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Genetic Pollution from Farm Forestry

using eucalypt species and hybrids

A report for the RIRDC/L&WA/FWPRDC
Joint Venture Agroforestry Program

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Foreword

The rapid expansion of eucalypt plantations and restoration plantings in Australia has increased concerns of the risk of genetic pollution of native eucalypt gene pools.

This publication reviews the risks of genetic pollution and potential impacts on local biodiversity from planting non-native eucalypt species and hybrids in Australia. It develops a framework for risk assessment and identifies key research required for the development of management strategies.

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This report, a new addition to RIRDC's diverse range of over 700 research publications, forms part of our Agroforestry and Farm Forestry R&D program, which aims to integrate sustainable and productive agroforestry within Australian farming systems.

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Executive summary

Plant invasions arising from agricultural, forestry and other activities are becoming of increasing concern worldwide. Such invasions have traditionally been viewed as plants dispersing by seed beyond their intended area of use and becoming weeds. However, in the last decade, genetic invasion by pollen dispersal and hybridisation has become of increasing concern. The risk of escape of transgenes from genetically modified organisms has focused public attention on the general issue of hybridisation and introgression of genes from planted (exotic species, provenances or selected genotypes) to native gene pools. Indeed, there are already overseas reports of several forest tree species or provenances being under threat of genetic swamping from large, non-native plantings.

In the case of eucalypts, the contamination of local, native gene pools via non-native pollen is of relevance as:

(i) pollen dispersal is believed to be much more widespread than seed dispersal;

(ii) reproductive barriers are often weak between closely related species;

(iii) European settlement has already had a major impact on Australia's eucalypt woodlands and mallee;

(iv) there has been a rapid expansion of eucalypt plantations and restoration plantings in Australia; and

(v) Australia is the custodian of an internationally important genetic resource.

The risks associated with the introduction of non-native species, hybrids and provenances are reviewed. These include direct effects on the gene pool through genetic pollution as well as indirect effects through impacts on other components of biodiversity. In many cases the risk of genetic pollution will be small due to strong barriers to hybridisation between distantly related species, differences in flowering time or differences in other floral traits. There is no risk of hybridisation between species from the different major eucalypt genera/subgenera (e.g. symphyomyrts, monocalypts, eudesmids, bloodwoods and angophora). The main plantation species are symphyomyrts and within this subgenus, the probability of successful hybridisation decreases with increasing taxonomic distance between species. This trend is not clear in other subgenera (e.g. *Corymbia* and *Monocalyptus*). Inter-sectional crosses within *Symphyomyrtus* are unlikely to be successful, or if they are then the hybrids are unlikely to be of sufficient vigour to survive in undisturbed native forests. For example, the probability of successful gene flow between *E. globulus* and the predominantly western distributed mallee groups (*Dumaria* and *Bisectaria*) and potentially the boxes (*Adnataria*) is likely to be low. Even hybrids between relatively closely related species often exhibit reduced vegetative vigour and reduced reproductive output compared to parental types which would limit the possibility of gene flow between planted and native forest gene pools.

No major additional genetic risk is seen from the deployment of exotic hybrids as opposed to an exotic species in the landscape. The only exception is where backcrossing to parental taxa may occur. No reports of genetically modified eucalypts being field tested in Australia were found and their release in Australia is likely to be a lengthy procedure and depend upon reproductive sterility. The planting of non-local provenances or improved material within the range of the native gene pool has the potential to genetically impact on local gene pools to varying degrees and gene pool management strategies should be developed for the major plantation species. Such strategies will require a detailed knowledge of the spatial patterns of genetic differentiation in the native forest gene pool of these commercial species, some knowledge of which is already available from breeding trials established in Australia or overseas.

Pollen flow between plantation and native forest eucalypt species has already been reported and implementation of strategies to minimise the risk and consequences of genetic pollution is important if Australian forestry is to be certified as sustainable. A framework for assessment of the risk of genetic pollution is developed herein, involving identification of the conservation status of the adjacent forest ecosystem or gene pool, the probability that pollen-mediated gene flow will occur, and the impact that such gene flow is likely to have on the adjacent population. Such risk assessment could be an integral part of environmental impact assessments of eucalypt plantations and farm forestry. While the crossability patterns of the major plantation species need to be determined more accurately for species in their planting zones, there will be many species or provenance combinations where the conservation status of adjacent forest and risk of hybridisation and introgression are assessed to be high. Naturally small or remnant populations are going to be at particular risk. Under such circumstances, the challenge is to define acceptable isolation distances, planting stock or silvicultural regimes that will decrease this risk.

Isolation distances will be variable and depend upon the relative population size and the numerous factors that affect the movements of the birds, insects, marsupials and other mammals that pollinate eucalypts. There are few detailed studies of pollinator movements and pollen dispersal with which to guide this choice, although powerful molecular techniques are now available to help resolve this issue. Current evidence would suggest that pollen will be distributed close flowering neighbours with a tail of long-distance dispersal events associated with pollinator escape, exploratory and migratory movements. The pattern of pollen dispersal will be expected to change with spatial and temporal variation in the flowering resource and pollinator community. Predominantly bird (and flying fox) pollinated eucalypts are likely to require larger buffer distances than those predominantly pollinated by insects. Isolation distances should be greater as the size of the ‘source’ population increases relative to the ’sink’ population and also greater for a patchy as opposed to a spatially continuous flowering resource.

While species choice will be one of the most important factors, there are genetic and silvicultural opportunites that will help minimise the risk of genetic pollution. For example, close spacing in plantations is also known to reduce the abundance of flowers and many of the plantation environments are not conducive to flowering. Flowering on plantation edges may be countered with guard rows of non-hybridising, inert genotypes. There is considerable genetic variation within the plantation species for reproductive traits and it would be feasible to deploy material secondarily selected for delayed onset or reduced abundance of flowering, or of different flowering time.

Key research required for the refinement of risk management is:

(i) Distance and levels of pollen dispersal and gene flow.

(ii) Crossability of the main plantation species with local native populations.

(iii) The potential of selecting for sustainability traits.

(iv) Spatial patterns of genetic variation within native gene pools of the main plantation species.

(v) Provision of base-line molecular data for long-term monitoring of introgression.

(vi) Impacts of plantings on local biodiversity.

SOME KEY POINTS (Highlighted throughout the document)

* 1 *Eucalypts often exhibit weak reproductive barriers between closely related taxa. Hybridisation is a natural process and evidence would suggest that it has been an integral part of the evolutionary history of the genus.* 14

* 2 *One of the major threats to the genetic integrity of native eucalypt gene pools currently would appear to be the introduction of exotic species into the range of potentially interbreeding native species.* 16

* 3 *Often species that have evolved in geographical isolation exhibit weaker barriers to hybridisation than those which naturally co-occur.* 16

* 4 *No major additional genetic risk is seen from the deployment of exotic hybrids as opposed to an exotic species in the landscape. The exception is where backcrossing to parental taxa may occur. The deployment of selected hybrids in the vicinity of natural populations of their parental (or closely related) taxa should therefore be avoided unless other barriers can operate. However, the susceptibility of eucalypt hybrids to pests is a key consideration in the Australian environment.* 19

* 5 *Remnant populations of the main plantation species in rural landscapes will be particularly at risk from genetic swamping from exotic provenances. However, in cases enhanced gene flow may be beneficial in overcoming inbreeding effects.* 22

* 6 *It is important that strategies for the management of the gene pools of the major commercial eucalypt species are developed.* 24

* 7 *No reports of GM eucalypts being field tested in Australia were found. The release of GM eucalypts in Australia is likely to be a lengthy procedure and depend upon reproductive sterility. GM* Pinus radiata *developed in New Zealand is likely to be the first GM forest tree tested in Australia.* 34

* 8 *Isolation distances should be greater as the size of the 'source' population increases relative to the 'sink' population.* 43

* 9 *The timing of the onset of first flowering and flower abundance can be genetically manipulated relatively simply to reduce the risk of genetic pollution.* 44

* 10 *Silvicultural regimes used in farm forestry such as increased spacing between trees required in drier regions, plantings with a high edge to area ratio and thinning for sawlog production may enhance flower and hence pollen production and increase the risk of genetic pollution.* 46

* 11 *Flowers are often more abundant on plantation edges and their abundance could be reduced by surrounding plantations with guard rows of reproductively inert stock.* 46

* 12 *Differences in flowering time will be a major barrier to gene flow between plantation and native forest eucalypts.* 46

* 13 *Because pollen is usually shed before the eucalypt stigma becomes receptive, later flowering trees are more likely to pollinate early flowering trees than visa versa.* 46

* 14 *Flowering time can be markedly influenced by site and seasonal effects requiring generalised flowering information to be supplemented with local observation. Nevertheless, flowering time is also under strong genetic control and there is often large genetic based variation within the plantation species that could be exploited to minimise flowering overlap with native provenances or species.* 47

* 15 *To predict the rate of introgression and define buffer distances it is essential to characterise the frequency distribution of pollen and seed dispersal distances under field conditions.* 50

* 16 *Within a continuous native forest abutting a plantation and with synchronous flowering, pollen immigration should be dramatically reduced by c. 1km from a source of exotic pollen.* 56

* 17 *Isolation distances should be greater for bird-pollinated than insect pollinated species.* 56

* 18 *Isolation distances should be greater for a patchy as opposed to spatially continuous flowering resource.* 56

* 19 *With a high conservation value, high risk situation (i.e. high probability of gene flow, large source population) a conservative approach should be adopted until further research is undertaken on pollen dispersal distances.* 56

* 20 *The probability of successful hybrid seed set will be reduced with increasing difference in flower size and increasing taxonomic distance between two species.* 57

*21 *The probability of* F_1 *hybrid inviability will generally increase with increasing taxonomic distance between the parent species.* 60

1. Introduction

1.1 Plant invasions

Plant invasions arising from agricultural, forestry and other activities are becoming of increasing concern worldwide, and may have gene pool to ecosystem wide impacts (Drake *et al.* 1989; Raybould and Gray 1994; Williamson 1996; Higgins and Richardson 1998). Often exotic species that are transported across large barriers have the advantage of escaping from predators, parasites and competitors (Elton 1958 cited in Huxel 1999), thereby increasing their fitness. A well recognised problem is plants dispersing by seed beyond their intended area of use and becoming weeds. The spread of wildlings from plantations of the exotic *Pinus radiata* in Australia is a classic example (Chilvers and Burdon 1983; Raybould and Gray 1994). While *Pinus radiata* is invasive of many natural eucalypt communities in Australia, the species is threatened in its native Californian habitat (Brown 1999), due in part to the pine blister disease as well as urbanisation. Similar problems have been reported when Australian native forest trees have been planted as exotics overseas. There are several reports of invasion of native plant communities by exotic eucalypts (e.g. *Eucalyptus globulus* in California Kirkpatrick 1977; Rejmanek 1989 p. 378; *E. cladocalyx*, *E. gomphocephala* and *E. lehmannii* in the Cape region of South Africa Heywood 1989; see also Pryor 1991). Indeed, the vigorous growth and competitive ability of several species of eucalypts has given the genus a reputation as ecologically aggressive (Drake *et al.* 1989), although this reputation has been disputed (Pryor 1991).

In the last decade, invasion by pollen (genetic pollution) rather than seed has become of increasing concern (Abbott 1992; Anttila *et al.* 1998; Rhymer and Simberloff 1996). This concern is mainly fuelled by the risk of escape of transgenes from genetically modified organisms (Tiedje *et al.* 1989; Ellstrand and Hoffman 1990; Raybould and Gray 1994; Dale 1992; James *et al.* 1998). Nevertheless, it has focused attention in Australia on the broader issue of genetic pollution of native forest from ornamental (garden and roadside plantings) and restoration plantings, but particularly farm and plantation forestry. Intensively managed plantation forestry has many analogies with agricultural systems. While studies of genetic pollution in forest trees are in their infancy (Barbour *et al.* 2000; DiFazio *et al.* 1999), the literature on the genetic interaction between agricultural crops and their wild relatives is extensive. Much can be learned from this literature as, while generation intervals are shorter, the experimental approaches adopted, the process involved and genetic impacts are effectively the same as in forest trees (see Section 3.5.2). Insights into the magnitude of this problem for Australia can also be obtained from continents subject to longer periods of anthropomorphic influence such as Europe.

