *Monocalyptus* are frequently salt sensitive (Benyon et al., 1999; Marcar, 1989; Sands, 1981). Increased salinity is often associated with reduced tree growth, this being manifested in decreased stem diameter and crown volume. Stomatal conductance and photosynthetic rates decrease under saline conditions; during summer, when water stress is more likely, the concentrations of salt in the leaves increases (Barrett, Preiss and Sinclair, 2005; Van der Moezel, Watson and Bell, 1989).

There are believed to be two general mechanisms of salinity tolerance in plants: 1) the ability of the plant to keep salt ions away from cells and/or tissues where they would be particularly harmful; and 2) the ability of a tissue to tolerate the elevated level of salt ions. In the former case, either active or passive methods are used to exclude and extrude ions, while in the latter the focus is on compartmentalising ions in cellular organelles such as vacuoles. It has been proposed that the relative tolerance of *E. camaldulensis* to salt is possibly linked to plant tissues being able to tolerate the ion, but in other *Eucalyptus* species, tolerance may be associated with reduced uptake of ions from the surrounding environment (Sands, 1981). Stomatal closure and a reduction in stomatal conductance is a feature of the response of *E. camaldulensis* and *E. lesouefii* to high salinity (Van der Moezel, Watson and Bell, 1989).

### ***Air pollution and global warming***

Gaseous pollutants arising from industry can affect the growth and survival of all living organisms. In many countries, forests nearby to industrial centres show obvious signs of damage from air pollutants. In China, sulphur dioxide and fluoride in the air have been linked to foliar damage in many trees, including *Eucalyptus* species adjacent to large cities (Shu-Wen et al., 1990), while pollution from cars can reduce the levels of photosynthetic pigments in *Eucalyptus* (Joshi and Swami, 2009). Other research has demonstrated that ozone (O<sub>3</sub>), which is a product of fuel combustion, can significantly reduce the weight and injure the leaves of certain species of *Eucalyptus* (Monk and Murray, 1995). *Eucalyptus* trees exposed to chemicals in the air respond by the activation of enzymes such as peroxidases, ascorbate peroxidases and catalases, as well as by

increasing the cellular levels of the antioxidant ascorbic acid, all of which help provide protection (Seyyednejad and Koochak, 2010).

The possible effects of global warming on plants have been the subject of much research as well as controversy. An increase in the levels of carbon dioxide may prove beneficial to certain species of *Eucalyptus*, providing they have an adequate supply of water (Ghannoum et al., 2010), but the possibility of increased droughts may negate this advantage. In Australia, it is likely that any reduction in rainfall will increase tree mortality, the frequency and intensity of bushfires, and change the nature of pest and pathogen risks (Booth, Kirschbaum and Battaglia, 2010). One study of the effect of global warming on plantations of *Eucalyptus* in the Brazilian states of Espírito Santo and Bahia has suggested that the yield from these forests could decrease by at least 24% by the end of this century due to an increase in the severity and duration of droughts (Baesso, Ribeiro and Silva, 2010).

## Biotic interactions

In their native environments in Australia, Papua New Guinea, Indonesia and the Philippines, as well as in many other countries to which they have been introduced, *Eucalyptus* species interact with mycorrhizal fungi and are affected by a wide range of diseases and animal pests. In particular, the effective management of pests and pathogens in plantations is a necessary prerequisite for their commercial success. As an exotic species, *Eucalyptus* trees are susceptible to elements of the biota of their new homes as well as known Australian pests that have been accidentally introduced. Nevertheless, there are many more pests and pathogens of *Eucalyptus* in their native habitats than occur outside their native range.

### *Mycorrhizas*

Mycorrhizal fungi form symbiotic relationships with the roots of most land plants, and this interaction needs to be studied to fully understand plant-soil relations (Rosendahl, 2008). Both arbuscular mycorrhizal fungi and ectomycorrhizal fungi are known to colonise the roots of *Eucalyptus*, individual fungal species having preferences for particular plant species (Pagano and Scotti, 2008). These fungi help provide plants with necessary minerals (such as nitrogen and phosphorus), while some protect plants from pathogenic fungi and toxic compounds, in return receiving carbohydrates from plants (van der Heijden, Bardgett and van Straalen, 2008). In nutrient-rich environments, the mycorrhiza may have little obvious effect on the plant, but in mineral-deficient environments the presence of the fungi may be essential for optimal growth and development (Schmidt, Handley and Sangtjean, 2006). Further, at least in some cases, mycorrhiza can protect *Eucalyptus* trees from the effects of elevated aluminium in the soil (Arriagada et al., 2007).

Species of these fungi have been introduced from Australia to other countries, almost certainly with the seedlings of the introduced plants (Vellinga, Wolfe and Pringle, 2009). Although it is not common for these fungi to form mycorrhizas with the local tree species, in these new environments some have spread from the native hosts to other plant species. For example, in the Iberian Peninsula, the ectomycorrhizal fungus *Laccaria fraterna* has spread from plantations of introduced *Eucalyptus* trees to a native *Cistus* sp. (Diez, 2005), while species of *Pilothus* have been introduced to many countries, including Brazil (Kasuya et al., 2010). On the other hand, in countries where it is an exotic,

*Eucalyptus* species have been colonised by members of the native mycorrhizal population.

### ***Pathogens and diseases***

Eucalypts in native forests in Australia have a wide range of co-evolved pathogens, mainly foliar pathogens in the Phylum *Ascomycota* (Park et al., 2000). These have only come to prominence with their increased incidence and severity in eucalypt plantations planted in the region. Perhaps the most important example is *Mycosphaerella* (*Teratosphaeria*) *cryptica*, causing serious leaf blight and defoliation in *E. globulus* plantations in southern Australia. Another highly destructive disease in native forests in southern Australia has been eucalypt dieback, caused by the oomycete *Phytophthora cinnamomi*, which is thought to have been introduced to the southern forests from tropical regions (Shearer and Smith, 2000). This pathogen has been particularly destructive in the jarrah (*Eucalyptus marginate*) forests of southern Western Australia.

Eucalypt species planted outside Australia are susceptible to a range of bacterial (including phytoplasma), fungal and viral diseases, many of which are caused by new-encounter pathogens. The most important of these are vascular wilts, mildews, leaf spots and blights, stem rots and cankers, and root rots. Especially amongst the fungi, pathogens of *Eucalyptus* come from a large number of different taxonomic groups, including *Basidiomycota*, *Cryptosporiopsis*, *Erysiphe*, *Erythrimum*, *Mycosphaerella*, *Phaeophleospora* and *Sphaerotheca*. Other than natural host resistance, factors such as climate and environment are principally responsible for determining the severity of disease caused by these organisms.

The response of any exotic species to exposure to new diseases is unpredictable in the absence of a long period of co-existence and co-evolution. Resistance by any plant species is often, but not always, dependent upon natural selection acting on the genetically variable population of individuals exposed to the pathogen, resistant individuals more often surviving infection and breeding. In this context, introduced *Eucalyptus* trees have undoubtedly been resistant to many local pathogens, but succumbed to others.

The characterisation of host shifts of pathogens to *Eucalyptus* is of such importance that not only have the identified examples been the subjects of study, but much research has been conducted into the potential occurrence of such shifts. The destructive epidemics of *Phytophthora cinnamomi* in southern Australia appear to be a classic example of a new-encounter disease (Keane et al., 2000). Several fungal pathogens present on certain Myrtaceae species native to South America and South Africa have been considered capable of infecting introduced *Eucalyptus* (Pavlic et al., 2007; Perez et al., 2010). In the reverse direction, the movement of pathogens accompanying introduced *Eucalyptus* plantation trees to other plants, especially those in the family Myrtaceae, is important (Perez et al., 2008). Even in the Australian context itself, *Eucalyptus* faces new pathogens when grown outside their native range. For example, *Botryosphaeria australis* has been found infecting plantations of introduced *E. globulus* in Western Australia, the fungus almost certainly coming from adjacent forest trees and representing an extension of its host range (Burgess, Sakalidis and Hardy, 2006).

The major pathogen-induced diseases affecting *Eucalyptus* species worldwide are listed in Table 6.4.



*Ralstonia solanacearum*, a phytopathogenic soil bacterium, is the causal agent of bacterial wilt. It colonises the xylem, usually causing decolouration of this tissue and wilting of either individual branches or the entire crown of plants, the end result often being the death of the plant (Old, Wingfield and Yuan, 2003). This pathogen has a wide host range, infecting over 200 plant species from over 50 plant families. Reports of it infecting eucalypts in plantation have come from Australia, Brazil, China, Indonesia, Chinese Taipei, Thailand, Bolivarian Republic of Venezuela, Viet Nam and a number of sub-Saharan African countries (Fouche-Weich et al., 2006; Old, Wingfield and Yuan, 2003). There is no effective control measure. Although the culling of infected trees is possible, the bacteria survive in the soil and any remaining roots. This disease is rarely seen in the native forests of Australia, but has become evident as a problem in plantations.