1.2 Genetic pollution

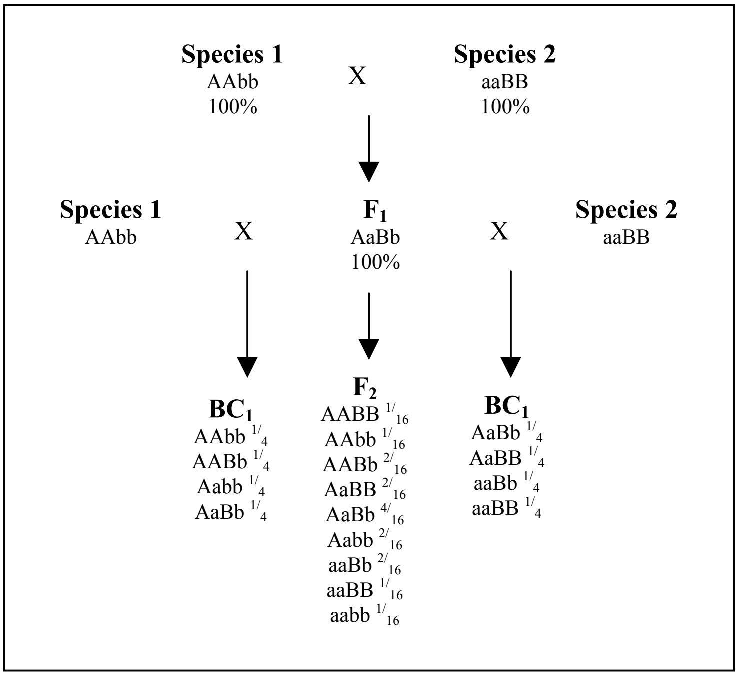
1.2.1 Definition

Genetic pollution is the movement or introgression of foreign genes from domesticated or other exotic populations into a native population via pollen (Hoffman 1990; Ellstrand and Hoffman 1990), with engineered fitness genes causing special concern (Daniels and Sheil 1999). Such hybridisation and introgression can refer to interbreeding between populations which vary in relatedness ranging from different families or provenances, through to different species (Arnold 1992). Introgression is gene flow between populations which hybridise, achieved when hybrids repeatedly backcross to one or both parents (Anderson 1949; Rhymer and Simberloff 1996). Repeated backcrossing either as a male or female to one or both parents can lead to the infiltration of genes from one population to another and result in the production of offspring more and more similar to the parental populations with each backcross, but which possess certain characteristics inherited from the donor (Abbott 1992; Box 1.1).

It may result in transfer of only a minor component of the donor genome to the native gene pool (as originally envisaged in the definition of introgression - Anderson 1949). However, introgression may extend to virtually complete introgressive displacement (also termed genetic assimilation) of the native population by an invader (e.g. Anttila *et al.* 1998).

Box 1.1 Hybridisation terminology

A scheme of hybridisation between two species showing the expected genotypes under a 2 locus model in the first (F_1), second (F_2) and first backcross (BC_1) generations . In the F_1 generation the hybrid will be uniformly heterozygous for species-specific genes at loci A and B, however segregation and recombination in the next generation will result in highly variable offspring in the backcross but particularly the F_2 generations. The frequency of the various multi-locus genotypes will depend upon how tightly the two loci are linked. The figures shown are the estimated proportions of each genotype assuming random recombination. Introgression would arise with the incorporation of the A or b alleles into the gene pool of Species 2 following sequential backcrossing to this species. In many cases in forest trees, genes will not be fixed, rather the original parents may be heterozygous which result in various allelic combinations in the F_1 hybrids.



Extensive discussion of the concepts and concerns associated with genetic pollution can be found in the literature (Hoffman 1990; Ellstrand and Hoffman 1990; Raybould and Gray 1993; Gliddon 1994, 1999; Rhymer and Simberloff 1996; Strauss 1997; Daniels and Sheil 1999). Mixing of gene pools through hybridisation and introgression is a natural evolutionary process in animals and particularly plants, and appreciation of the potential for introgression and introgressive displacement is not new (Anderson 1953; Baker 1957). However, the increased use of molecular markers over the last decade has focused attention on the extent of hybridisation in both natural and man-influenced systems that is not always apparent from morphological observations alone (Rhymer and Simberloff 1996; Jackson *et al.* 1999). The term 'genetic pollution' has deleterious connotations and, as most highlighted cases are a result of human activities leading to the introgression of foreign genes, it would appear that the term should be restricted to situations initiated or significantly influenced by human activity. This would include situations where non-native species have been intentionally or non-intentionally introduced or the habitat modified bringing previously isolated species into geographic contact. Hybridisation, with or without introgression, may threaten the genetic integrity of a wide variety of plant and animal taxa because of human activities. Furthermore, Rhymer (1996) notes that the very factors that threaten extinction by hybridisation – habitat destruction, fragmentation, and species introductions – are all increasing and often act synergistically. However, Daniels (1999) considers that the risks of genetic pollution are decreased where populations/species are distantly related, the communities containing them are stable and closed, and where ecological conditions are such that selection operates strongly in favour of the locally-adapted genotypes.

1.2.2 The process of invasion

There is increasing modelling of the spread of genes through hybridisation (Gliddon 1994; Gliddon 1999; Huxel 1999). The introduction of exotic populations can lead to the competitive exclusion (displacement) of native populations through seed dispersal, but this can be exacerbated by the potential for hybridisation (Huxel 1999). Immigration and selection appear to act in two different ways: increasing immigration results in displacement by overwhelming the native; whereas increasing the selection differential in favor of the invader leads to displacement via genetic assimilation (Huxel 1999). Factors affecting the spread of genes through a population by introgression are discussed by Gliddon (1994). Fitness is only one of the evolutionary forces that may affect the flow of genes into a population. The first hybridisation event (F_1) will normally be rare in the native population and the major determinant of its fate will be random genetic drift. In addition, the rounds of sexual reproduction, after escape, will be mainly backcrosses between the hybrid and native species. However, the magnitude of recurrent gene flow from the crop into the native species will be a major factor affecting the fate of the hybrids. This will depend on the dispersal distances, probability of hybrid formation and the scale on which the crop is grown relative to the size of the native recipient population. In fact, the magnitude of this directional gene flow may be sufficient to overcome any slight fitness disadvantages of the hybrid. Thus if the hybridising crop species is grown on a large scale, Gliddon (1994) suggests that the risk of genetic pollution will only be small when the hybrid can be shown to be markedly less fit than the native species in the native habitat.

1.2.3 Importance of hybridisation in plants

Hybridisation and introgression are believed to be more common in plants than animals (Harrison 1993), with 70% of plant taxa commonly quoted as potentially originating from hybridisation (Ellstrand *et al.* 1996; Ellstrand *et al.* 1999). Contemporary natural hybridisation appears to be concentrated in specific families and genera, most of which are primarily outcrossing perennials (Stace 1975; Ellstrand *et al.* 1996). The frequency of hybridisation in forest tree genera is amongst the highest. For example, for the 23 British willow (*Salix* sp.) species, 123 hybrid combinations have been recorded. This was the highest proportion for the 7 genera examined in Britain (Stace 1975). Natural interspecific hybrids have been found in 25 of the 125 plant families represented in the USSR; introgressive hybrids have been described in most forest tree genera including spruce (*Picea*), larch (*Larix*), oak (*Quercus*), birch (*Betula*), linden (*Tilia*) and poplar (*Populus*) (Milyutin *et al.* 1989). The weak reproductive barriers amongst forest tree taxa would make them particularly vulnerable to genetic pollution. However, the longer generation times means that the time frame is longer, but the concerns and risks are no different from that posed for crop plants.

1.2.4 Common examples of genetic pollution

1.2.4.1 Introduced species

The global scale of the problem of invasion and genetic pollution from exotic species can be gauged from Staces' (Stace 1975) New Flora of the British Isles, one of the few floras to detail the number of native, aliens and hybrid combinations (reviewed in Abbott 1992 and Raybould and Gray 1993). The flora treats 2834 species of which 1264 (45%) are believed to be aliens, many of which are quite widespread. Of the 715 hybrids reported, 70 are hybrids between native and introduced species. However, hybrids are generally rare, often sterile and relatively few populations persist, except where the parents remain in contact or where the hybrids are able to spread vegetatively. Nevertheless, 7% of the introduced species that have produced hybrids with native species and are now considered part of the flora of the British Isles. If this is an indication of the potential for introgression associated with plant invasions, then the threat of genetic pollution of natural communities across the globe is significant. However, the extent to which these hybrids have invaded undisturbed natural communities is not given.

The extent of introgression may vary markedly, but can potentially result in complete introgressive displacement of native species with wide ranging consequences. This would appear to be the case following the spread of the cord grass *Spartina alterniflora* into a native population of *Spartina foliosa* in the salt marshes of San Francisco Bay (Anttila *et al.* 1998). The invader produces much more pollen, has superior siring ability and is rapidly genetically swamping the local species. Serial genetic assimilation of the very large native population is likely with potential ecosystem wide consequences. Unlike Californian cordgrass, the invading cordgrass can grow into low intertidal habitats and cover open mud necessary to foraging shorebirds and other marine life. The hybrids are more similar to the invader in this respect and introgression will lead to loss of habitat for shore birds and marine life as well as genetic pollution of native California cordgrass. Other plant examples include the succulant perennial *Carpobrotus edulis* which was introduced to California from South Africa for dune stabilisation and has now extensively hybridised with a presumed native species *C. chilensis* (Gallagher *et al.* 1997; Vila *et al.* 1998). The Belgium riverbank species complex of the genus *Scirpus* is also reported to be threatened from introgression from an introduced species (De Greef and Triest 1999).

The problem of genetic pollution of native gene pools is equally relevant to animal species. For example, fishes introduced into natural rivers and lakes accidentally, or for commercial and recreational fishing, have been reported to have caused genetic pollution by hybridisation with native strains (e.g. Japan - Yuma *et al.* 1998; Texas - Echelle and Connor 1989; Echelle and Echelle 1994; Echelle and Echelle 1997; western USA - Rhymer and Simberloff 1996). This process can be extremely rapid. For example, Echelle and Echelle (1997) report complete introgression of introduced alleles into extensive distribution of the native pump-fish (*Cyprinodon* spp.) populations occurred approximately 15 years from the isolated introduction of a related species as bait fish. Other well known examples involving species introductions include extensive hybridisation of introduced mallard and ruddy ducks with endemic duck species (*Anas* spp.) in many countries (e.g. New Zealand, Hawaii, Australia, south Florida, eastern USA), feral house cats hybridising with wild cat (*Felis* spp.) species and domestic dogs hybridising with wolves and jackals (*Canis* spp.) (reviewed in Rhymer and Simberloff 1996).

1.2.4.2 Crop-weed-wild relative hybridisation

With forestry plantations being increasing intensively managed and treated as fibre crops, the agricultural literature on gene flow between crops and wild relatives is becoming increasingly relevant. Sexually compatible crops and related wild species co-occur frequently in agroecosystems (Ellstrand and Hoffman 1990) and every level of gene flow can be found between them ranging from absolute reproductive isolation to unrestricted crossing (reviewed in de Vries *et al.* 1992; Raamsdonk and van der Maesen 1996; Ellstrand *et al.* 1999). Spontaneous hybridisation and introgression of genes from domesticated plants to wild relatives is commonly reported, with experimentally measured rates of hybridisation typically exceeding 1%, sometimes even over distances of 100m (Bateman 1947; Klinger *et al.* 1991; reviewed in Ellstrand *et al.* 1999). For example, hybrid swarms of wild and cultivated varieties and species of rice have been reported by several workers (see Majumder *et al.* 1997) and gene flow among rice cultivars and a locally sympatric conspecific weed varied from 1.0%

to 52% in mixed stands (Langevin *et al.* 1990b). Studies of crop hybridisation have even detected pollen-mediated gene flow at distances of 700m to 1300m from a planted pollen source (Kirkpatrick and Wilson 1989; Daniels and Sheil 1999).

An increasing number of studies have shown specific cases where genes have passed to wild relatives from different crops (reviewed in Raybould and Gray 1993; Ellstrand *et al.* 1999). The main harmful consequences of such gene flow are seen as the evolution of increased weediness and the extinction of wild relatives. Introgression may promote the persistence of the weedy populations in cultivated habitats by allowing the weed to become more adapted to man-made habitats (Langevin *et al.* 1990b). Hybridisation between a crop and wild relative has been implicated in the extinction of certain wild crop relatives in rice and cotton (Daniels and Sheil 1999; Ellstrand *et al.* 1999) and potentially in hemp (*Cannabis sativa*), capsicum (*Capsicum frutescens*), date palm (*Phoenix daclifera*) and sweet pea (*Lathyrus odoratus*) (Small 1984). In all cases, the emphasis has been on the loss of identity at the species or subspecies level with the rarer relative subsumed into the more common relatives.

1.2.4.3 Threats to rare taxa

The problem of genetic pollution is clearly enhanced with small populations. Differences in the relative size of populations may result in different rates of hybridisation with larger populations tending to swamp smaller populations (reviewed in Ellstrand 1992b; Ellstrand *et al.* 1993; Levin *et al.* 1996). Hybridisation with or without introgression may, nevertheless, threaten a rare species' existence (Rhymer and Simberloff 1996). A classic forest tree example is Catalina Mahogany, *Cercocarpus traskiae*, a rare island endemic that is hybridising with the more abundant *C. betuloides* (Rieseberg *et al.* 1993). Outbreeding depression from detrimental gene flow may reduce the fitness of a locally rare species making it vulnerable to extinction. Alternatively, pollen swamping may result in its loss of genetic integrity and it may become assimilated into the gene pool of the common species. Hybridisation is a major problem in plant conservation because so many plant species, even from different genera, can hybridise (Abbott 1992; Ellstrand 1992b; Ellstrand *et al.* 1993; Arnold 1997; Carney *et al.* 2000). Introgression is also believed to be a substantial contributing factor for 3 of the 24 animal species listed under the ESA that are now extinct and many of the high profile endangered vertebrates are perceived as potentially threatened or “irrevocably contaminated” by hybridisation and introgression (Rhymer and Simberloff 1996). These plant and animal examples are believed to be ‘the tip of the iceberg’ as the great majority of introgression is likely to be undetected (Rhymer and Simberloff 1996; Rieseberg and Wendel 1993) without the use of expensive molecular technologies. However, it should be noted that in some cases there is a positive benefit from hybridisation with the introduction of new genes allowing threatened taxa to survive. For example, in the early 1900’s to the 1950’s an introduced fungus (*Cryphonectria parasitica*) destroyed virtually the entire American chestnut population of the widespread forest species *Castanea dentata*. Backcrossing of survivors to Chinese and Japanese species is being used to breed disease resistant American chestnuts (Burnham 1990; Carney *et al.* 2000).

1.2.4.4 Forest tree examples

There are several reports of forest tree taxa threatened by genetic pollution from exotics. The California black walnut (*Juglans hindsii*) is thought to have hybridised with numerous congeners imported from all over the world for commercial purposes (Rhymer and Simberloff 1996). One of the most highlighted cases is the native European species *Populus nigra* L. (Black Poplar) which was once widespread, but is now considered to be on the verge of extinction in a large part of western Europe (Smith and Sytsma 1990a; Cagelli and Lefevre 1995; Heinze 1998; Cagelli and Lefevre 1995). Its natural habitat is being gradually reduced by human activity, and the gene pool is further threatened by the large-scale presence of cultivated hybrids as well as the ornamental cultivar 'Lombardy poplar' (*P. nigra* var. *italica*), which spontaneously hybridize with it. One of the major hybrid cultivars responsible is *P.* x *canadensis* (also known as x *euramericana*) which is derived from the progeny of crosses between *P. deltoides* females and *P. nigra* males. Raybould (1993) notes that for both pines and poplars, there is a high probability of gene flow between crop and native or feral populations in the UK. *Populus alba* and various poplar hybrids are widely planted in the UK and while the grey poplar (*P. alba* x *P. tremula*) is planted, it has also arisen spontaneously throughout the UK (Stace 1975).

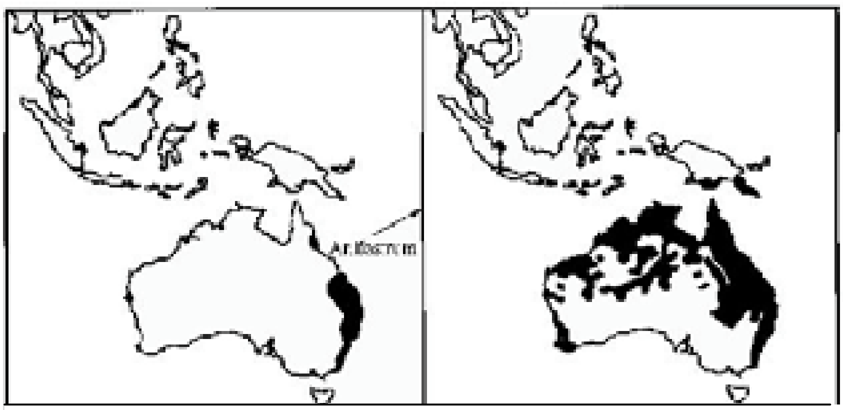
Another example is the Californian sycamore (*Plantanus racemosa*) which Rhymer (1996) reports is being lost from the Sacramento River and its tributaries in the USA, through introgression with the London plane (*P.* x *acerifolia*). The London Plane is well known for its tolerance of coal dust, smoke and other aspects of the urban environment and is a hybrid of the American sycamore (*P. occidentalis*) and oriental plane (*P. orientalis*), both of which were introduced to England in the seventeenth century. In contrast, Raybould (1993) notes that there is no risk of hybridisation between commonly planted spruce (*Picea* ssp.) or Douglas fir (*Pseudotsuga menziesii*) and wild populations of Scots pine (*Pinus sylvestris*).

1.3 Australian eucalypt forests and plantations

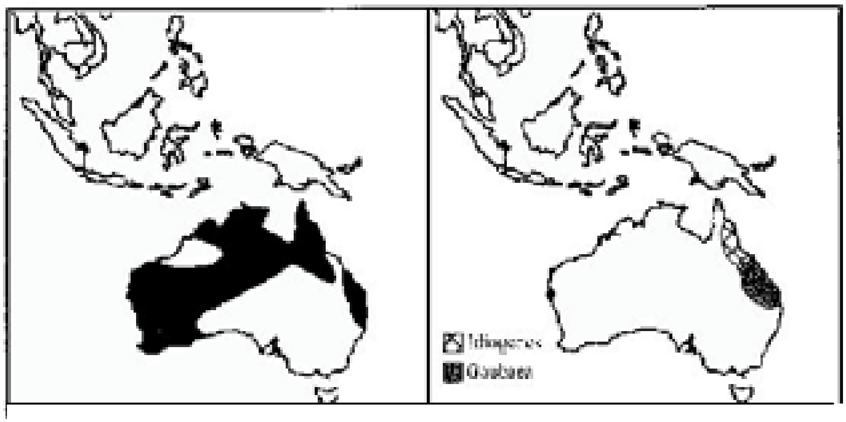
Eucalypts are an internationally utilised genetic resource (Eldridge *et al.* 1993), with the total plantation area worldwide anticipated to reach 15-20 million hectares by 2000 (Turnbull 1999). However, virtually all the 800 or more taxa (including *Eucalyptus*, *Corymbia* and *Angophora*; Hopper 1997) are endemic to Australia and surrounding islands (Figure 1.1). Australia has an international obligation for the long-term management of this native genetic resource. The development of strategies to manage the gene pools of major plantation species and to minimise the impacts of genetic pollution are among the Commonwealth's indicators for sustainable forestry in Australia (Ministerial Council on Forestry 1997 p. 14). European settlement has already had a substantial effect on Australia's native vegetation. Hopper (1997), for example, notes that only a highly fragmented 10% of the once extensive Australian temperate woodlands and mallee remain. Currently, 74 species of eucalypts are listed as endangered or vulnerable (Environment Australia 2000). This issue is further accentuated (see Gliddon 1994) by the rapid expansion of eucalypt plantations in Australia in recent years, with plans to treble the overall plantation estate from 1 million hectares to 3 million by the year 2020 (Ministerial Council on Forestry 1997; Stanton 1999).

Eucalyptus globulus and *E. nitens*, are the major hardwood plantation species in temperate regions of Australia (Tibbits *et al.* 1997). The *E. globulus* plantation estate in particular is rapidly increasing, with 60-80,000 ha likely to be planted in 2000 (Figure 1.2). There are also plantation initiatives in sub-tropical regions of Australia with *E. grandis*, *E. pellita, E. pilularis, E. cloeziana, E. dunnii, Corymbia henryi* and *C. variegata* and various artificial hybrids (Nikles and Lee 1998). Species such as *E. cladocalyx*, *E. occidentalis*, *E. camaldulensis*, *E. sideroxylon*, *E. tricarpa Corymbia maculata*, *C. variegata* (Harwood and Arnold 1999) and the oil mallees *E. kockii*, *E. horistes* and *E. polybractea* (e.g. Byrne and Macdonald 2000) and various hybrids (Harwood and Arnold 1999) (see Table 3.1) are being developed for plantations in the drier zones (400-600mm/yr). Part of this plantation expansion is fuelled by desires to counter the deleterious effects of land degradation (i.e. restoration plantings) such as salinity (Marcar *et al.* 1995), and to accrue greenhouse credits through carbon sequestration (Borough 1998; O'Neill 1999). However, it is important to consider and minimise deleterious impacts on other aspects of the environment (see also Mott 1999). Such impacts include changes in biodiversity in adjacent or remnant native forest as well as seed or pollen-mediated invasion of the native forest by plantation species. Eucalypt species are well known for their propensity to hybridise (Griffin *et al.* 1988; Potts and Wiltshire 1997) and it is important to assess the risk of introgression of genes from plantations into native forests (e.g. Byrne and Macdonald 2000; Barbour *et al.* 2000; Jones *et al.* 2000). The majority of the Australian eucalypt plantation estate has been planted in the last 5 years (Figure 1.2) and is currently reproductively immature. As these plantations reach reproductive maturity, they have the potential to constitute a significant source of exotic pollen that through dispersal and hybridisation may impact on adjacent native forest gene pools. The effects of hybridisation have also been shown to extend beyond the tree species gene pool to the composition and structure of arthropods and fungi communities dependent on eucalypts (Morrow *et al.* 1994; Whitham *et al.* 1994; Whitham *et al.* 1999). These impacts may even flow to higher trophic levels (Whitham *et al.* 1999). Hence, if there is a risk of genetic pollution of native eucalypt forest then this may have unappreciated ecosystem wide consequences.

a) Angophora b) Corymbia



c) Eudesmia d) Idiogenes and Gaubaea



e) Monocalyptus f) Symphyomyrtus

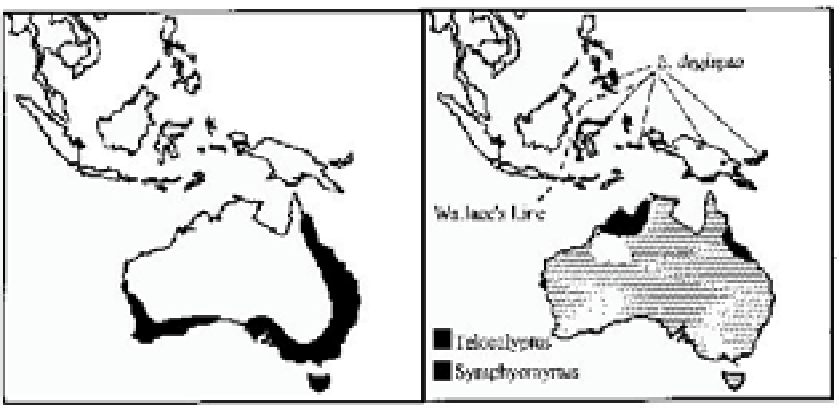


Figure 1.1 The natural distribution of eucalypts
The natural distribution of *Angophora* (a), *Corymbia* (b) and the *Eucalyptus* subgenera *Eudesmia* (c), *Idiogenes* and *Gaubaea* (d), *Monocalyptus* (e) and *Symphyomyrtus* (f). The distribution of the genus *Arillastrum* in New Caledonia is indicated in (a), Wallace's Line and the extra-Australian distribution of *E. deglupta* in (f) (adapted from Potts and Pederick 2000). Australia is the main custodian of this internationally important genetic resource.

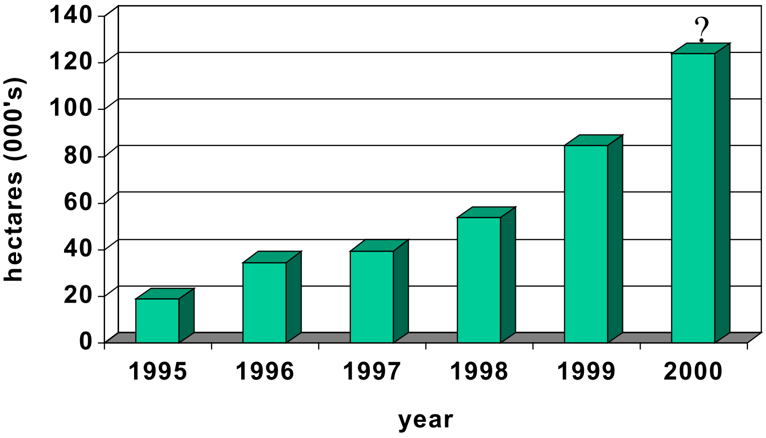


Figure 1.2 Annual plantings of new hardwood plantations in Australia.
The total area of new hardwood plantation in Australia planted each year from 1995-1999 (source: Inventory 2000; http://www.brs.gov.au/nfi/forestinfo/info.html). The predicted plantings for the year 2000 are indicated. The majority of these new hardwood plantations are *Eucalyptus globulus*.

2. Natural hybridisation in eucalypts

2.1 Introduction

Natural and artificial hybridisation in eucalypts is reviewed by Pryor and Johnson (1971), Pryor (1976), Griffin *et al.* (1988) and Potts and Wiltshire (1997). As with many forest tree genera, hybridisation among recognised species is relatively common (Pryor 1976; Potts and Wiltshire 1997). Natural hybrids may occur (i) along species boundaries, as sporadic individuals, (ii) in hybrid swarms where hybridisation has extended beyond the first generation, or (iii) in zones of introgression. Pragmatic criteria for the identification of hybrids in natural populations are given in Hopper *et al.* (1978):

- Intermediate morphology
- Phenotypic segregation in the progeny
- Occurrence in sympatric parental stands
- Close resemblance between suspected and manipulated hybrids
- Occurrence in disturbed or relatively youthful habitats
- Impaired reproductive capabilities of hybrid relative to parental individuals (i.e. F_2 breakdown)
- Occurrence of interspecific pollen exchange by indiscriminant vectors in sympatry.