Table 6.4. **Major pathogens affecting commercial *Eucalyptus* species in plantations**

Causal organism	Country of occurrence	Damage to plant	Reference
<i>Ralstonia solanacearum</i> (race1 and either biovar. 1 or 3) (Bacterium)	Australia, Brazil, China, Democratic Republic of the Congo, Indonesia, South Africa, Chinese Taipei, Thailand, Uganda, Venezuela, Viet Nam	Infection of xylem causing wilting (vascular wilt)	Old, Wingfield and Yuan (2003)
<i>Botryosphaeria</i> spp. (Ascomycota)	Worldwide	Stem cankers which may girdle the stem	Old, Wingfield and Yuan (2003); Pavlic et al. (2007)
<i>Chrysosporthe cubensis</i> (Ascomycota)	Africa, Caribbean (Cuba, Puerto Rico), Mexico, South America, South East Asia (Indonesia, Thailand, Viet Nam), United States	Cankers at the base of plants, but may extend up the stem	Rodas et al. (2005a)
<i>Coniothyrium zuluense</i> (anamorph of Ascomycota)	Argentina, Ethiopia, Hawaii, Mexico, South Africa, Thailand, Uganda, Uruguay, Viet Nam	Cankers in young green tissue	van Zyl, Coutinho and Wingfield (2002); Wingfield, Crous and Coutinho (1996)
<i>Cylindrocladium</i> spp. (anamorph of Ascomycota)	Australia, Colombia, India, South East Asia	Foliar and shoot blights, leaf spots, root lesions	Blum and Dianese (1993)
<i>Erythricium</i> ( <i>Corticium</i> ) <i>salmonicolor</i> (Basidiomycota)	Brazil, Costa Rica, India, Indonesia, Philippines, South Africa, Viet Nam, Zambia	Pink-coloured pustules on branches and stems ("pink disease")	Seth et al. (1978)
<i>Mycosphaerella</i> spp.; <i>Teratosphaeria</i> spp. (particularly <i>T. cryptica</i> ) (Ascomycota)	Worldwide (particularly Australia, Brazil, New Zealand, South Africa)	Leaf blotches, defoliation, shoot die-back	Crous et al. (2006); Hunter et al. (2011)
<i>Puccinia psidii</i> (guava rust or myrtle rust) (Basidiomycota)	North and South America (recently found in Australia)	Yellow or brown pustules on leaves, stems or fruits	Coutinho et al. (1998)

*Coniothyrium* stem canker caused by the fungus *Coniothyrium zuluense* is a serious disease of *Eucalyptus* species in plantations outside Australia (van Zyl, Coutinho and Wingfield, 2002). It was first reported in South Africa, but since has been found in a number of other countries, both in Africa, South East Asia, Hawaii and South America (Cortinas et al., 2004; Gezahgne et al., 2005). The earliest indication of infection is usually lesions on young green tissue, which then coalesce to produce large cankers. A plant suffering from an advanced infection will have cankers along its entire stem, leading to malformation of the stem, and often death of the tops of branches. At present, the only effective management strategy is the selection and breeding of resistant lines for release into plantations.

*Chrysosporthe cubensis* (formerly *Cryphonectria cubensis*) is a fungal pathogen of *Eucalyptus* species in all continents, although particularly in South America where it may have originated (Rodas et al., 2005a). It is relatively rare in Australia and is especially

rare in native forests (Pegg et al., 2010). The cankers caused by this pathogen are usually located at the base of trees, although they may sometimes occur higher up in branches. Once a tree has been girdled, it may wilt and in severe cases die. In Brazil, the selection for resistant lines of *E. grandis* x *E. urophylla* hybrids has proven a successful strategy in dealing with this disease. This pathogen has also been recorded outside the Myrtaceae (Wingfield et al., 2008).

Species of *Cylindrocladium* infect a wide range of plants including *Eucalyptus*, particularly affecting plantations in tropical and sub-tropical regions of India, South East Asia and South America (Blum and Dianese, 1993; Rodas et al., 2005b). Plants infected by these fungi exhibit a wide range of symptoms, including foliar and shoot blights, leaf spots, root lesions and cankers which girdle stems. In nurseries, fungicides have proven effective in controlling this pathogen, but along with management by chemical means, the selection of resistant clones has been actively pursued.

*Puccinia psidii* (guava rust) is the only rust fungus that has been well documented to infect eucalypts (Coutinho et al., 1998; Glen et al., 2007; Langrell, Glen and Alfenas, 2008). It is a typical new-encounter pathogen, having transferred to eucalypts growing in extensive plantations in Brazil from its native myrtaceous host guava (*Psidium guajava*). Although a native of South America, it now occurs in Central America, the Caribbean, and the states of California, Florida and Hawaii in the United States (Loope, 2010), infecting species belonging to a number of Myrtaceae genera. Usually it infects young tissues, causing the deformation and often death of leaves and flower buds. In severe cases, it stunts the growth of trees and sometimes even leads to their death, but most young infected trees show few symptoms as they grow older. Furthermore, infection is sporadic, being at least partly dependent upon climatic variables. Control of the rust is possible by the use of fungicides, but in Brazil resistant lines of both *E. grandis* and the hybrid *E. grandis* x *E. urophylla* have been selected and used in plantations. The ability of *P. psidii* to find new hosts in *Eucalyptus* and other Myrtaceae is of particular importance to Australia (Coutinho et al., 1998). Nearly half of the classified genera of Myrtaceae occur there, and most of the native species belong to that family. Indeed, a form of *P. psidii*, designated by the common name “myrtle rust”, has been recently found infecting a wide range of native myrtaceous hosts, including *Eucalyptus*, in Australia (Carnegie et al., 2010). Its discovery in Australia in 2010, clearly linked to a breakdown in quarantine restrictions in the nursery industry, represents the first time any member of the *P. psidii* group has been found on that continent. Although its host range consists of many species in the family Myrtaceae, it has not been recorded commonly on *Eucalyptus*. Nevertheless, the common occurrence of the fungus on eucalypts in Brazil makes it a serious threat to eucalypts in Australia. Management of this rust in nurseries is dependent upon the destruction of infected plants and the application of fungicides, although these measures are of limited usefulness once the fungus has spread to native vegetation. The full impact of this recent pathogen introduction to Australia is yet to be determined.

Another example of a likely host shift which may prove to be significant in the future is the infection of *Eucalyptus* trees in Argentina and Uruguay with the bacterium *Erwinia psidii*, also a well-known pathogen of guava (Coutinho et al., 2011). Infection of *Eucalyptus* trees is characterised by the die-back of branches and stems, symptoms similar to those observed after infection of guava.

Although virus or virus-like diseases have been reported in *Eucalyptus*, there has been little research in this field. Infection by viruses appears to result in only limited symptoms, which may be transitory and disappear as the trees get older. At present, virus

diseases make a negligible impact on the commercial cultivation of *Eucalyptus* (Randles, 2010; Wardlow, Kile and Dianese, 2000).

### **Pests**

In Australia, there are a large number of bird species that feed on either *Eucalyptus* nectar or the insects that commonly inhabit these plants (Landsberg and Cork, 1997). However, there are few species that feed on fruits and no known leaf-eating species. Insectivorous birds must play a role in controlling the number of insects, but the extent to which this occurs is still debated, especially in relation to years where there is an abnormal increase in insect numbers. It should also be appreciated that in Australia, the level of native vegetation in an area is proportional to the level of bird species (Ford, 2011). In Brazil, which has extensive *Eucalyptus* plantations with varying degrees of intensity of understory clearing, the diversity of bird species is likely to be dependent upon the richness of the understory, but none have been identified as major pests of eucalypts (Marsden, Whiffen and Galetti, 2001).

The major mammalian herbivores of *Eucalyptus* in Australia are possums, gliders, koalas, kangaroos and wallabies (Dungey and Potts, 2002; Landsberg and Cork, 1997). Possums can eat leaves, nectar, gums and fruit, while koalas almost exclusively target leaves, and even then they prefer the leaves of only a minority of all the *Eucalyptus* species. Kangaroos, and especially the smaller wallabies that occur more in the forested areas, can be important grazers of young plants in plantations.

As with other plants, insects target a wide variety of tissues in *Eucalyptus*; damage ranges from mild to severe and may even result in tree death. Numerous native Australian insect species have been recorded on *Eucalyptus*, both in the Australasian region and in other countries where these plants and their co-evolved insect herbivores have been introduced. Such insects include defoliators, leaf chewers, stem borers (affecting both bark and wood), sap suckers, and others which target seeds, pollen and nectar. Outside the Australian region, the insect pests include some originating in Australia itself and many local indigenous species. For example, in China, approximately 300 species of insect, mainly native to China, have been identified on *Eucalyptus*. Among these, about 30 cause severe damage and a further 60 moderate damage (Pang, 2003), while one study in India found more than 60 species on trees of this genus (Sen-Sarma and Thakur, 1983). In New Zealand, there are now over 50 species of insects which feed on *Eucalyptus*, of which approximately one-half specialise in plants of this genus (Withers, 2001).

The ability of an insect to move hosts appears to depend upon factors such as the physical structure of the leaf and the chemical nature of the plant cells, and pests usually choose plants of similar chemistry and/or taxonomic relatedness to those to which they are adapted (Becerra, 1997). In this context, it should be noted that Australia, southern Africa and South America have a greater diversity of Myrtaceae plants than is found anywhere in the northern hemisphere (Paine, Steinbauer and Lawson, 2010). *Eucalyptus* trees in Brazil, for example, are often grown with internal strips of native vegetation, which may act as sources of insects that may be able to switch hosts. However, *Eucalyptus* has also attracted pests with no known preference for plants from the Myrtaceae.

*Eucalyptus* plantations have sometimes become a “refuge” for insect pests indigenous to the new countries in which they are planted, this being due to predators of these pests preferring not to live in the plantations (Grosman et al., 2005). The problem of insect pests has been tackled by a number of different measures, including chemical sprays and

the implementation of management practices based on biological control. In a number of cases, the introduction of a parasitoid insect has been effective in reducing the numbers of *Eucalyptus* insect pests (Dahlsten et al., 1998; Hanks, Paine and Millar, 1996; Luhring et al., 2000). Table 6.5 summarises the major insect pests of *Eucalyptus*. Some of these are discussed in more detail below.

Table 6.5. Major insect pests affecting commercial *Eucalyptus* species

Causal organism	Country of occurrence	Damage to plant	Reference
<i>Ctenarytaina</i> spp. (particularly <i>C. eucalypti</i> )	Australia, France, Italy, New Zealand, Portugal, South America, Spain, United States, Uruguay	Sucks the sap from trees	Gill (1998); Queiroz Santana and Burckhardt (2007)
<i>Eriococcus coriaceus</i>	Australia, New Zealand	Sucks the sap from trees	Vranjic and Gullan (1990)
<i>Eupseudosoma involuta</i> and <i>E. aberrans</i>	Brazil	Defoliation by caterpillar (larva)	Zanuncio et al. (1994)
<i>Goniapterus gibberus</i> , <i>G. scutellatus</i>	Argentina, Australia, Brazil, France, Italy, Kenya, Madagascar, Malawi, Mauritius, Mozambique, New Zealand, Uganda, United States, Uruguay, Zimbabwe	Damage to edges of leaves, defoliation, stunting and possible death of trees	Clarke, Paterson and Pennington (1998)
<i>Isoptera</i> (termites)	Worldwide	Bark and wood	Constantino and de Almeida Pessoa (2010); Landsberg and Cork (1997)
<i>Phoracantha semipunctata</i> and <i>P. recurva</i>	Argentina, Australia, Brazil, Chile, Cyprus*, Israel, New Zealand, South Africa, United States, Zimbabwe	Bark and cambium, possible girdling of trees and death	Paine and Millar (2002)
<i>Sarsina violascens</i>	Argentina, Brazil	Defoliation by caterpillar (larva)	Zanuncio et al. (1994)
<i>Stenalcidia grosica</i>	Brazil	Defoliation by caterpillar (larva)	Pereira et al. (2001)
<i>Thyreteina amobia</i>	Brazil	Defoliation by caterpillar (larva)	Batista-Pereira et al. (2006)

\*Note by Turkey: The information in this document with reference to “Cyprus” relates to the southern part of the Island. There is no single authority representing both Turkish and Greek Cypriot people on the Island. Turkey recognises the Turkish Republic of Northern Cyprus (TRNC). Until a lasting and equitable solution is found within the context of the United Nations, Turkey shall preserve its position concerning the “Cyprus issue”.

\*Note by all the European Union Member States of the OECD and the European Union: The Republic of Cyprus is recognised by all members of the United Nations with the exception of Turkey. The information in this document relates to the area under the effective control of the Government of the Republic of Cyprus.

A number of psyllids have been introduced from Australia into the Americas and Europe. In California, both the blue gum psyllid (*Ctenarytaina eucalypti*) and the red gum lerp psyllid (*Glycaspis brimblecombei*) have proven to be significant pests, damaging or killing thousands of *Eucalyptus* trees. However the use of parasitoid wasps such as *Psyllaephagus pilosus* and *P. bliteus* has helped limit the problem (Dahlsten et al., 2005; 1998).

Larvae and adults of the weevils *Goniapterus gibberus* and *G. scutellatus* (*Eucalyptus* snout beetle) feed mainly on the edges of *Eucalyptus* leaves, often leading to the defoliation and death of young plants. Originating in Australia, they have spread to most countries that grow *Eucalyptus* plantations (Clark, Paterson and Pennington, 1998). At least in some countries, effective management of these pests has been achieved by the use of the parasitoid wasp *Anaphes nitens*, the larvae of which eat the eggs of *Goniapterus scutellatus* (Huber and Prinsloo, 1990).

*Phoracantha recurva* and *P. semipunctata* (Eucalyptus longhorned borers) are beetle pests of *Eucalyptus* that are native to Australia and have spread around the world (Luhring et al., 2000; Paine and Millar, 2002; Paine et al., 2000). Their larvae tunnel into the bark and cambium of trees causing extensive damage, frequently girdling trees and leading to their death. Use of natural enemies, such as the parasitic wasp *Avetianella longoi*, which lays its eggs within the eggs of these beetles, has proven to be an effective method of biological control (Hanks, Paine and Millar, 1996).

Termites (*Isoptera*) are another prominent pest of *Eucalyptus*, although infestation by these insects frequently does not result in the death of trees. In the Australian environment, termites often only attack *Eucalyptus* after fire or other damage to the tree, their activity being most common in tropical climates (Landsberg and Cork, 1997). Regarding other continents, native termites and the larvae of certain beetles (*Lepidiota stigma*, *Anomala* spp.) are prominent pests of *Eucalyptus* in Brazil, China and southern Africa, although their prominence as a pest is dependent upon regional factors (Calderon and Constantino, 2007; Constantino and de Almeida Pessoa, 2010; Pang, 2003). In China, termites usually infect the tap roots of seedlings and frequently lead to their death (Pang, 2003).

Other examples in countries of host shifts of native insect pests onto *Eucalyptus* include species of ants in Brazil, the lepidopterans *Sarsina violascens*, *Stenalcidia grosica* and *Thyrintina arnobia* in Brazil (Paine, Steinbauer and Lawson, 2010) and the lepidopteran *Coryphodema tristis* in South Africa (Gebeyehu, Hurley and Wingfield, 2005). In Brazil, the moth *T. arnobia* is known to attack a number of native species within the Myrtaceae, including guava and jaboticaba, but since the introduction of *Eucalyptus* to that country, it has extended its host range to become a frequent pest of trees from this genus (Batista-Pereira et al., 2006; Grosman et al., 2005). The wood boring moth *C. tristis*, which in South Africa has long been known as a pest of native and introduced trees, has recently been found to be capable of damaging trees of *E. nitens* (Gebeyehu, Hurley and Wingfield, 2005).

Although examples are known of parasitic nematodes which infect *Eucalyptus*, none are important pathogens of these plants (Wardlow, Kile and Dianese, 2000). Studies in a number of countries have indicated that nematodes can indeed cause mortality of plants, but their effect on the commercial success of plantations is minimal.

### **Additional interactions**

*Eucalyptus* oils have been shown to be effective pesticides and repellents, acting against a range of bacteria, fungi, nematodes and arthropods (Batish et al., 2008). Further, due to the environmental problems of synthetic chemical-based approaches, the use of natural product-based pesticides and repellents has become more attractive. In the case of *Eucalyptus*, the oils are easily extractable from leaves, and their chemical diversity provides a variety of candidates that can be screened for their effectiveness against given targets.

For example, the oils from a number of *Eucalyptus* species, in particular *E. dunnii*, have distinct insecticidal and repellent properties against *Sitophilus zeamais*, a species of weevil that is commonly found in maize (Mossi et al., 2011). Oils from the three species *E. staigeriana*, *E. citriodora* and *E. globulus* all act as insecticides of the egg, larval and adult phases of the sand fly (*Lutzomyia longipalpis*) (Maciel et al., 2010). The most effective oil is that of *E. staigeriana*, which consists primarily of (+)-limonene, Z-citral and E-citral. The major constituents of the oils of *E. citriodora* and *E. globulus* are

$\beta$ -citronellal and 1,8-cineole, respectively. In certain situations 1,8-cineole can be used as an insecticide against mosquitoes (Klocke, Darlington and Balandrin, 1987), but it has only moderate toxicity against flies (Sunkontason et al., 2004). The oils from *E. camaldulensis* and *E. urophylla*, in particular the chemical constituent  $\alpha$ -terpinene, have been recorded as larvicides against some species of mosquito (Cheng et al., 2009). Anti-microbial properties include action against *Staphylococcus aureus*, *Pseudomonas aeruginosa*, *Bacillus subtilis* and *Candida albicans* (Hendry et al., 2009; Marzoug et al., 2011).

*Eucalyptus* oils have also been demonstrated to have herbicidal properties. The oil from *E. citriodora* inhibits the germination and growth of *Bidens pilosa*, *Amaranthus viridis*, *Rumex nepalensis* and *Leucaena leucocephala*, all of which are weeds in India (Batish et al., 2004; Setia et al., 2007). The findings from such research may prove the basis of the development of bioherbicides. Although the oil from *Eucalyptus* itself can produce allergic contact dermatitis, it can be an effective insecticide against house dust mites, reducing the allergens associated with these insects in children's soft toys (Chang et al., 2011).

## Weediness

### *Weediness status on a global scale*

A weed can be defined as a plant that causes significant levels of one or more harms in a given geographical area. The most important of these harms are: 1) adverse effects on the health of people and/or animals; 2) reduction in the establishment and/or yield of desired plants; 3) restriction in the physical movement of people, animals or vehicles; and 4) adverse effects on environmental health, such as adverse changes to soil, salinity and the habitat of desirable organisms. Potential adverse effects on the environment from *Eucalyptus* include possible negative impacts on biodiversity, water quantity and quality, and fire risk.