In most cases, morphological and physiological traits are inherited in a more or less intermediate manner in first generation (F_1) hybrids, although there are exceptions, since the exact degree of dominance may vary between traits and species combinations (e.g. Pilipenka 1969; Cauvin *et al.* 1987; Tibbits *et al.* 1991).

2.2 Patterns and levels of natural hybridisation

Eucalypts are well known for weak reproductive barriers between many recognised taxa (Pryor 1976). Of the 528 species examined in Griffin *et al.*'s (1988) review, 289 (55%) were recorded as being involved in at least one natural hybrid combination. However, across the genus, natural hybridisation was actually found to be rather restricted with only 15% of sympatric (geographically co-occurring) combinations recorded. Nevertheless, of the 883 described taxa listed in Pryor and Johnson (1971), at least 124 (14%) are species, subspecies or variants subsequently considered to be of hybrid origin, and the number is increasing (e.g. Rossetto *et al.* 1997). While many new hybrid combinations have since been recorded, the appendix of Griffin *et al.*'s (1988) review is still the most comprehensive listing of natural and artificial hybrid combinations in the genus. The frequency of natural hybridisation was found to broadly decrease with increasing taxonomic distance between parents (i.e. inter-subgeneric < inter-sectional < inter-series < intra-series). This trend is also reflected in the taxonomic relationships between the putative parental species of the 124 described taxa which were subsequently considered to be of hybrid origin by Pryor and Johnson (1971; Table 2.1). However in this case, the frequency of interseries hybrid combinations was greater than the intra-series combinations, which may reflect their greater ease of detection.

Griffin *et al.*'s review is based on the informal taxonomic treatment of Pryor and Johnson (1971) and Johnson (1976) which dominated the literature for nearly 30 years and recognised 8 subgenera (Table 2.2). For consistency with historical literature the treatment of Pryor and Johnson (1971) has been followed in this review. Although many features of this taxonomic treatment have survived the test of time (Brooker 2000), the abnormally high frequency of hybrids between some taxonomic groups within the subgenus *Monocalyptus* and subgenus *Corymbia* (Griffin *et al.* 1988) signalled some problems. Indeed, even in Hill and Johnson's (1995) classification of *Corymbia*, intersectional hybrids were reported to link virtually all major sections. How well the patterns of hybridisation match the latest taxonomic treatment of the genus (Brooker 2000) has yet to be examined in detail but the taxonomic treatment has not changed substantially for the general purpose of this review, although several new minor subgenera and sections have been now recognised. Hybridisation between species from the major subgenera in either treatment does not occur either naturally or artificially (Pryor and Johnson 1971; Griffin *et al.* 1988; Potts and Wiltshire 1997). However, natural hybrids between the subgenus *Eucalyptus* and the closely related, monotypic, subgenera *Idiogenes* have been verified (*E. cloeziana* x *E. acmenoides* Stokoe *et al.* 2000).

Table 2.1 The relatedness amongst putative parental species of 'hybrid' taxa.

The taxonomic relatedness amongst the putative parents of described taxa that are listed by Pryor and Johnson (1971) as likely to be of hybrid origin. The table shows the percentage of hybrid taxa, reported natural hybrids (from Griffin et al. 1988) and species combinations in close geographic proximity (G_1 10'x10' window; 23 x 19km) in each category of taxonomic relatedness. More taxonomically divergent species tend to co-occur more frequently yet account for a smaller proportion of the 'hybrid' taxa (at the sectional level) and reported natural hybrids.

Taxonomic relatedness between putative parents	**% 'hybrid' taxa**	**% natural hybrids**	**% G_1 species combinations**
Different subgenera	0	-	-
Different sections	12	9	48
Different series	54	39	37
Species within series	34	52	16

Within subgenera, the extent of natural hybridisation between species varies considerably, depending upon numerous factors, including the degree of spatial and taxonomic separation and flowering synchrony between putative parents (Griffin *et al.* 1988; Potts and Wiltshire 1997). In native forest there is a low background level of natural crossing continually occurring between species. This background level of F_1 hybridisation was found to average 1.62% across 13 species, and range from 0.03% to 3.5% at the species level (Table 2.3). There has been several suggestions that human activity may have enhanced this rate of hybrid formation and survival through, for example the introduction of honey bees and habitat disturbance respectively (Pryor 1953; Chappill *et al.* 1986). Regardless, there is little doubt that hybridisation in the genus is natural, pre-dates European settlement and has been a significant factor in eucalypt evolution. DNA markers have revealed large patches of a single hybrid genotype of the mallee habit in Western Australia (*E. graniticola* = *E. rudis* x *E. drummondii* Rossetto *et al.* 1997) and Tasmania (*E. amygdalina* x *E. risdonii* - Tyson *et al.* 1998) which must clearly pre-date European settlement. Further, while there has been some debate as to the evolutionary significance of hybridisation in the genus (see Potts and Wiltshire 1997; Ladiges 1997), DNA markers have recently provided strong evidence that hybridisation and introgression have played an intimate role in the evolution of the genus. This evidence is based on the extensive sharing of similar maternally inherited chloroplast types across species in the same geographic area (Steane *et al.* 1998; McKinnon *et al.* 1999; Jackson *et al.* 1999) (Figure 2.1).

Table 2.2 The eucalypt subgenera
The alignment of the eucalypt subgenera as detailed by Pryor and Johnson (1971; Johnson 1976) and Brooker (Brooker 2000) and the number of species in each of Brooker's subgenera and % natural hybrid combinations recorded by Griffin *et al.* (1988) for geographically close species combinations (10' x 10'). Hybridisation between species from the major subgenera does not occur either naturally or artificially. However, natural hybridisation has been verified between *Idiogenes* and *Monocalyptus* and between several of the *Blakella* and *Corymbia* species (Wardell-Johnson *et al.* 1997) which require verification.

Pryor & Johnson	**Brooker**	**No. Species**	**% Hybrids**
Angophora (genus)	*Angophora*	14	33
Blakella[1]	*Blakella*	16	13
Corymbia[1]	*Corymbia*	70	18
Eudesmia	*Eudesmia*	20	14
Gaubea	*Acerosae*	1	
"	*Cuboidea*	1	
Idiogenes	*Idiogenes*	1	
Monocalyptus	*Primitiva*	1	
"	*Eucalyptus*	104	37
Symphyomyrtus	*Cruciformes*	1	
"	*Alveolata*	1	
"	*Symphyomyrtus*	467	19
Telocalyptus	*Minutifructus*	5	

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[1] Combined into the genus *Corymbia* by Hill and Johnson (1995; see also Ladiges and Udovicic 2000)

Table 2.3 The rate of F_1 hybridisation in eucalypts.

Estimates of the rate of first-generation hybridisation (F_1) in natural eucalypt populations (updated from Potts and Wiltshire 1997). The % of putative F_1 hybrids in open-pollinated seed-lots from range wide native stand collections of 13 Tasmanian eucalypt species and *E. nitens*. Plants were assessed as seedlings while in the nurseries. Vigorous plants that were relatively rare and markedly different on several morphological criteria from others of the same family were classified as putative F_1 hybrids. In many cases these phenotypes could be matched to known F_1 hybrid phenotypes.

Species	**Total (n)**	**% hybrids**
Subgenus *Symphyomyrtus*		
E. globulus	30 582	0.06
E. urnigera	3 715	0.27
E. cordata	870	1.84
E. morrisbyi	5 073	1.12
E. subcrenulata	2 090	0.38
E. gunnii	10 181	3.48
E. archeri	2 695	1.34
E. rodwayi	488	0.61
E. nitens	135 816	0.03
Subgenus *Monocalyptus*		
E. risdonii	2 569	2.37
E. tenuiramis	3 001	3.90
E. coccifera	104	2.88
E. nitida	142	2.82
TOTAL	197 326	1.62 (mean)

2.3 Introgression and genetic invasion

The processes that will potentially allow the spread of genes from eucalypt plantations to native forest gene pools are the same natural processes that have already shaped the evolution of the genus. Studies of natural eucalypt populations clearly indicate their propensity for introgression. Despite their longevity, eucalypts were amongst the plant genera in which pollen-mediated invasion was first documented as a natural process, intimately linked with species range expansion and contraction (reviewed in Potts and Jackson 1986; Potts 1990; Potts and Wiltshire 1997). There was early recognition that some taxonomically intermediate populations that were isolated from one or both putative parent species may be the result of hybridisation. In cases, it was argued that such populations were the genetic remnants of past distribution of the parental taxa, termed 'phantom hybrids' (Pryor and Johnson 1971; Parsons and Kirkpatrick 1972). In this case, pollen swamping and hybridisation may have resulted in the complete introgressive displacement of small relic populations leading to complete extinction or assimilation of the genetic remnants into the gene pool of the surrounding, more abundant species. In other cases, these intermediate populations are suggested to be the products of long-distance pollen dispersal followed by hybridisation (Potts and Reid 1983; Potts and Reid 1988; Ashton and Williams 1973; Ashton and Sandiford 1988).

It is unlikely that long distance seed dispersal would be implicated in the origin of isolated hybrid patches. Seed dispersal in the genus appears to be extremely limited, although there are exceptions where dispersal is enhanced by water (e.g. *E. camaldulensis*) or rarely animal (e.g. bees in *E. torelliana* Wallace and Trueman 1995) transport (reviewed in Cremer 1977; Potts 1990; Potts and Wiltshire 1997). Seed is mainly dispersed by wind and gravity following release from canopy-stored capsules. The distance of seed fall is essentially proportional to canopy height, seed weight (i.e. terminal velocity) and wind speed, with virtually all seed deposited within a radius of twice the tree or canopy height (Cremer 1977). Such seed dispersal is often highly asymmetrical, with a nearly 15 fold increase in the number of seed dispersed downwind of a source having been reported (Potts and Wiltshire 1997). The movement of seed once deposited on the ground is probably fairly limited in most species. Rare, long distance dispersal events necessary for colonisation and invasion may occur under abnormal circumstances where seed or capsules may be dispersed by birds, floods, storms, or in fire updrafts. However, with pollen dispersed by active, non-specific pollinators such as birds, bats and insects (see 5.4), it has been argued that in eucalypts, pollen-mediated gene dispersal would far exceed that through seed dispersal, particularly in the tail of the dispersal curve (Potts and Reid 1990).

The dynamics of invasion through pollen dispersal and hybridisation has been studied between two closely related species, *E. amygdalina* and *E. risdonii*, in southeast Tasmania (reviewed in Potts and Reid 1985; Potts 1986; Potts and Reid 1988; Potts and Reid 1990). In this case, *E. risdonii* appeared to be invading the range of *E. amygdalina* by both pollen and seed dispersal. The invasion appears to have persisted for at least several regeneration cycles. However, there was marked inertia in the species boundary due to extremely slow population turnover (due to extensive vegetative regeneration from lignotubers) and limited seed dispersal. Despite a low rate of hybridisation at the boundary between these two species (ca 3%), seed dispersal was so limited compared to pollen dispersal (which appears typical of eucalypts), that hybridisation effectively doubled the rate of gene flow from *E. risdonii* into the range of *E. amygdalina*. This conclusion was consistent across both pre- and post-dispersal seed samples. It appears that when seed dispersal is limited, a moving front may be heralded by a wave of hybridisation. Most cases of long-distance pollen dispersal and hybridisation probably result in extinction and have no impact on the local gene pool. However, in some cases, such hybridisation may not only represent a source of novel genetic variability in the 'sink' population, but may provide a means of invasion by the 'source' population which is independent of seed dispersal. Evidence for this mechanism was obtained from the *E. amygdalina* x *risdonii* hybrid system, partly because the species were so morphologically distinctive in the seedling and adult stage (Potts and Reid 1988). This mechanism involves long-distance pollen-dispersal and hybridisation followed by selection resurrecting, to varying degrees the phenotype of the pollen parent from a segregating hybrid swarm. With intermediate flowering time, such hybrid patches would act as focal points for future long-distance gene exchange that would enhance the resurrection process.

Similar scenarios for long-distance pollen dispersal have been proposed for other eucalypt species in Australia (Ashton and Williams 1973; Potts and Reid 1983; Ashton and Sandiford 1988) and *Nothofagus* in New Zealand (Wardle *et al.* 1988). While these cases involve spatial replacement of one species by another through hybridisation, such invasion has been reported to occur temporally in oaks. In this case, sessile oak (*Quercus petraea*) and the pioneer pedunculate oak (*Q. robur*) frequently form mixed forests in Europe, and successional replacement of pedunculate oak by sessile oak appears to be reinforced by genetic invasion through hybridisation (Bacilieri *et al.* 1996). Such processes are difficult to actively observe or document in forest trees due to their longevity. Nevertheless, the models of range expansion and contraction through pollen-mediated invasion that have been proposed for eucalypts are consistent with observations of the extant variation patterns (e.g. Potts and Jackson 1986; Potts 1990) and recent molecular evidence for ancient hybridisation and reticulate evolution in the genus (Steane *et al.* 1998; Jackson *et al.* 1999; McKinnon *et al.* 1999; McKinnon *et al.* 2000) (Figure 2.1). They also appear to be generally applicable to forest tree taxa, at least in temperate regions of the world, and explain molecular patterns of variation in a range of genera such as poplar (Smith and Sytsma 1990b) and oaks (Whittemore and Schaal 1991; Ferris *et al.* 1993; Dumolin-Lapegue *et al.* 1999).

* 1 *Eucalypts often exhibit weak reproductive barriers between closely related taxa. Hybridisation is a natural process and evidence would suggest that it has been an integral part of the evolutionary history of the genus.*

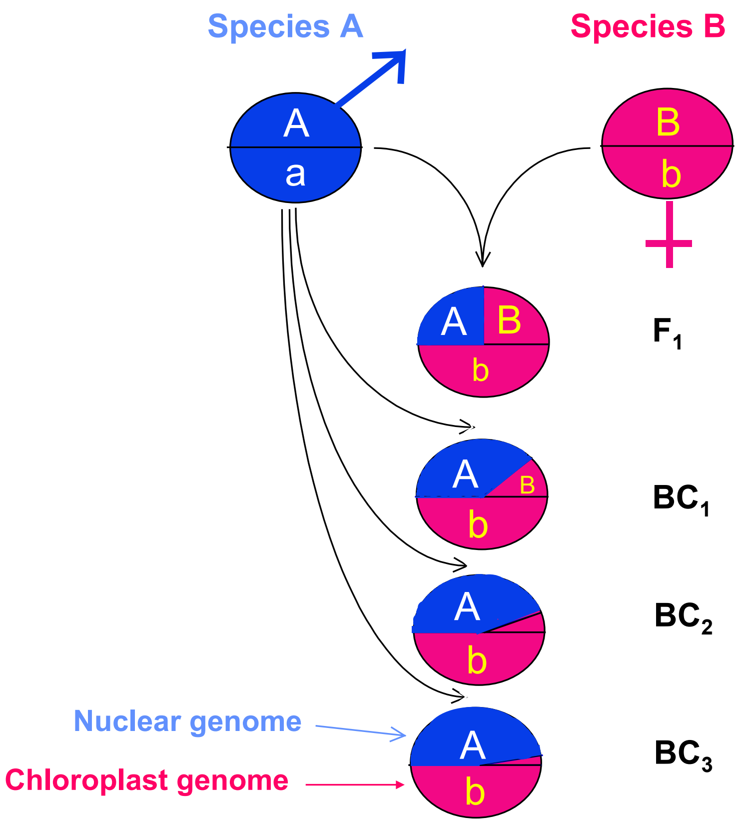

Figure 2.1 Chloroplast capture by hybridisation.
The manner in which the maternally inherited chloroplasts of one species may be introgressed into the gene pool of another species through hybridisation and backcrossing. Some components of the genome are inherited in a uniparental manner, and are thus only passed to the hybrid offspring through the female or male line. For example, the small circular DNA in the chloroplast is inherited asexually (i.e. without recombination) and normally maternally in most angiosperms (e.g. *Eucalyptus*) but paternally (through the pollen) in most conifers. In eucalypts for example, after several generations unilateral pollen flow from a plantation into the range of a native species could result in trees which resemble the exotic species but which have the chloroplast genome (haplotype) of the native species. This process is known as *chloroplast capture* and is the basis of the evidence for historical hybridisation and introgression in many recent studies (e.g. Jackson *et al.* 1999) (Figure provided courtesy of D. Steane).

3. Potential sources of genetic pollution of eucalypt forest

Potential sources of genetic pollution of native eucalypt gene pools are exotic species, artificial hybrids, exotic provenances or selected material and in the future, genetically modified eucalypts.

3.1 Exotic species

One of the major potential sources of genetic pollution of native eucalypt gene pools would appear to be exotic species that have been introduced into the range of closely related, potentially interbreeding native species (see Ellstrand 1992b). Often naturally sympatric species have evolved stronger barriers to hybridisation than those which have evolved in geographical isolation (Huxel 1999; Butlin 1989). This would exacerbate gene flow when previously isolated species are brought together. In eucalypts it is significant that there is a broad trend for closely related taxa to not co-occur frequently in close geographic proximity (Table 2.1). The extent of hybridisation that may occur when geographic barriers between previously isolated eucalypt species are removed is evident from the levels of spontaneous hybridisation that occurs in multi-species eucalypt plantings overseas. Large forest bases have been established from nineteenth century introductions of eucalypt species from Australia into countries such as France and Algeria (Trabut 1914; Pilipenka 1969). Hybrids arose in the multi-species plantings and in one case, Trabut (1900) reported that 60% of the progeny of a relatively isolated *E. botryoides* tree were of hybrid origin. Many of these exotic hybrids were described as new species (e.g. *E.* x *algeriensis* Trabut (initially considered a *E. rostrata* x *rudis* hybrid; but later *E. camaldulensis* x *rudis* - Trabut 1914), *E.* x *antipolitensis* Trabut (*E. globulus* x *viminalis*), *E.* x *Cordieri* (*E. globulus* x *cypellocarpa*) (Pilipenka 1969). The Algerian eucalypt (*E.* x *algeriensis*) is widely distributed in Algeria where it grows on the banks of streams and is cited as an example of acclimation by means of hybridisation (Pilipenka 1969). Similarly in India, the widely planted Mysore gum is believed to be a stabilised hybrid between *E. tereticornis* and *E. camaldulensis* (Boden 1964). Such examples clearly indicate the potential of eucalypts to hybridise and rapidly develop stabilised hybrid populations in exotic environments.

The main commercial species of eucalypts likely to be used in farm forestry in various regions of Australia are listed in Appendix 1. These species are mainly from the *Symphyomyrtus* subgenus with the exception of the monocalypt, *E. pilularis*, *E. cloeziana* from *Idiogenes,* and the *Corymbia* species (*C. henryi*, *C. variegata*, *C. maculata*, *and C. citriodora*). The *Symphyomyrtus* species are from virtually all major sections within this subgenus including *Transversaria* (*E. grandis*, *E. pellita*), *Exertaria* (*E. camaldulensis*), *Maidenaria* (*E. globulus*, *E. nitens*, *E. dunnii*), *Bisectaria* (*E. cladocalyx*, *E. horistes*, *E. kochii*, *E. occidentalis* and *E. polybractea* and *E. kochii*) and *Adnataria* (*E. sideroxylon* and the closely related *E. tricarpa*) (see 5.8.2).

The potential for plantation and native forest eucalypts to hybridise has already been demonstrated on the island of Tasmania (Barbour *et al.* 2000). Four percent of seedlings grown from open-pollinated seed collected from the native *E. ovata* trees in a stream reserve were found to be F_1 hybrids with the exotic *E. nitens*. These trees were within 300m of a small, mature *E. nitens* plantation. All 11 *E. ovata* trees sampled produced hybrids, with individual tree values ranging from 0.1 to 16%. In contrast, no hybrids were found involving the adjacent *E. viminalis* that does not overlap with the flowering of *E. nitens* at this site. Whether the F_1 hybrids observed in the present study can survive to reproductive maturity in the wild and allow the introgression of *E. nitens* genes into the native gene pool is yet to be determined. Nevertheless, these first results clearly indicate the potential for pollen flow from exotic plantings into the range of an adjacent native species.

3.1.1 How genetically different are species?

The potential for introgression will depend upon numerous factors (see Section 5). Its impact will in part depend upon the level of genetic and phylogenetic divergence between the species (Wilson 1990; Ellstrand *et al.* 1999). On the one hand, the greater the divergence the less likelihood hybridisation and introgression will be successful (see 5.6 and 5.7), but if it is, the impact on the native gene pool will be potentially greater. On the other hand, poorly differentiated species may hybridise more readily, but the impact of the gene flow on the native species gene pool will be less. The degree of genetic differentiation between some forest tree taxa can be relatively small, certainly in terms of the allelic difference at random neutral marker loci. In the case of oaks, allozyme and nuclear DNA markers have revealed low genetic distances between many species (Dumolin-Lapegue *et al.* 1999 c.f. Howard *et al.* 1997). For example, a screening of 2800 PCR amplification products using random primers on 22 trees of each of *Quercus petraea* and *Quercus robur* revealed that only 2% of the amplified fragments exhibited significant frequency differences between the two species (Bodenes *et al.* 1997; see also Moreau *et al.* 1994). None of these were specific to a species. In such cases, the absence of species specific alleles would mean that very few novel alleles would be introduced into the gene pool by introgression. However, for diploid species, there is increasing evidence that differentiation and speciation involves not only differences in gene frequency (additive genetic effects), but is due to differences in gene combinations and their interactions (epistatic gene effects; e.g. co-adapted gene combinations) (Rieseberg *et al.* 1996; Wu and Li 1999).

In the case of eucalypts, no major differences in chromosome number or arrangement have been detected to date, with virtually all species examined having a haploid chromosome number of n=11 (reviewed in Eldridge *et al.* 1993 and Potts and Wiltshire 1997). No marked differences in chromosome morphology have been reported between species to date (Moran *et al.* 2000; Thamarus *et al.* 2000). However, there do appear to be differences in genome size and DNA content. For example, within the *Symphyomyrtus*, species from the same section tend to have similar DNA content, which was nearly double the DNA content of species from the genus *Corymbia* (Grattapaglia and Bradshaw 1994). Further, minor inversions and deletions have been reported in some genes (e.g. Steane *et al.* 1999), but the extent to which they are species-specific remains to be determined.

Many closely related eucalypt species also show poor molecular differentiation with no species-specific markers detected, despite marked morphological differences. Examples reported included *E. amygdalina* and *E. risdonii* (Sale *et al.* 1996), *E. risdonii*, *E. tenuiramis* and *E. coccifera* (Turner *et al.* 2000), *Corymbia ficifolia* and *C. calophylla* (Wardell-Johnson and Coates 1996), and the *E. dendromorpha* complex (Prober 1990). Such poor differentiation could reflect either recent differentiation or gene flow between taxa. By contrast, more distantly related species can often be clearly differentiated with fixed allelic differences (*E. jacksonii* and *E. brevistylis* Wardell-Johnson and Coates 1996). In such cases, hybridisation could result in the introduction of novel alleles into the 'sink' population. However, neutral molecular markers do not necessarily detect the quantitative genetic variation that is significant in physiological and morphological differentiation of the species. For example, many closely related species are markedly differentiated in ecological and morphological characteristics, yet exhibit poor molecular differentiation (e.g. *E. risdonii* and *E. amygdalina*). In such cases, the observed phenotypic differences between species are likely to be controlled by few genes.

* 2 One of the major threats to the genetic integrity of native eucalypt gene pools currently would appear to be the introduction of exotic species into the range of potentially interbreeding native species.

* 3 *Often species that have evolved in geographical isolation exhibit weaker barriers to hybridisation than those which naturally co-occur*

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3.2 Artificial hybrids

3.2.1 General

Artificial interspecific hybrids have been used in forestry world-wide for many decades with the main genera including *Acacia*, *Larix*, *Picea*, *Pinus*, *Populus* and *Eucalyptus* (reviewed in Griffin *et al.* 1988; Martin 1989; Nikles and Griffin 1992; Nikles and Lee 1998; Khurana 1998; Dungey 1999). Most hybrids deployed are from the first generation crossing (F_1's), although advanced generation material is often considered due to greater ease of seed production (see Dungey 1999). In Australia, the only interspecific hybrids being deployed for forestry on a commercial scale appear to be mainly in Queensland. These are F_1 and advanced generation hybrids of the exotic tropical *Pinus* species (mainly *P. elliottii var. elliottii* x *P. carribaea* var. *hondurensis*) (Nikles 1996; Nikles and Lee 1998; Nikles 2000).

Artificial hybrids represent sources of unique combinations of genes that may or may not be found in nature. In the case of *Populus*, strong incompatibility barriers occur between species from different sections. However, these barriers have been broken with a variety of artificial manipulations (mentor pollens, pollen extracts, solvent treatments) (Smith and Sytsma 1990a) and some of the poplar clones being deployed in the USA and Europe are the result of intersectional crossing (Stettler *et al.* 1996). In the case of *Eucalyptus*, hybrid combinations are being tested for forestry purposes that involve species that would not normally hybridise due to temporal and geographic barriers (*Eucalyptus nitens* x *globulus*). Further, many are intersectional hybrids (e.g. *E. camaldulensis* x *globulus*, *E. grandis* x *globulus*; Table 3.1) that have only been selected after extensive screening (Griffin *et al.* 2000) and therefore involve species combinations which would rarely occur in nature due to their poor average fitness, although specific individuals may show good fitness. Techniques have also been developed to allow hybridisation between species which exhibit physiological (Pryor and Willing 1974) or morphological (Harbard *et al.* 2000; Barbour and Spencer 2000) barriers to crossing.