Standard agricultural practices reduce biological diversity when compared to previous more natural ecosystems, and a eucalypt monoculture is not expected to be greatly different in this respect. It is unsurprising, then, that Stewart (2011) found that water quality and biodiversity values at a number of *E. globulus* plantation sites were inferior to those at remnant native vegetation sites. However, when compared with "pasture unfenced" and some "pasture fenced" sites", the plantation sites often had better water quality, riparian condition and biodiversity (Stewart, 2011). Studies in Brazil have shown that both *Eucalyptus* plantations and areas that were once planted with *Eucalyptus* trees but have been allowed to regenerate forest naturally, have fewer species of birds, ferns, epiphytic angiosperms and other organisms than observed in natural forests (Barlow et al., 2007; Fonseca et al., 2009). However, at least in some cases, plantations of *Eucalyptus* provide a unique habitat that is attractive to some species of birds with lifestyles that can benefit from the monocultures (Loyn et al., 2007).

Eucalypts are widely used in agroforestry and can provide environmental benefits for degraded landscapes. However, broad areas of revegetation may provide a large source of foreign genes in landscapes where small remnant native populations act as a sink (Byrne and Stone, 2011). Genetic change from hybridisation can threaten persistence of such populations through genetic assimilation or demographic swamping. The potential for gene flow and natural hybridisation of *Eucalyptus* is considered later in this chapter.

*Eucalyptus* trees are also known to be able to suppress the growth of understorey plants and adjoining crop plants, through the release of allelopathic chemicals (Zhang et al., 2010).

As outlined above, eucalypts may use extensive and deep root systems to access water. As a consequence, eucalypt plantations have been the subject of concerns about their potential for high water use and possible effects on groundwater (Almeida et al., 2010a; Morris et al., 2004). A number of authors have examined the impacts of such plantations on the environment, concluding that although they have adverse effects, if well managed they can provide benefits such as acting as wind breaks, reducing wind erosion and providing shelter for humans and animals (Poore and Fries, 1985). Nonetheless, there is data indicating that afforestation with *Eucalyptus* species can affect stream flow (Scott and Prinsloo, 2008; Silveira and Alonso, 2009); the degree to which this occurs has been found to depend on rainfall intensity and distribution, soil texture, tree age and stocking (Almeida et al., 2007).

Detailed data on water use and water balance of plantations are required to evaluate their environmental impact and to design optimal land-use strategies in catchment areas where wood production is an important economic component. Hydrology research for eucalypt and other exotic tree plantations has therefore received increasing attention in recent years. In Brazil, for example, studies of evapotranspiration and catchment water balance in eucalypt plantations have found that, in some parts of the country, catchment-scale plantation evapotranspiration did not differ from the climatic mean, whilst under other conditions it was higher (Lima et al., 2012a; 2012b). These authors concluded that, in general, there is no reason to expect that forest plantations are inherently detrimental to water availability, or that they would produce hydrological effects of the same magnitude in all situations. Instead, these and other studies' results show that the control of water impacts is very much dependent on the implementation of sustainable strategies of forest plantation management practices based on practical local experience and incorporating results from experimental studies and monitoring programmes (Lima et al., 2012a; 2012b). Selection of clones for water-use efficiency can also play a part in such strategies (Dye, 2012). Comparisons of water loss between *Eucalyptus* and pine plantations have also been conducted, with at least some work suggesting that plantations of the latter have less effect on stream flow (Dvorak, 2012).

Characteristics of weeds may be related to potential invasiveness, such as high seed output, rapid growth to flowering, self-fertilisation and secondary seed dormancy. Further, the ability of a plant to spread (the ease and range of the dispersal of seed) and persist (establish and reproduce in a new location) affects its likelihood of being classified as a weed.

In general, *Eucalyptus* species do not figure prominently as weeds around the world. This is perhaps surprising given that many eucalypts produce large quantities of seeds and possess diverse adaptations for dealing with disturbance. However, compared to species of *Pinus* (which have also enjoyed worldwide popularity as plantation trees), and members of the family Leguminosae, eucalypts are poor invaders (Richardson, 1998). Eucalypt seeds are generally small, but have no adaptation for dispersal and there is a high mortality amongst seedlings (see discussion earlier in this chapter). Due to their relatively long lifecycles, even under ideal circumstances they are slow to spread and establish, with the growth of many species being restricted by their preference for specific soils and climatic regimes. One study in Brazil, specifically designed to examine the abilities of *E. grandis* and *E. grandis* x *E. urophylla* to invade and establish in areas of

native vegetation lying adjacent to plantations, demonstrated that neither plant could effectively do so (da Silva et al., 2011). However, factors such as soil and climatic preferences do not altogether explain the comparatively poor invasive abilities of plants from this genus. The potential of mycorrhizal fungi for improving the establishment and performance of exotic eucalypts is still not fully explored (Chilvers et al., 2000; see above), but a lack of compatible ectomycorrhizal fungi has also been suggested as a factor limiting invasiveness (Rejmanek and Richardson, 2011).

Nevertheless, in a number of countries and environmental contexts, species of *Eucalyptus* have been classified as weeds. An Australian report prepared for the World Wildlife Fund lists five species (*E. botryoides*, *E. camaldulensis*, *E. citriodora*, *E. cladocalyx* and *E. maculata*) as posing a significant weed risk in some Australian states (Groves, Boden and Lonsdale, 2005). However, the online database from the Australian Weeds Committee National Initiative<sup>8</sup> records only *E. maculata* (spotted gum) as a weed anywhere in the country, while the database from the Australian Department of Environment<sup>9</sup> fails to list any *Eucalyptus* species. A study in Western Australia has reported that *E. megacornuta* has invaded areas of urban bushland, perhaps due to factors linked to the increased germination of seed and survival of seedlings after fire (Ruthrof, 2004).

Outside Australia, several species of *Eucalyptus* have been classified as weeds. The CABI Invasive Species Compendium<sup>10</sup> lists the following four *Eucalyptus* species as invasive: *E. sideroxylon*, *E. camaldulensis*, *E. cladocalyx* and *E. paniculata*. All four are reported to be invasive in South Africa and classified as category 2 under the South African Conservation of Agricultural Resources Act (1983). *E. camaldulensis* has been described as transforming large expanses of riverbanks in South Africa, and *E. grandis* and *E. lehmannii* have also been noted as weeds in that country (Forsyth et al., 2004). The Invasive Plant Atlas of the United States<sup>11</sup> designates six species as invasive of natural areas, including *E. camaldulensis* and *E. globulus*. Using the Australian Weed Risk Assessment System (Pheloung, Williams and Halloy, 1999), Gordon et al. (2012) evaluated the invasive potential of 38 species of *Eucalyptus* that, at the time of the study, were being tested or cultivated in the United States for pulp, biofuel or other purposes. It was found that 15 species (39%) had a low risk of invasion, 14 (37%) were high risk while the remainder needed further information to establish their status. The high risk species included *E. camaldulensis*, *E. globulus*, *E. grandis* and *E. saligna*, while the hybrid *E. urophylla* x *E. grandis* (*E. urograndis*) required further evaluation. In another study, Gordon et al. (2011) used the Australian Weed Risk Assessment System to explore the invasiveness of a range of plants that were under study as biofuels. Likewise, *Eucalyptus* species such as *E. camaldulensis* and *E. grandis* were concluded as having a high risk of invasiveness (Figure 6.16).

In both Nepal and South Africa, the invasion of areas by species of *Eucalyptus* has been linked to problems with the amount of water flowing in streams, and in turn the quantity of water in dams (Kunwar, 2003; Richardson and van Wilren, 2004). However, in some countries where *Eucalyptus* species have been extensively grown as a plantation crop for many years, such as Brazil and India, none have been classified as a weed (Pasquali, 2010; Reddy, 2008; Reddy et al., 2008).

When assessing the weediness of any given *Eucalyptus* species, it should not be forgotten that it relates to trees used for plantation in most cases. The invasive spread of trees from large-scale plantings (commercial plantations) into surrounding regions is usually greater than from areas under agroforestry practices (Richardson, 1998). This is



likely due to a number of factors, including the larger expanses of commercial plantations and the greater concern with the environment associated with agroforestry. Hence, the management practices of the plantations in question may form a major part of any weed risk assessment.

Figure 6.16. Young *E. camaldulensis*, growing beside waterway at the Australian National Botanic Gardens



Source: Courtesy Alison Wardrop, OGTR.

### **Control measures**

*Eucalyptus* seedlings can be killed by the surface application of herbicides. In the case of adult trees, it is possible to drill holes around the perimeter of the trunk, or use an axe to place a series of cuts around the base; then a syringe is used to inject an herbicide, such as glyphosate, into the interior tissues. Climate and the time of the year are factors which must be kept in mind before using an herbicide. Burning, either by the controlled lighting of a fire around the target trees or the use of a flame gun, are also possible measures to kill trees. Large *Eucalyptus* trees can be felled by standard procedures, ideally this being coupled with the disposal of the timber, either as chips, mulch or its conversion to wooden products such as flooring. Ring barking (girdling), in which a strip of bark is removed all the way around a trunk, thus breaking the phloem tissue, can also be used to kill the upper portions of trees. This practice was commonly used to kill eucalypts on agricultural land during the early days of European settlement of Australia.

The clearing of a weed from an area is only the first step in its reclamation. Ideally, a linked strategy for the colonisation of the cleared area needs to be in place and acted upon, or else it is possible that another weed will take the place of the eradicated weed. For instance, when *E. grandis* was cleared from the banks of one river in South Africa, it was found that a group of unwanted weeds almost immediately sprouted to fill the ecological niche (Koenig, 2009).

### **Mating system and hybridisation in *Eucalyptus***

The possibility of genes transferring from any one of the *Eucalyptus* species to other organisms is addressed below. Potentially, genes could be transferred to: 1) plantation eucalypt populations; 2) other cultivated and naturalised eucalypt species; 3) other plant

genera; and 4) other organisms. For gene transfer beyond species, potential barriers must be overcome before gene flow can occur successfully. Pre-zygotic barriers include differences in floral phenology, different pollen vectors and different mating systems, such as stigmatic or stylar incompatibility systems. Post-zygotic barriers include genetic incompatibility at meiosis, selective abortion, lack of hybrid fitness, and sterile or unfit backcross progeny. Even where pre-zygotic and post-zygotic barriers do not exist, physical barriers created by geographic separation can still limit gene transfer to other plants.

Successful gene transfer requires that three criteria are satisfied. The plant populations must: 1) overlap spatially; 2) overlap temporally (including flowering duration within a year and flowering time within a day); and 3) be sufficiently close biologically that the resulting hybrids are fertile, facilitating introgression into a new population (den Nijs, Bartsch and Sweet, 2004).

### ***Intraspecific crossing***

As outlined above, *Eucalyptus* species are often capable of self-fertilisation, but in most cases breed by a combination of self-pollination and outcrossing, with a marked tendency to outcross (Pryor, 1976). This tendency is reinforced by protandry and by selection against the products of self-fertilisation in later stages of life; self-pollination often results in severe inbreeding depression for growth and survival, manifested as a reduction in capsule production, seed yield, and seedling growth and vigour compared with cross-pollination (Hardner and Potts, 1995; Potts, Hamilton and Blackburn, 2011; Potts and Wiltshire, 1997). Nonetheless, open pollinated seed collected from native stand and seed orchard trees still contain significant proportions of self-pollinated seed (Eldridge et al., 1994; Potts and Wiltshire, 1997).

### ***Estimates of outcrossing rate***

Quantitative estimates of outcrossing in several eucalypt species have been made on the basis of allozyme variants. From such studies, outcrossing has been shown to predominate, averaging about 75% in seed from natural populations of 18 species (Eldridge et al., 1994; Potts and Wiltshire, 1997). Subsequent estimates using values averaged over 23 species show a mean outcrossing rate of 0.74<sup>12</sup> (Byrne, 2008). Where comparisons have been made for species using both microsatellite markers and allozyme markers, it appears that the allozyme estimates may underestimate true outcrossing rates by up to 10% (Byrne, 2008). Estimates of the outcrossing rate in natural populations using rare morphological seedling markers range from 0.70 to 0.92 (McGowen et al., 2004), and in exotic stands the range is 0.62-0.90.

For individual species, estimates of outcrossing in native populations of *E. globulus* range from 0.65 to 0.89 (Mimura et al., 2009) and in seed orchards from 0.60 to 0.90 (Potts et al., 2008). McGowen et al. (2004) used a single locus morphological marker to estimate outcrossing in *E. globulus* and suggested that pollinator activity and flower abundance had little effect on outcrossing rate, rather the self-incompatibility of a tree is probably the primary determinant of its outcrossing rate.

Only seed orchard estimates of outcrossing rates have been published for *E. nitens*, and these range from 0.75 to 0.87 (reviewed in Grosser, Potts and Vaillancourt, 2010). This is similar to outcrossing rates estimated in natural seed orchards and breeding populations of other eucalypt species: *E. camaldulensis*: 0.75; *E. regnans*: 0.91;

*E. urophylla*: 0.89-0.93 (Jones et al., 2008), and *E. grandis*: 0.84 (House, 1997; James and Kennington, 1993).

### *Self-incompatibility*

Self-incompatibility has been studied in only a few species of *Eucalyptus*. These studies indicate that there may be more than one self-incompatibility mechanism in eucalypts and that both pre- and post-zygotic mechanisms may operate (Ellis and Sedgley, 1992; Horsley and Johnson, 2007; McGowen et al., 2010; Pound et al., 2003a, 2003b, 2002a, 2002b; Sedgley and Granger, 1996; Sedgley et al., 1989; Sedgley and Smith, 1989).

In *E. globulus*, self-incompatibility is probably the primary determinant of outcrossing rate rather than pollinator activity or flower abundance (McGowen et al., 2010, 2004; Patterson et al., 2004). Self-incompatibility in this species is estimated at 87-89% and is thought to be mainly due to late-acting mechanisms operating in the ovary, with post-zygotic abortion of self-fertilised ovules (Pound et al., 2002a). Similarly, ovule breakdown has been suggested in *E. nitens* as a late-acting self-incompatibility response (Pound et al., 2003b). Studies of the breeding systems of *E. urophylla* and *E. grandis* suggest that, in addition to a late-acting self-incompatibility barrier, cryptic self-incompatibility in the form of self-pollen tube growth retardation could be responsible for the preferential outcrossing observed for these two species (Horsley and Johnson, 2007).

### *Natural and manipulated hybridisation*

A comprehensive overview of natural and manipulated hybridisation patterns within the genus *Eucalyptus* L'Hérit can be found in reviews by Griffin, Burgess and Wolf (1988) and Pryor and Johnson (1981; 1971). In addition, Potts, Barbour and Hingston (2001) and Potts et al. (2003) have compiled a large volume of published work on the characteristics of plantation eucalypt species and hybrids, in the context of assessing the risk of genetic pollution from farm forestry. A comprehensive list of reports relating to natural and manipulated hybrids of the major plantation *Eucalyptus* species was tabulated in Potts, Barbour and Hingston (2001) and includes a vigour rating for hybrid seedlings; extracts from that publication are reproduced in Annex 6.A1. In addition, the potential for gene flow from exotic eucalypt plantations into Australian native eucalypts has been explored by Barbour et al. (2010). Some of the key conclusions and summaries from those reports are included in the discussion below.

The degree to which hybridisation may occur is limited by pre-mating barriers such as spatial isolation and flowering asynchrony (Keatley, Hudson and Fletcher, 2004; Potts and Wiltshire, 1997), and by post-mating crossing incompatibilities. Pollination mechanisms are a major determinant of gene flow in plants; species which are located, by distance or other physical features, beyond the normal range of pollen transfer are unlikely to hybridise (Duncan, 1989). This is particularly the case for eucalypts, for which gene flow by seed dispersal is quite limited (see above; Byrne, 2008). Pollen transfer between eucalypts occurs via the activities of non-specific biotic vectors such as birds and insects rather than wind, and the extent of pollen dispersal is influenced by the type and efficiency of pollinators (see above).

Other determinants of gene flow are: 1) season of flowering (phenology); and 2) lack of reproductive compatibility. Seasonal differences in flowering time are one of the major pre-zygotic barriers to gene flow within *Eucalyptus* (Drake, 1980; Pryor, 1976). For

inter-provenance crossing in a seed orchard of *E. regnans*, for example, differences in peak flowering time of only two weeks was enough to reduce crossing to 65% of that expected under random mating (in Potts, Barbour and Hingston, 2001). However, flowering within eucalypt species may be highly variable and influenced by numerous other factors (Eldridge et al., 1994; House, 1997; Potts and Wiltshire, 1997). Most eucalypts display protandrous flower development and, because pollen is usually shed before the eucalypt stigma becomes receptive, late-flowering trees are more likely to pollinate early-flowering trees (see above). A summary of relative flowering times in Australia for a range of plantation species can be found in Table 5.3 of Potts, Barbour and Hingston (2001).

In addition to premating barriers such as geographic isolation and flowering asynchrony, post-mating crossing incompatibilities will also determine the level of gene flow. Controlled crossing experiments have shown that there are two major pre-zygotic barriers to hybridisation. The first is a structural barrier which is unilateral, and due to the pollen tubes of small-flowered species being unable to grow the full length of the style of large-flowered species (see above; Gore et al., 1990). The resulting reduction in seed set has hindered attempts to produce F<sub>1</sub> hybrids between *E. globulus* and smaller flowered species such as *E. gunnii*, *E. camaldulensis*, *E. nitens*, *E. grandis* or *E. dunnii*. However, since flower and style size are inherited in an intermediate manner, once F<sub>1</sub> hybrids are obtained, the physical barrier between species can be broken down (Potts, Barbour and Hingston, 2001).

The second barrier is physiological and results in pollen tube abnormalities and pollen tube arrest in the pistil. This prevents successful hybridisation between the three genera of eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*), as well as between the major subgenera within *Eucalyptus* (Griffin, Burgess and Wolf, 1988; Potts et al., 2003; Pryor and Johnson, 1971).