All eucalypt hybrids being developed or introduced into Australia are still at the stage of field testing (Table 3.1). The oldest and largest program is that of North Forest Products aimed at developing *E. nitens* x *E. globulus* F_1 hybrids which commenced in 1986 (Tibbits 1986; Tibbits *et al.* 1995). However, this program has now been suspended due to the difficulties and high costs of cloning elite F_1 genotypes with current technology (Tibbits 2000). F_1 combinations involving more easily cloned species (e.g. *E. camaldulensis* and *E. grandis*) are now being investigated by other organizations (Table 3.1). Seedlings or clones of other combinations derived from crossing programs in either South Africa or South America are currently being tested or are in quarantine. These included intersectional crosses (*E. pellita* x *maidenii, E. pellita* x *globulus, E. urophylla* x *dunnii, E. urophylla* x *maidenii, E. urophylla* x *globulus, E. maidenii* x *saligna, E. maidenii* x *urophylla, E. maidenii* x *grandis, E. saligna* x *maidenii, E. grandis* x *maidenii*), intrasectional crosses (*E. grandis* x *urophylla, E. grandis* x *botryoides, E. pellita* x *deanei*, *E. urophylla* x *deanei, E. saligna* x *urophylla*) and two- and three-way species backcrosses (*E. grandis x [grandis x camaldulensis]*, *E. grandis x [grandis x tereticornis], E. urophylla x [grandis x camaldulensis]* and *E. urophylla x [dunnii x grandis]*) (D. Boomsma pers com).

3.2.2 Are hybrids any more risky than exotic species?

The key issue for deployment of hybrids is whether hybrids *per se* constitute a greater risk for genetic pollution of native species than already exists with the use of exotic species.

Relevant features of these hybrids are:

(i) floral morphological traits, such as style length, are likely to be intermediate to their parental taxa (but biased toward the smaller flowered species) (McComb *et al.* 2000; Tilyard and Potts unpubl. data);

(ii) flowering time is likely to be intermediate between the parental flowering times (Lopez *et al.* 2000a);

(iii) if closely related, their pollen is likely to be as viable as parental pollen (e.g. *E. nitens* x *globulus* Tilyard and Potts unpubl. data) (intersectional crosses have not yet been reported);

(iv) on average they may be more susceptible to insect and fungal pests than their parental taxa (Morrow *et al.* 1994; Whitham *et al.* 1994; Whitham *et al.* 1999; Dungey *et al.* 2000; Lawrence *et al.* 2000); and

(v) clonal propagation is likely to be the preferred means of deployment (Griffin *et al.* 2000; Tibbits 2000; Verryn 2000), although in some cases seed from F_1 hybrid orchards is being deployed (Nikles and Lee 1998).

The risk of genetic pollution from these, usually F_1, hybrids will depend upon whether one or other of the parents is in close proximity. If a parental species is in close proximity then backcrossing may occur. Backcrossing may be enhanced by the weakening of any post-zygotic barriers between the species as flowering time and other characteristics such as morphology are often inherited in an intermediate manner. Further enhancement could occur due to most F_1's deployed having been heavily selected from a highly variable pool of often poor performing F_1's (Griffin *et al.* 2000; de Assis 2000). In these elite F_1's, any complementary dominant genes or chromosomal effects responsible for deleterious interaction between the parental species would have been heavily selected against. Nevertheless, any progeny derived from hybrids crossing to either their parental species or an unrelated third species is still likely to exhibit considerable loss of fitness due to segregation and recombination resulting in advanced generation hybrid breakdown (see 5.7.3). Many of the F_1 hybrids currently being tested are inter-sectional hybrids, which due to their distant phylogenetic relationship are likely to produce offspring which are particularly prone to advanced generation breakdown (outbreeding depression) (see 5.7.3). Certainly, abnormalities and dwarfism is a common feature of many advanced generation eucalypt hybrids. Pilipenka (1969) notes that dwarfs and abnormal phenotypes may represent up to 90-95% of some advanced generation eucalypt hybrid combinations and cites the intersectional F_2 between *E. viminalis* and *E. camaldulensis* as an example.

If such outbreeding depression is evident in the F_2 it will also be expected, but to a lesser extent, following any back-crossing between plantation F_1's and native forest species regardless of whether they are related or not to the hybrids' parental taxa (see Section 5.7.3). This would reduce offspring fitness and hence the chance of introgression and would seem to occur regardless of whether the F_1 has been heavily selected or not. For example, following backcrossing of *E. grandis* x *globulus* F_1's to unrelated trees of either parental taxa, Griffin *et al.* (2000) noted that the selection of a good F_1 phenotype does not, *per se*, eliminate the genes responsible for the progeny inviability. High levels of abnormal phenotypes were still produced, although in this case it did improve the proportion of normal plants relative to the initial F_1 population (Table 3.2). de Assis (2000) and Pilipenka (1969) also noted that selected F_1's had been used in backcrossing, three-way and four-way crosses and that these crosses were also subject to the same abnormality problems as F_1 hybrids. Indeed, it is possible that where three-way crossing is involved, viability problems may be increased, confounding problems of recombination in the F_2 with new incompatibilities with a third genome. These results suggest that there should be no less of a barrier to genetic pollution through planting selected F_1 hybrids than from planting the parental species themselves. The only exception is where backcrossing to parental taxa may occur more readily than F_1 hybridisation and progeny may be of higher fitness, but this will be countered by the contribution of novel genes being less. There is a high probability they will be intermediate in flowering time and other physical characteristics such as flower size. These hybrids will therefore be a conduit for the flow of genes between the parental taxa.

*** 4** *No major additional genetic risk is seen from the deployment of exotic hybrids as opposed to an exotic species in the landscape. The exception is where backcrossing to parental taxa may occur. The deployment of selected hybrids in the vicinity of natural populations of their parental (or closely related) taxa should therefore be avoided unless other barriers can operate. However, the susceptibility of eucalypt hybrids to pests is a key consideration in the Australian environment.*

Table 3.1 Eucalypt hybrids being developed in Australia.
The main eucalypt hybrid combinations that are currently being field tested in Australia for forestry purposes, hybrid type, reference and organisation responsible. * both reciprocals being tested

Hybrid	Type	Organisation	Reference	Comment
INTER-SECTIONAL HYBRIDS				
E. camaldulensis x *grandis**	F_1 BC_1	XYLONOVA	Dale *et al.* 2000 Sasse *et al.* 2000	Imported clones are being developed in Australia for salt tolerance
	F_1		Robson 2000	Field trials just planted
		QFRI CSIRO-FFP	Harwood unpubl. D. Kleinig pers.com.	Imported clones currently being deployed
E. camaldulensis x *globulus*	F_1 BC_1	CALM, Murdock Univ-NFP XYLONOVA	McComb *et al.* 2000 Sasse *et al.* 2000	Being developed for salt-tolerance
E. grandis x *nitens*	F_1		Shelbourne *et al.* 1999	High % of inviable F_1 plants but rest normal
E. grandis x *tereticornis*		QFRI	Robson 2000	Imported hybrids
E. saligna x *camaldulensis*	F_1	CSIRO-FFP	Harwood unpubl.	Field trials just planted
E. saligna x *tereticornis*	F_1	CSIRO-FFP	Harwood unpubl.	Field trials just planted
E. urophylla x *camaldulensis*		QFRI	Robson 2000	Imported hybrids
INTRA-SECTIONAL HYBRIDS				
Corymbia torelliana x *C. citriodora*			D. Kleinig pers.com.	Imported hybrids
E. grandis x *urophylla**	F_1	FIOBIO	Shepherd 1998 D. Kleinig pers.com.	Imported hybrids
		QFRI	D. Lee pers. com.	
E. grandis x *pellita*	F_1	QFRI	Lee *et al.* 2000	
E. urophylla x *pellita*	F_1	QFRI	Lee *et al.* 2000	
E. saligna x *grandis*	F_1	CSIRO-FFP	Harwood unpubl.	Field trials just planted
E. gunnii x *globulus*	F_1, F_2, BC_1	CRCSPF-NFP	Potts *et al.* 1992 Scott *et al.* 2000	Susceptibility to marsupial browsing and poor performance relative to *E. nitens* has stopped F_1 development
E. nitens x *globulus*	F_1	NFP, CSIRO-NFP-CRCSPF	Potts *et al.* 1992 Volker 1995 Tibbits *et al.* 1995 Tibbits 2000	F_1's show high levels of inviability but survivors can be vigorous. High cost of cloning has prohibited F_1 hybrid deployment to date in Australia
	F_1, F_2, BC_1	CRC-SPF	Tilyard and Potts 1996 Potts *et al.* 2000	F_1 & F_2 hybrids show many inviabless, survivors support greater numbers of insect species than pures

Table 3.2 Germination and seedling viability of some eucalypt F_1 hybrids

Summary of germination and seedling viability of hybrid combinations evaluated by Shell Forestry (from Griffin *et al.* 2000). The data is averaged over different sites and years. Normally with pure species outcrosses the percentage germination and normal plants in the nursery would be expected to be greater than 90% (e.g. Potts *et al.* 1992; Potts *et al.* 2000; Lopez *et al.* 2000b).

Cross	% germination	Normal seedlings as % germinated	Normal seedlings in nursery as % of seed sown
Inter-series			
E. nitens x *globulus*	48	91	44
E. dunnii x *globulus*	31	63	20
Intersectional			
E. urophylla x *globulus*	42	47	20
E. urophylla x *dunnii*	17	54	9
E. grandis x *globulus*	9	80	7
E. dunnii x *grandis*	50	18	6
E. grandis x *dunnii*	17	39	6
Backcrosses			
E. grandis x (*grandis* x *globulus*)[1]	61	77	47
E. globulus x (*grandis* x *globulus*)[2]	57	71	41

[1] Calculated using data from 2 families derived from backcrossing with an outstanding F_1 selection in Table 4 of Griffin *et al.* (2000). The percentage of seed giving normal plants in the field after 2 years was 17%, as 46% of the field grown plants were of poor viability with abnormal phenotypes. [2] As above but only a single family. No field data was available.

3.3 Exotic provenances

3.3.1 General

Gene exchange between locally adapted plant populations of the same species can have significant evolutionary consequences, including changes in genetic diversity, introduction of adaptive or maladaptive traits, disruption of coadaptive gene complexes, as well as the creation of new ecotypes or even species (Nagy 1997). Ultimately, changes in local diversity will depend upon levels of allelic richness and genetic diversity of the source population (e.g. plantation) relative to that of the sink populations (wild populations) (Ellstrand *et al.* 1999) and the strength of selection against non-native characters (Nagy 1997).

A key issue is the conservation value of genetic diversity below the species level. The existence of genetically distinctive populations, whether or not the differences among them are adaptive, has fostered widespread concern for the conservation of intraspecific entities (Rhymer and Simberloff 1996). Why should we worry about loss of entities such as subspecies, races and local populations? Often one of the major components of genetic variation within species is among populations, and eucalypts are no exception (see Potts and Wiltshire 1997). Daniels and Sheail (1999) argue that maintenance of biodiversity requires the retention of not only a range of habitats and species, but also the separate gene pools giving rise to the uniqueness of species and variants at the intra-specific level. They suggest individual, isolated populations become worthy of conservation because their genetic structure may endow them with a suite of characteristics that may be unique. Gene flow from external sources may compromise this uniqueness, placing individual local populations and rare species at particular risk.

In a review of the probability of hybridisation and gene flow between crops and wild species in the UK, Raybould and Gray (1993) assessed the risk of genetic pollution for four forest tree taxa. They considered the risk of gene flow between cultivated and wild Scots pine (*Pinus sylvestris*) was high. While they are the same species outside of Scotland, 'wild' Scot's pines are often introductions from Russia. New genotypes or genes of the same species could swamp the local gene pool. Of particular concern are small local gene pools associated with naturally or artificially remnant populations. For example, isozyme studies have demonstrated that the small relic population of *Abies alba* in the Bialowieza Primeval Forests is genetically distinctive and at risk of genetic pollution from adjacent man-made forest of exotic *Abies alba* (Mejnartowicz 1996). This remnant forest is the only natural lowland forest remaining in Europe on the expansive "Dikij Nikor" bogs. The problem of introduction of genetically differentiated exotic provenances is also an increasing issue in restoration ecology where efforts to restore the natural biodiversity may result in remnant populations of the same species being genetically swamped (Handel *et al.* 1996; Jones and Johnson 1998).

*** 5** *Remnant populations of the main plantation species in rural landscapes will be particularly at risk from genetic swamping from exotic provenances. However, in cases enhanced gene flow may be beneficial in overcoming inbreeding effects.*

Figure 3.1 Remnant stands of *E. globulus* ssp. *globulus* in southern Gippsland.

3.3.2 How different are provenances of *Eucalyptus*?

The key factors determining the genetic impact of exotic provenances on the local gene pools are, firstly, how genetically differentiated are the two populations and, secondly, whether the local provenance will have an adaptive advantage resulting in non-local genes failing to introgress into the native gene pool. Eucalypt species are well known for the large amount of genetic variability between populations within recognised species (reviewed in Potts and Wiltshire 1997), and the major plantation species are not exceptions (Eldridge *et al.* 1993; Table 2.1). Such variation may occur over steep habitat gradients as well as over large geographic distances. There are certainly broad trends for genetic differences between native eucalypt populations to increase with an increasing geographic distance between populations (Moran and Hopper 1983; Sampson *et al.* 1988). Molecular studies have shown that greatest population differentiation, at least for neutral markers, occurs between populations of regionally distributed species as opposed to populations of species with localised or widespread distributions (Moran 1992; Potts and Wiltshire 1997). Nevertheless, marked genetic differentiation in quantitative traits at least can occur over very short distances, even within continuous populations (e.g. Jordan *et al.* 2000). Key studies or sources of information on the patterns of genetic differentiation within the major plantation species likely to be used in farm forestry in Australia are given in Table 3.3 .

Of the eucalypts, the genetic diversity within *E. globulus* ssp. *globulus* and its intergrades with mainland subspecies has been the best studied (reviewed in Eldridge *et al.* 1993; Dutkowski and Potts 1999; Potts *et al.* 1999) (Table 3.3). Considerable molecular and quantitative genetic differentiation is known to occur across its geographic range which has recently been summarised by dividing this gene pool into 13 geographically and genetically differentiated races (Dutkowski and Potts 1999). This broad scale genetic variation is superimposed upon fine scale genetic differentiation in response to local habitat gradients (e.g. Jordan *et al.* 2000) as well as a local family group structure (Hardner *et al.* 1998; Skabo *et al.* 1998). A key point emerging from these studies is that the closer a gene pool is examined the more diversity is discovered in ecological (e.g. drought) and traits of economic importance. In some cases advances in technologies are allowing unexpected facets of this variation to be revealed (Jackson *et al.* 1999). This better knowledge of the gene pool or changes in breeding objectives can lead to different areas of the gene pool being valued for exploitation. In the case of *E. globulus*, King Island was the favoured seed source for plantations during the 1980's due to its fast growth. However, as breeding objectives became more focused on pulpwood production, emphasis has now shifted to intergrade populations in the Strezlecki Ranges (Potts *et al.* 1999). While most seed for future plantations will be derived from seed orchards established from breeding populations, the future requirements on a genetic resource are difficult to predict. Current *E. globulus* plantations in Australia are either derived from seed collected from first generation, multi-provenance seed orchards or open-pollinated seed collected directly from favoured native stands. The Strezlecki Ranges race has been a major source of seed, although with the huge demand for *E. globulus* seed many other native stand seed sources have been utilised (e.g. Otway Ranges, King Island, Furneaux Group, Southern Tasmania).

The molecular genetic differentiation within the Western Australian oil mallees *E. kochii* ssp. *kochii*, *E. kochii* ssp. *plenissima* and *E. horistes* has recently been studied by Byrne and Macdonald (Byrne 1999; Byrne and Macdonald 2000). The complex shows high overall levels of genetic diversity. However, differentiation between populations in nuclear allele frequencies was low, yet populations could be grouped according to taxa in most cases. Diversity in the chloroplast genome revealed by RFLP markers was also high but most diversity was distributed between populations. *E. kochii* ssp. *kochii* could be differentiated on nuclear allele frequencies, although its chloroplast genomes were not monophyletic. Both data sets revealed close identity of the three taxa and it was suggested that they be treated as a single large, genetically and morphologically variable species for breeding purposes. While the three taxa are not rare or threatened, much of their distribution has been reduced to remnant vegetation on farmlands, often comprising small populations. It was argued that planting trees in the vicinity of existing trees or adjacent areas should be beneficial, restoring gene flow levels more consistent with historical levels. The planting of non-native provenances in the vicinity of these remnants was addressed. It was argued that the use of seed from the remnants themselves should be avoided since they may suffer from reduced variation and inbreeding depression. Accordingly, it was concluded that germplasm from larger populations in the provenance would be more appropriate. The genetic architecture suggests three provenances (*E. horistes* and southern *E. kochii* ssp. *plenissima*: northern region of *E. kochii* ssp. *plenissima*; and *E. kochii* ssp. *kochii*) should be recognised for restoration of areas of remnant vegetation.

**** 6 It is important that strategies for the management of the gene pools of the major commercial eucalypt species are developed.***

3.3.3 Fitness of local gene pools

A major determinant of the potential for genes from other provenances to introgress into native provenance gene pools will be the relative fitness of the native and non-native provenances (e.g. Nagy 1997). Many studies have demonstrated better growth of local provenances (see Potts and Wiltshire 1997), yet there are an increasing number of reports of local provenances being out-performed in growth by exotic provenances at least in plantation trials. For example, in trials established from range-wide provenance collections of both *E. delegatensis* and *E. regnans*, exotic provenances often outperformed local provenances in growth (Raymond and Volker 1993; Raymond and Volker 1994). However, it is debatable as to whether growth *per se* is an adequate measure of population fitness and while local provenances of *E. delegatensis* were generally outperformed in growth rate, their survival was amongst the best at all sites (Raymond and Volker 1994). The better growth of exotic provenances could arise where local populations have undergone natural selection to maximize reproductive fitness, which may or may not be correlated with plant vigour. In addition, most provenance trials are relatively young (less than 15 years old) in terms of tree generation time and may not account for the suite of catastrophic selection events (e.g. drought - Davidson and Reid 1989 and frost - Davidson and Reid 1985) that play a major role in shaping variation patterns in natural forests. Experimental trials also often have uniformity imposed by site preparation and lower competition than that experienced in natural stands, both of which may affect the comparison between experimental and natural sites. Nevertheless, such results do question the fitness of local gene pools and whether natural populations are in equilibrium with prevailing selection regimes (see Potts 1986).

Disequilibrium could arise through endogenous (inbreeding, genetic drift) or exogenous factors (climate change, pests). Floyd *et al.* (1994) note that local provenances of *E. camaldulensis* were the most susceptible to insect herbivory and suggested that local provenances may not be best adapted to resisting the local suite of phytophagous insects. Eucalypts usually exhibit marked inbreeding depression and there is increasing evidence of local populations accumulating a level of inbreeding through self-pollination and crossing between related neighbours (see Potts and Wiltshire 1997). Such inbreeding occurring within local populations means that the products of unrelated matings would tend to be favoured by natural selection (Hardner and Potts 1997; Hardner *et al.* 1998; Skabo *et al.* 1998). In the case of natural systems, this would mean the products of longer-distance pollen dispersal would be favoured. In the case of native forest/plantation boundaries, this means that the products of crossing between the exotic and native provenance could have at least some selective advantage. This could arise simply through removal of deleterious inbreeding effects, but would be counteracted by differences in local adaptation and co-adaptation (Moritz 1999).

Table 3.3 Provenance variation in plantation eucalypts
Key studies or reviews on genetic variation amongst provenances of the main plantation eucalypts. Provenance variation in *E. grandis*, *E. globulus*, *E. nitens*, *E. camaldulensis* are reviewed in detail in Eldridge *et al.* (1993) and studies post-dating this review are indicated.

Species	Molecular genetic studies	Quantitative genetic studies
Temperate species		
E. globulus ssp. *globulus*	Nesbitt *et al.* 1995, RAPDs Jackson *et al.* 1999, cpDNA Steane *et al.* 2001, microsatellites	Eldridge *et al.* 1993 (review) Carnegie *et al.* 1994 Farrow *et al.* 1994 Jordan *et al.* 1993 Potts and Jordan 1994 Jordan *et al.* 1994 Almeida *et al.* 1995 Dutkowski 1995 Ferrari and Mughini 1995 Zang *et al.* 1995 Lopez *et al.* 2000a Chambers *et al.* 1996 Chambers *et al.* 1997 MacDonald *et al.* 1997 Soria *et al.* 1997 Soria and Borralho 1998 Jordan *et al.* 1999 Potts *et al.* 1999 Dutkowski and Potts 1999 Tibbits *et al.* 1997
E. nitens	Moran 1990, isozymes Byrne and Moran 1994, cpDNA Byrne *et al.* 1998, nuclear RFLPs Cook and Ladiges 1998, isozymes	Eldridge *et al.* 1993 (review) Li *et al.* 1994 Johnson 1996 Tibbits *et al.* 1997 Gea *et al.* 1998

Table 3.3 Provenance variation in plantation eucalypts *cont.*

Species	**Molecular genetic studies**	**Quantitative genetic studies**
Tropical and subtropical species		
E. grandis		Eldridge *et al.* 1993 (review) Ferreira and Santos 1995 Varghese *et al.* 1995 Arnold *et al.* 1996
E. pellita	House and Bell 1994, isozymes	Harwood 1997 Harwood 1998 (review)
E. pilularis		Florence 1964 Florence 1969 Burgess 1975 de Castro Pasztor 1977
E. cloeziana	Turnbull 1980, isozymes	de Aguiar *et al.* 1988 Vigneron 1989 Manaturagimath *et al.* 1991 Marques-Junior *et al.* 1996 Lee *et al.* 1997 Doimo *et al.* 1999
E. dunnii		Pereira *et al.* 1986 Benson and Hager 1993 Stanger 1993 Ferreira and Santos 1995 Marco and Lopez 1995 Gerischer and van Wyk 1998
Corymbia henryi/variegata/maculata/ citriodora complex	McDonald *et al.* 2000, isozymes	Larsen 1965 Andrew 1970 Darrow 1985 de Castro Pasztor 1977 Dias and Kageyama 1991 Hill and Johnson 1995 Mazanec 1999 Larmour *et al.* 2000

Table 3.3 Provenance variation in plantation eucalypts *cont.*

Dry land species		
E. cladocalyx		Groves 1967
E. occidentalis		Zohar 1991
E. camaldulensis	McDonald *et al.* 1995, isozymes	Midgley *et al.* 1989 (review) Eldridge *et al.* 1993 (review) Floyd *et al.* 1994 Doran and Burgess 1996 Pinyopusarerk *et al.* 1996
E. sideroxylon		Bramwells and Whiffin 1984 Hill and Johnson 1991
E. tricarpa		Hill and Johnson 1991
E. kochii	Byrne 1999, nuclear RFLP Byrne and Macdonald 2000, cpDNA	
E. horistes	Byrne 1999, nuclear RFLP Byrne and Macdonald, 2000 cpDNA	
E. polybractea		

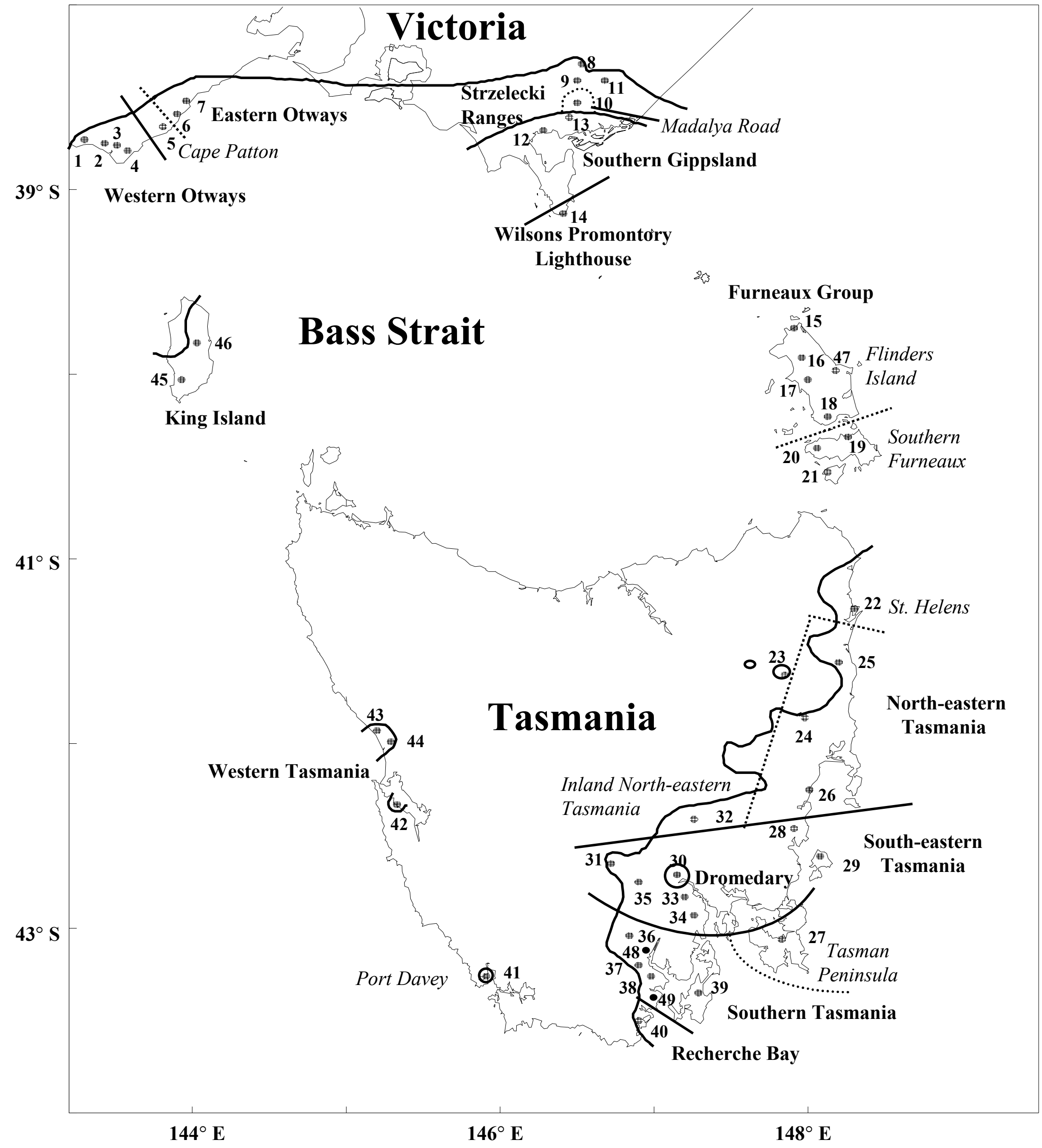

Figure 3.2 Distribution of genetically differentiated races of *E. globulus* ssp. *globulus*
The native populations of the major plantation species, *E. globulus* ssp. *globulus* and its intergrades with other subspecies, are genetically differentiated on numerous traits. The distribution of this genetic diversity has been summarised by classifying the gene pool into 13 geographically based races (in bold; from Dutkowski and Potts 1999). These races could form an initial framework for a gene pool management strategy for this species. (Reproduced with permission of CSIRO Publishing, from Dutkowski GW, Potts BM, (1999) Australian Journal of Botany Vol. 46, fig. 6, p. 254)