### *Natural hybridisation*

Griffin, Burgess and Wolf (1988) examined patterns of both natural and manipulated hybridisation within the genus *Eucalyptus* and, consistent with earlier work by Pryor and Johnson (1971; 1981), found that the occurrence of hybrid combinations reflects the degree of taxonomic distance. Barriers to hybridisation between species within subgenera are often weak (Griffin, Burgess and Wolf, 1988; Hardner and Potts, 1995; Potts et al., 2003), and natural hybridisation and introgression between recognised taxa is relatively common (Butcher and Williams, 2002; Field et al., 2011; Griffin, Burgess and Wolf, 1988; Potts and Gore, 1995; Potts and Wiltshire, 1997). In decreasing order of frequency, hybrids are found to occur within series, between series and between sections. Thus, interspecific hybridisation between species from the same section is commonly reported, but hybridisation between species from the major subgenera or genera does not occur.

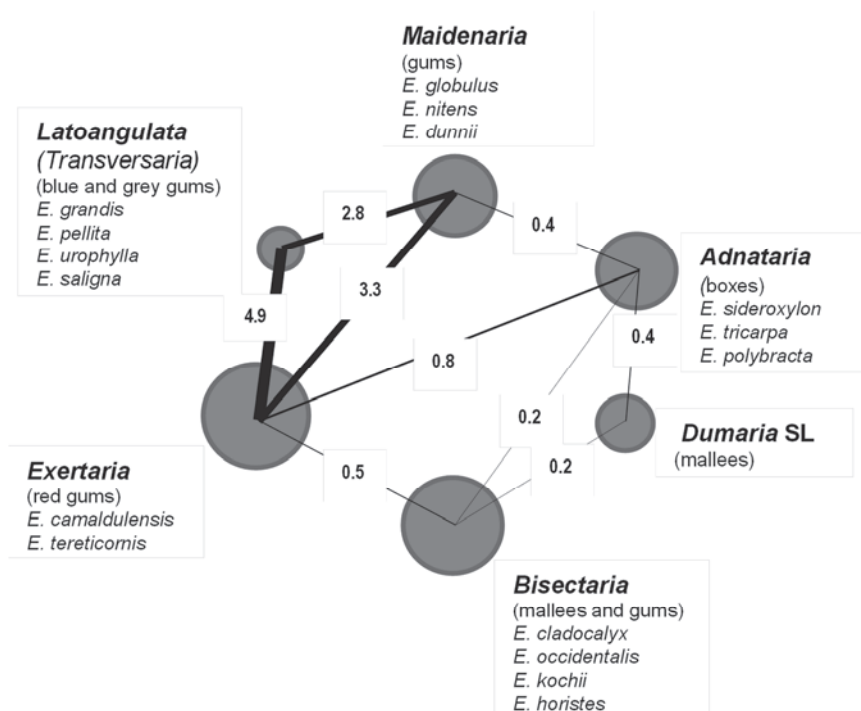
Natural hybridisation may be rather restricted (Griffin, Burgess and Wolf, 1988) since, amongst recorded natural hybrids only 15% of combinations expected on geographic and taxonomic grounds had been recorded. Nonetheless, it appears that in native forest there is a low background level of natural crossing continually occurring between species. In Australian native forests, this background level of F<sub>1</sub> hybridisation was found to average 1.62% across 13 species, and from 0.03% to 3.5% at the individual species level (see Table 3 in Potts et al., 2003). While it has been suggested that human activity may have enhanced this rate of hybrid formation and survival (e.g. through the introduction of honey bees and habitat disturbance), there is no doubt that hybridisation in

the genus is natural and has been a significant factor in eucalypt evolution (Potts, Barbour and Hingston, 2001).

### Within and between sections

The occurrence of natural and artificial hybrids of the main *Symphyomyrtus* plantation eucalypt species (data from Griffin, Burgess and Wolf, 1988) is summarised in Annex 6.A1, and the frequency of inter-sectional hybridisation is shown diagrammatically in Figure 6.17. Only 40 natural intersectional hybrids were reported in *Symphyomyrtus*.

Figure 6.17. Natural inter-sectional hybridisation in *Symphyomyrtus*



*Note:* The figure shows the frequency of natural inter-sectional hybrids as a percentage of the number of intersectional combinations possible amongst proximal species (within 10 x 10 minutes of longitude and latitude). The area of the circle indicates the number of species in each section. Sections follow Pryor and Johnson (1971). Section *Transversaria* was renamed *Latoangulatae* by Brooker (2000).

*Source:* Adapted from Potts et al. (2003) (reproduced from Steane et al. (2002)).

The summarised data suggest that species from *Exertaria* (e.g. *E. camaldulensis*) can potentially hybridise with all other major sections except *Dumaria*. Plantation species from the *Latoangulatae* (e.g. *E. grandis*, *E. pellita*) are more likely to hybridise with species from the *Exertaria* or *Maidenaria* than with other sections of *Symphyomyrtus*. No natural hybrids have been reported between *Maidenaria* and either *Bisectaria* or *Dumaria* species.

Within the section *Maidenaria*, the potential for natural hybridisation of eucalypts from plantations and native forests has been documented by Barbour, Potts and Vaillancourt (2003; 2005) and Barbour et al. (2002) on the island of Tasmania. Hybrids between *E. ovata*, which is native to the island, and the introduced plantation species

*E. nitens*, were found in a number of locations, and it was concluded that such hybrids were establishing in the wild (Barbour, Potts and Vaillancourt, 2003; Barbour et al., 2002). Further studies of pollination from *E. nitens* plantations showed that *E. ovata* plants within 100 m of *E. nitens* produced approximately 7% hybrids, but after 200 m the number of hybrids had dwindled to less than 1% per plant (Barbour, Potts and Vaillancourt, 2005).

### Between genera and subgenera

Post-mating crossing incompatibility prevents successful hybridisation between the three genera of eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*), as well as between the major subgenera within *Eucalyptus* (Griffin, Burgess and Wolf, 1988; Potts et al., 2003). Only two records were found of imputed natural hybrids between *Eucalyptus* subgenera; both proved to be misidentifications when re-examined (Griffin, Burgess and Wolf, 1988).

### Manipulated hybridisation

Controlled pollination, or manipulated/artificial hybridisation, is used for the generation of interspecific hybrids for plant improvement (Eldridge et al., 1994). It has been widely used as a breeding strategy in eucalypts in subtropical and tropical regions of the world, but to a lesser extent in temperate regions (Harwood, 2011; Potts and Dungey, 2004).

Most records of manipulated hybrids are derived from the subgenus *Symphyomyrtus*. As part of a review of the risks of genetic pollution from planting non-native eucalypt species and hybrids in Australia, Potts, Barbour and Hingston (2001) and Potts et al. (2003) summarised Griffin's data and supplemented it with new records of manipulated and artificial hybridisation. Annex 6.A1 is adapted from tabulated data presented in Potts, Barbour and Hingston (2001), and some of the major conclusions drawn in that review are outlined below.

### Within sections

Reports of successful manipulated interspecific hybridisation within sections are relatively common (Delaporte, Conran and Sedgley, 2001; Griffin, Burgess and Wolf, 1988) (see Annex 6.A1), some of the hybrids having become of significant commercial importance. *E. grandis* x *E. urophylla* hybrids are planted extensively in Brazil (Goncalves et al., 2008; Potts and Dungey, 2004). In Australia and South America, there has been considerable research on artificial hybridisation of the major plantation species *E. nitens* and *E. globulus*, which would not normally hybridise due to temporal and geographic barriers (Potts and Dungey, 2004; Potts et al., 2000; Tibbits, 2000). Hybrid clones between these species have been developed in Chile (Griffin et al., 2000), but attempts in Australia have been unsuccessful, in part due to the inability to achieve clonal propagation (Potts, Hamilton and Blackburn, 2011).

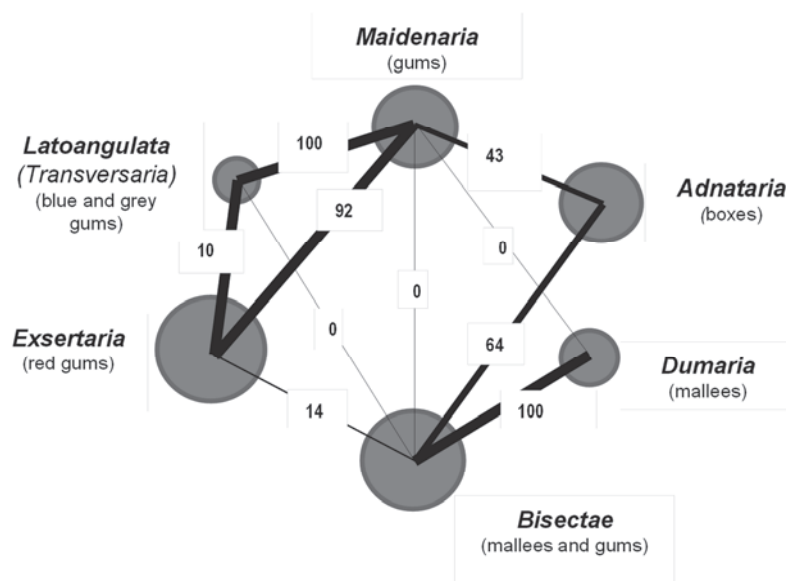
### Between sections

Data from manipulated hybridisation studies are consistent with the observations outlined for natural hybrids (see previous section and Figure 6.18.). Thus, within *Symphyomyrtus*, it appears that plantation species from the section *Exertaria* can potentially hybridise with all other major sections except possibly the mallees (Griffin, Burgess and Wolf, 1988; Potts, Barbour and Hingston, 2001). Plantation species from the

section *Latoangulata* (*Transversaria*) are more likely to hybridise with species from either the *Exsertaria* or *Maidenaria* than the other *Symphyomyrtus* sections. Overall, *Latoangulata* has the highest number of intersectional hybrids.

Delaporte, Conran and Sedgley (2001) reported on 36 individual crosses between series in section *Bisectaria* and between section *Bisectaria* and section *Adnataria*. The results confirmed and extended earlier findings that crosses between species from *Bisectaria* and *Adnataria* have a relatively high chance of success (Ellis, Sedgley and Gardner, 1991). This study also confirmed that crosses between closely related species have a greater degree of success than those between distant crosses, as do those between species with similar flower size (Delaporte, Conran and Sedgley, 2001). The resulting hybrid seedlings displayed leaf and stem characteristics that were intermediate between the maternal and pollen parents, albeit closer to the maternal parent.

Figure 6.18. **Manipulated inter-sectional hybridisation in *Symphyomyrtus***



*Note:* The figure shows the percentage of successful species combinations produced from manipulated inter-sectional cross-combinations within *Symphyomyrtus*. Sections follow Pryor and Johnson (1971). Also see Annex 6.A1.

*Source:* Adapted from Potts et al. (2003).

Even if interspecific mating occurs and seed is produced, it is not certain that hybrids will survive and introgression will occur. Hybrid offspring are also usually intermediate between parental taxa for flowering time and physical characteristics such as flower size (Lopez et al., 2000; McComb et al., 2000) and this may potentially enhance backcrossing to parental species. However, progeny derived from hybrids crossing to either of the parental species or an unrelated third species are likely to exhibit loss of fitness due to advanced generation breakdown (outbreeding depression). Some interspecific crosses of *Symphyomyrtus* are reported to be more susceptible to insects and fungal pests than parental species (Harwood, 2011) and impaired reproductive capability, abnormalities and dwarfism are common features of many later generation eucalypt species (Delaporte, Conran and Sedgley, 2001; Pilipenko, 1969; Potts, Barbour and Hingston, 2001).

## Between genera and subgenera

There are a few reports of manipulated intersubgeneric hybrids, but seedlings from such crosses either died or showed very poor vigour or results need further validation (Ladiges, 1997; Meddings et al., 2003). In documenting extensive work in the Russian Federation on eucalypt hybridisation, Pilipenko (1969) mentioned 17 combinations of manipulated hybrids between subgenera. Of these, 13 were unsuccessful in that they produced no viable seed.

## Human health

Potential allergens and toxins from *Eucalyptus* are the products of flowers, especially pollen, gums from stems and branches, and the oils that are extracted from leaves.

*Eucalyptus* pollen can cause an allergic reaction in many people, but it is not considered a severe problem. One Internet database, providing details of the allergenicity of pollen from various plants native and introduced to the United States, lists four *Eucalyptus* species, and in each case classifies their pollen as a mild allergen.<sup>13</sup> In India, although pollen from *Eucalyptus* has been commonly found, it is not regarded as of allergenic importance (Singh and Dahiya, 2008). Allergenic symptoms from pollen include irritation to the respiratory tract and skin, conjunctivitis, asthma, nasal congestion and even malfunction of the vocal cords. Such symptoms in susceptible individuals are invariably seasonal, corresponding to the time when the relevant *Eucalyptus* trees release pollen, but environmental factors such as the level of humidity can influence the responses of people.

The oils from *Eucalyptus* leaves have long been extracted and used in various commercial and medicinal capacities. In medicine, such oils have been used to relieve the symptoms of respiratory tract infections and inflammations, and reduce the effects of asthma (Juergens et al., 2003).

Although eucalyptol can be ingested in small quantities (such as in mouthwash and through application to the nose and other parts of the skin), it is toxic when consumed in high dose, with an oral LD50 in rat of 2 480 mg/kg. It is oxidised by cytochrome p450 enzymes to one of two metabolites which are then excreted in urine (Duisken et al., 2005). Rarely, application to the skin of *Eucalyptus* oil (which often consists mostly of eucalyptol) can induce significant symptoms of toxicity. In one case, the use of *Eucalyptus* oil to treat urticaria (hives) induced severe nervous system toxicity, evidenced by slurred speech, muscle weakness and unconsciousness (Darben, Cominos and Lee, 1998). In addition, eucalyptol has been recorded as producing an allergic response in some people, usually characterised by a rash and the desire to scratch the infected areas (Vilaplana and Romaguera, 2000). Use of a corticosteroid can relieve the symptoms.



## Notes

1. This citation was added as an update in January 2016.
2. This citation was added as an update in January 2016.
3. This citation was added as an update in January 2016.
4. This citation was added as an update in January 2016.
5. Clinal variation: continuous variation in form between individual leaves.
6. Protandry: anthers dehisce and shed pollen before the stigma becomes receptive.
7. [www.phytozome.net/eucalyptus.php](http://www.phytozome.net/eucalyptus.php).
8. Weeds Australia website at: [www.weeds.org.au](http://www.weeds.org.au).
9. Weeds Australia website at: [www.weeds.org.au](http://www.weeds.org.au).
10. CABI Invasive Species Compendium website at: [www.cabi.org/isc](http://www.cabi.org/isc).
11. Invasive Plant Atlas of the US website at: [www.invasiveplantatlas.org/index.html](http://www.invasiveplantatlas.org/index.html).
12. t; 0 = complete self-fertilisation, 1 = complete outcrossing.
13. [www.pollenlibrary.com](http://www.pollenlibrary.com).

### ***Annex 6.A1.***

## **Compilation of natural and manipulated hybrids of major eucalypt plantation species<sup>1</sup>**

Vigour rating (V)

- 1: apparently healthy seedlings or trees
- 2: below mid parent performance noted
- 3: some vigorous but also others with viability problems
- 4: successful seed set and early seedling growth but failed to survive in later years
- 5: seedlings or trees with stunted growth
- 6: fruit set or seed only
- 7: failed hybrid combinations
- S: successful seed set only reported, not planted

Female/male (f/m): whether the species listed was used as the female or male in the cross.

Table 6.A1.1. *Eucalyptus globulus*

A. Natural hybrids

Species	Reference
<i>E. barberi</i>	Williams and Potts (1996)
<i>E. brookeriana</i>	Williams and Potts (1996)
<i>E. ovata</i>	Jordan et al. (1993); Williams and Potts (1996)
<i>E. kitsoniana</i>	Griffin, Burgess and Wolf (1988)
<i>E. goniocalyx</i>	Griffin, Burgess and Wolf (1988)
<i>E. nortonii</i>	Griffin, Burgess and Wolf (1988)
<i>E. cypellocarpa</i>	Kirkpatrick, Simmons and Parsons (1973)
<i>E. pseudoglobulus</i>	Griffin, Burgess and Wolf (1988)
<i>E. bicostata</i>	Griffin, Burgess and Wolf (1988)
<i>E. johnstonii</i>	Griffin, Burgess and Wolf (1988)
<i>E. viminalis</i>	Griffin, Burgess and Wolf (1988)
<i>E. cordata</i>	Williams and Potts (1996)
<i>E. rubida</i>	Griffin, Burgess and Wolf (1988)
<i>E. urnigera</i>	Griffin, Burgess and Wolf (1988)
<i>E. perriniana</i>	Williams and Potts (1996)

1. Adapted from Potts, Barbour and Hingston (2001) and based on data from Griffin, Burgess and Wolf (1988).

Table 6.A1.1. *Eucalyptus globulus* (continued)

## B. Manipulated hybrids

Species	V	FM	Reference
<i>E. urophylla</i>	3	f	Griffin et al. (2000)
<i>E. grandis</i>	3	f	Griffin et al. (2000)
<i>E. robusta</i>	1		Griffin, Burgess and Wolf (1988)
<i>E. pellita</i>			D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
<i>E. longifolia</i>			Griffin, Burgess and Wolf (1988)
<i>E. loxophloebe</i>			Griffin, Burgess and Wolf (1988)
<i>E. camaldulensis</i>	3	f	McComb et al. (2000); Mesbah (1995); Sasse, George and Dale (2000)
<i>E. dunnii</i>	3	f	Griffin, Burgess and Wolf (1988) ; Griffin et al. (2000); Barbour and Spencer (2000) (cut style)
<i>E. nitens</i>	3	f	Griffin et al. (2000); Potts et al. (2000)
<i>E. maidenii</i>	1	m	Potts unpublished data
<i>E. bicostata</i>	1	f	Potts unpublished data
<i>E. viminalis</i>	1		Griffin, Burgess and Wolf (1988)
<i>E. gunnii</i>	1	f	Potts et al. (2000)
<i>E. sideroxylon</i>	7	f	Griffin, Burgess and Wolf (1988)

Table 6.A1.2. *Eucalyptus nitens*

## A. Natural hybrids

Species	Reference
<i>E. quandrangulata</i>	Tibbitts, Boomsma and Jarvis (1997)

## B. Manipulated hybrids

Species	V	FM	Reference
<i>E. grandis</i>	3	f	Shelbourne, Hong and McConnochie (1999)
	2		Verryn (2000)
			Tibbitts (2000)
<i>E. saligna</i>	2	m	Tibbitts (2000)
<i>E. botryoides</i>	4	m	Tibbitts (2000)
<i>E. oldfieldi</i>	7	m	Tibbitts (2000)
<i>E. camaldulensis</i>	3	m	Tibbitts (2000; 1989; 1988)
	3	m	
<i>E. rudis</i>	4	m	Tibbitts (2000)
<i>E. ovata</i>	1	m	Tibbitts (2000)
<i>E. rodwayi</i>	2	m	Tibbitts (2000)
<i>E. neglecta</i>	2	m	Tibbitts (2000)
<i>E. parvifolia</i>	1	m	Tibbitts (2000)
<i>E. dunnii</i>	2	m	Tibbitts (2000)
<i>E. cypellocarpa</i>			Griffin, Burgess and Wolf (1988)
<i>E. globulus</i>	3	m	Griffin et al. (2000);
		m	Potts et al. (2000);
		m	Tibbitts (2000; 1989; 1988)
<i>E. quandrangulata</i>	6	m	Tibbitts (2000)
<i>E. johnstonii</i>	1	m	Tibbitts (2000)
<i>E. macarthurii</i>	6	m	Tibbitts (2000)
<i>E. viminalis</i>	1	m	Tibbitts (2000; 1989; 1988)
<i>E. dalrympleana</i>	1	m	Tibbitts (2000)
<i>E. rubida</i>	1	m	Tibbitts (2000)
<i>E. glaucescens</i>	7	m	Tibbitts (2000)

B. Manipulated hybrids (*continued*)

Species	V	FM	Reference
<i>E. gunnii</i>	1	mf	Tibbits (2000; 1989; 1988)
<i>E. morrisbyi</i>	2	m	Tibbits (2000)
<i>E. urnigera</i>	S	m	Tibbits (2000)
<i>E. perriniana</i>	2	mf	Tibbits (2000)
<i>E. cordata</i>	1	m	Tibbits (2000)
<i>E. decipiens</i>	7	m	Tibbits (2000)
<i>E. gillii</i>	7	m	Tibbits (2000)
<i>E. incrassata</i>	7	m	Tibbits (2000)
<i>E. tereticornis</i>	7	m	Tibbits (2000)
<i>E. pulverulenta</i>	7	m	Tibbits (2000)
<i>E. lansdowneana</i>	7	m	Tibbits (2000)
<i>E. fibrosa</i>	7	m	Tibbits (2000)

Table 6.A1.3. *Eucalyptus grandis*

## A. Natural hybrids

Species	Reference
<i>E. saligna</i>	Griffin, Burgess and Wolf (1988)
<i>E. robusta</i>	Griffin, Burgess and Wolf (1988)
<i>E. pellita</i>	Griffin, Burgess and Wolf (1988)
<i>E. tereticornis</i>	Griffin, Burgess and Wolf (1988)

## B. Manipulated hybrids

Species	V	FM	Reference
<i>E. urophylla</i>	1		de Assis (2000); Vigneron and Bouvet (2000); Wu, Wu and Xu (1996)
	1		D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
<i>E. botryoides</i>			D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
<i>E. pellita</i>	1		Griffin, Burgess and Wolf (1988)
	1		de Assis (2000)
<i>E. alba</i>	1	f	Griffin, Burgess and Wolf (1988)
<i>E. tereticornis</i>	1		Griffin, Burgess and Wolf (1988); Verryn (2000); Vigneron and Bouvet (2000)
<i>E. camaldulensis</i>	1		Griffin, Burgess and Wolf (1988)
	1		de Assis (2000)
	1	f	Verryn (2000)
<i>E. dunnii</i>	1		Dale, Aitken and Sasse (2000); Sasse, George and Dale (2000)
	3	fm	Griffin et al. (2000)
	3		de Assis (2000)
<i>E. nitens</i>	3	m	Shelbourne, Hong and McConnochie (1999); Tibbits (2000); Verryn (2000)
	2		
<i>E. maidenii</i>		fm	D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
	3		de Assis (2000)
<i>E. globulus</i>	3	m	Griffin et al. (2000)
<i>E. gunnii</i>	3	f	Potts unpublished data (in Potts, Barbour and Hingston, 2001)
<i>E. pulverulenta</i>			Paton (1981)
<i>E. leucoxylon</i>	7	m	Griffin, Burgess and Wolf (1988)
<i>E. resinifera</i>			David Lee personal communication (in Potts, Barbour and Hingston, 2001)

Table 6.A1.4. *Eucalyptus pellita*

## A. Natural hybrids

Species	Comments	Reference
<i>E. grandis</i>	Griffin, Burgess and Wolf (1988)	
<i>E. resinifera</i>	Griffin, Burgess and Wolf (1988)	
<i>E. punctata</i>	Griffin, Burgess and Wolf (1988)	
<i>E. brassiana</i>	Harwood (1998)	

## B. Manipulated hybrids

Species	V	FM	Reference
<i>E. deglupta</i>	7	m	Griffin, Burgess and Wolf (1988)
	5		Vigneron and Bouvet (2000)
	1?		Sariot (2013)
<i>E. urophylla</i>	1	fm	Harwood (1998); Vigneron and Bouvet (2000)
	3		de Assis (2000); Wu, Wu and Xu (1996)
<i>E. deanei</i>			D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
<i>E. grandis</i>	1		Griffin, Burgess and Wolf (1988)
	1		de Assis (2000)
<i>E. alba</i>	6	f	Griffin, Burgess and Wolf (1988)
<i>E. tereticornis</i>	1	f	Griffin, Burgess and Wolf (1988)
<i>E. camaldulensis</i>			Harwood (1998)
<i>E. maidenii</i>			D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
<i>E. globulus</i>			D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)

Table 6.A1.5. *Eucalyptus dunnii*

## A. Natural hybrids

Species	Comments	Reference

## B. Manipulated hybrids

Species	V	FM	Reference
<i>E. urophylla</i>		f	Griffin et al. (2000)
			D. Boomsma personal communication (in Potts, Barbour and Hingston, 2001)
<i>E. grandis</i>	3	mf	Griffin et al. (2000)
	3		de Assis (2000)
<i>E. maidenii</i>	1		de Assis (2000)
<i>E. globulus</i>	3	m	Griffin et al. (2000)
		f	Barbour and Spencer (2000) (cut style)

Table 6.A1.6. *Eucalyptus camaldulensis*

## A. Natural hybrids

Species	Comments	Reference
<i>E. robusta</i>	Spontaneous in exotic plantations	Kha and Cuong (2000)
<i>E. cladocalyx</i>		Griffin, Burgess and Wolf (1988)
<i>E. alba</i>		Griffin, Burgess and Wolf (1988)
<i>E. bigalerita</i>		Griffin, Burgess and Wolf (1988)
<i>E. tereticornis</i>		Griffin, Burgess and Wolf (1988)
<i>E. blakelyi</i>		Griffin, Burgess and Wolf (1988)
<i>E. dwyeri</i>		Griffin, Burgess and Wolf (1988)
<i>E. rudis</i>		Griffin, Burgess and Wolf (1988)
<i>E. ovata</i>		Griffin, Burgess and Wolf (1988)
<i>E. bridgesiana</i>		Griffin, Burgess and Wolf (1988)
<i>E. viminalis</i>		Griffin, Burgess and Wolf (1988)
<i>E. largiflorens</i>		Griffin, Burgess and Wolf (1988)
<i>E. melliodora</i>		Griffin, Burgess and Wolf (1988)
<i>E. leucoxylon</i>		Griffin, Burgess and Wolf (1988)

## B. Manipulated hybrids

Species	V	FM	Reference
<i>E. diversicolor</i>		m	Mesbah (1995)
<i>E. grandis</i>	1		de Assis (2000)
	1	m	Mesbah (1995)
	1		Dale, Aitken and Sasse (2000); Sasse, George and Dale (2000)
<i>E. botryoides</i>	1		Griffin, Burgess and Wolf (1988)
<i>E. cladocalyx</i>		m	Mesbah (1995)
<i>E. urophylla</i>	1		de Assis (2000)
	1		Kha and Cuong (2000); Wu, Wu and Xu (1996)
<i>E. tereticornis</i>	1	m	Griffin, Burgess and Wolf (1988)
			Mesbah (1995)
<i>E. blakelyi</i>	1	f	Griffin, Burgess and Wolf (1988)
<i>E. macarthurii</i>	1	f	Griffin, Burgess and Wolf (1988)
<i>E. viminalis</i>	1	fm	Griffin, Burgess and Wolf (1988)
<i>E. exerta</i>	1		Kha and Cuong (2000)
<i>E. maidenii</i>		m	Mesbah (1995)
<i>E. globulus</i>	3	m	McComb et al. (2000)
			Sasse, George and Dale (2000)
<i>E. gunnii</i>	5	mf	Griffin, Burgess and Wolf (1988)
<i>E. laevopinea</i>	7	f	Griffin, Burgess and Wolf (1988)
<i>E. fastigata</i>	7	f	Griffin, Burgess and Wolf (1988)

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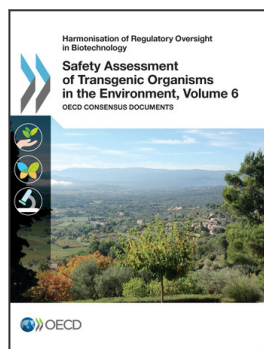
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