3.4 Artificially selected plants

The extent of domestication, reflecting the degree of genetic separation of the crop from wild relatives through breeding is a key issue. Domestication usually leads to the loss of traits that are important to fitness in natural environments and would be expected to result in reduced potential to invade natural habitats (James *et al.* 1998). Identification of genetically differentiated crop/weed elements often has proven not to be straight forward with regard to either morphological (Small 1984) or molecular (Wilson 1990) variation. In comparison to crop species, most forest tree species have undergone little domestication and where hybrids have been produced this usually involves parents that are only one or two generations from the wild (James *et al.* 1998). This is certainly the case for eucalypts currently being deployed in Australia. As noted above (section 3.3.2) the vast majority of eucalypt plantations in Australia are established from seed collected directly from native stands or from seed orchards resulting from the culling of trials established from open-pollinated seed lots collected directly from the wild. In the case of *E. globulus*, the major Australian breeding programs are currently testing their second generation crosses and some imported second generation material is being tested. The most advanced *E. nitens* breeding program is also testing second generation controlled crosses (Tibbits and Hodge 1998).

As well as natural communities, genetic pollution may affect cultivated communities or populations and the dispersal of pollen from congeneric native species represents a major source of genetic diversity to a population that requires a homogeneous structure. Maize, potato, quinua, barley, soyabean and lentils have all been identified as being vulnerable to such introgression (Bateman 1975; Wilson 1990). When the product of a crop is required for the growth of later generations, hybridisation can reduce the quality of the produce. The main issue of crop contamination with forest trees is the loss of genetic gain from open-pollinated seed orchards. Seed orchards are developed to provide a consistent and reliable supply of genetically improved seed for the establishment of tree plantations, and hence the production of intra- or interspecific hybrids poses a threat to the consistency and quality of the yield. Such orchards developed for gymnosperms are particularly at risk as they rely on wind as their vector for pollen dispersal, resulting in foreign pollen being transported from great distances (Caron 1994; Stoehr *et al.* 1994; Adams *et al.* 1997). Little is known of the contamination rates of eucalypt seed orchards in Australia, although 2.8-14.2% has been reported from seed orchards in Brazil (see Table 5.4). Recently, Barbour *et al.* (2000) reported low levels of interspecific hybridisation (0.14%) which was spread relatively uniformly through an *E. nitens* seed orchard in north-west Tasmania.

3.5 Genetically modified (transgenic) plants

3.5.1 General

There is considerable debate concerning the risks of releasing genetically engineered crops. The primary risk is the sexual transfer of transgenes to related wild plants via natural cross-pollination (Klinger *et al.* 1991). However, it is thought that increased 'weediness', invasive ability or persistence of the transgenic plant itself could be a problem if transgenes provide a large fitness advantage (e.g. herbicide, pest or disease resistance; Ellstrand and Hoffman 1990; Raybould and Gray 1993; Raybould and Gray 1994). There may also be direct impact of the gene product on the environment (James *et al.* 1998). Sexually compatible crops and related wild species co-occur frequently (Ellstrand and Hoffman 1990; but is not for example the case of cotton in Australia Brown and Brubaker 2000). If mating results in aggressive hybrids these could present an economic threat as weeds or an environmental threat as competitors in natural assemblages. It is unlikely that genetic modification will change the rate at which crop plants hybridise with wild relatives, or the range of species that are sexually compatible (de Vries *et al.* 1992). Modifications may however, alter the fitness of hybrids and this may result in greater persistence, faster rates of spread or the ability to invade new habitats (Raybould and Gray 1994). However, Hoffman (1990) notes that breeders have been introducing new genes into organisms by crossing with wild relatives for decades with no apparent harm. With genetic engineering it is the novelty of the introduced traits that distinguishes crop breeding using genetic engineering techniques from traditional breeding methods.

One of the most obvious risks with genetically engineered plants involves the introduction of genes for herbicide resistance. If these genes were captured by wild relatives, herbicides considered environmentally safe would no longer be effective against weeds, potentially requiring the use of more dangerous chemicals (Ellstrand and Hoffman 1990; Hoffman 1990; Dale 1992). The risk of the introduction of insect resistant genes, such as the *Bacillus thuringensis* (Bt) toxins (Table 3.4), is that this could result in decreased resistance to other pests, increased resistance in target pest populations, alteration of natural gene pools, and reduction of biodiversity (Duchesne 1993; Harcourt *et al.* 2000). Further disruption of pollinator and plant communities may occur if the toxin is expressed in plant nectar or pollen (Hoffman 1990; Losey *et al.* 1999). Indeed, Poppy (1998) considers that risk assessment should be required to ensure modified plants are not grown if significant direct effects on bees were demonstrated.

Raybould (1993) regards a transgene as having escaped from a crop if any of the criteria listed in Box 3.1 apply. The first route involves either vegetative propagation or transmission via seed. The later route is most likely to be a concern for the release of genetically modified *Pinus radiata* in Australia. The second route is similar to the first apart from transmission of the transgene via pollination to another crop and the third, which is of particular concern with genetically modified eucalypts in Australia, is transfer to a related species, particularly a wild relative.

Box 3.1 Criteria used to determine transgene escape.

A transgene may be regarded as having escaped from a crop if any of the following criteria apply (following Raybould and Gray 1993).

1a The plant containing it persists after harvesting of the crop, possibly becoming a weed of agricultural, especially arable, land
1b The plant containing it persists in the disturbed habitats associated with agriculture or other human activities (e.g. headlands, verges, ditches, roadsides, waste tips)
1c The plant containing it persists and invades semi-natural *or natural* habitats
2a The transgene is transferred by pollination to another crop which persists in agricultural habitats
2b As above, but the plant occupying disturbed habitats
2c As above, but the plant invades semi-natural habitats
3a. The transgene is transferred by pollination to a related wild plant which (possibly by introgression) persists in agricultural habitats
3b As above, but the plant occupying disturbed habitats
3c As above, but the plant occupying semi-natural *or natural* habitats

3.5.2 Genetically modified forest trees

There is general interest in genetic engineering of forest tree species to increase disease, pest, drought and heat resistance, tolerance of low nutrition, growth, herbicide resistance and decreasing lignin synthesis (for easy pulping) and male sterility (Duchesne 1993; Table 3.4). This research has been recently reviewed in Bajaj (1999). Genetic engineering of forest trees has lagged behind that of agricultural crops due to the long rotation times and early difficulties in adapting methodologies. Most field trials testing transgenic material have been established with reporter genes, and only recently have trials been established with genes of interest (Leplé 1999). Transformation is being undertaken in numerous forest tree genera such as *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Populus* and *Eucalyptus* (Table 3.4). Of these genera, genetic engineering of poplars is the most advanced and they are considered models for tree genetic engineering (James *et al.* 1998). They were the first hardwood species to be transformed with a herbicide resistance gene in 1987 and are one of the few examples of a tree species which is readily transformable with *Agrobacterium* (Walter 1999; Leplé 1999). Field trials have been established with transgenic material (Leplé 1999) and they are likely to be the major tree group where transgenic plants are widely used. It is important to note that the full potential of genetic engineering can only be realised by its integration into conventional clonal propagation programs (MacRae and Cotterill 2000). For example, in many European countries the majority of poplar plantations are established from only 5 clones and thus the commercial use of transgenic trees is facilitated as few clones would have to be transformed (Leplé 1999).

Extensive research on genetic engineering of *Populus* is being undertaken by the Tree Genetic Engineering Research Cooperative (TGERC; http://www.fsl.orst.edu/tgerc/index.htm) at Oregon State University. This group is actively assessing the environmental risks associated with the use of transgenes in forest trees (Strauss *et al.* 1995; Strauss 1997; James *et al.* 1998; DiFazio *et al.* 1999). Leplé *et al*. (1999) consider that the development of sterility in trees is probably a prerequisite for the commercial use of transgenic poplars. This would not only prevent pollen mediated gene flow, but could also enhance vegetative growth through reallocation of resources previously devoted to reproduction (see also James *et al.* 1998).

Key features by which forest tree taxa may differ from crop plants are overviewed by James *et al.* (1998). These include:

(i) extent of domestication

Most forest trees, even poplars have undergone little domestication and where hybrids have been produced this usually involves parents that are only one or two generations from the wild (James *et al.* 1998). This may mean for example, that transgenic varieties of forest trees may have a greater propensity to invade natural habitats compared with agricultural crop plants.

(ii) dispersal potential

Hoffman (1990) suggests that genetic manipulation of forest species such as pines and poplars, which are wind pollinated and disperse pollen and seeds over relatively long distances could have an even greater potential to disrupt natural community dynamics than many crop species. However, recent surveys of poplar regeneration in the vicinity of flowering hybrid poplar plantations in the Pacific Northwest of the USA have indicated extremely low levels of hybrid progeny (James *et al.* 1998).

(iii) breeding system

Many agricultural crop species are selfers and thus outcrossing is not promoted. By contrast most forest tree species are outcrossers and reproductive barriers between species are often weak.

(iv) time to reach reproductive maturity

(see Table 5.2)

(v) *longevity*

> The longer rotation interval poses considerable risk with regard to the long-term continued and controlled expression of transgenes (Walter 1999). Indeed, the expression of many transgenes would only be required in a specific tissue or stage in the life cycle. Their expression over the full life span of a forest tree could pose environmental risks, such as the development of resistance in insects against a toxin produced by a tree (Walter 1999; James *et al.* 1998). For example, although the Bt toxin has been applied as an insecticide commercially in agriculture for years, it degrades rapidly in the field. It thus only exerts a short-term selective pressure against insects whereas organisms genetically modified to produce the toxin would exert a constant selection pressure on the pests communities (Hoffman 1990).

The potential environmental hazards of transgenic trees are discussed in detail by James *et al.* (1998). It is argued that risk assessment should focus exclusively on the transgene phenotype within a given plant host and environment, weighing both the costs of foregoing the benefits a transgenic variety can provide and the possibility of adverse environmental effects. They consider that basic principles of population genetics can be used to facilitate prediction of the potential for transgenes to spread and establish in natural ecosystems. For example, transgenes that are expected to have neutral or deleterious effects on tree fitness, including those for lignin modification, reproductive sterility and antibiotic resistance, should be of little environmental concern in most biomass crop systems. In contrast, transgenes that are likely to substantially affect host fitness are believed to pose a greater risk, as are plants with transgenes which produce a substance known to disrupt ecological processes. Field experiments to determine population replacement and transgene flow are desirable for testing such predictions; however, the long generation times of tree crops makes such studies prohibitive. It is argued that a combination of demographic data from existing non-transgenic populations, simulation modeling of transgene dispersal, and monitoring field releases can be used to guide current risk assessment and can be used to further scientific knowledge for future assessment.

Table 3.4 Forest trees being genetically modified.

The major forest tree taxa that are being genetically transformed, their transformation status, and the key genes being transferred or traits being modified.

Taxa	**Transformation status**	**Genes transferred**	**Reference**
Larix sp.	3 species stably transformed, greenhouse evaluation (oldest 4 year old trees), no field evaluation reported	Markers, genes affecting herbicide resistance, insect tolerance (Bt toxin synthesis), lignin metabolism	Pilate 1999
Picea sp.	Greenhouse evaluation only	Markers	Tian 1999
Pinus radiata	Plants transformed with marker and herbicide resistance genes are in greenhouses and being field tested in NZ	Markers, herbicide resistance, exploring down regulation or change of lignin genes; genes advancing and delaying reproduction and affecting insect and fungal pests	Walter 1999
Populus sp.	Glasshouse and many field trials, likely to be the first commercially used GMO forest tree	Bt resistance, herbicide resistance (Glycophosphate, Basta, chlorsulfuron), insect resistance (e.g. Bt, proteinase inhibitor), lignin composition and content (including down regulation), resistance to oxidative stress, changing hormone metabolism, and reproductive sterility	Strauss *et al.* 1995 Leplé 1999 James *et al.* 1998
Eucalyptus sp.	Field trials 1995 in UK and Spain, Portugal and South Africa in 1997	Markers, herbicide resistance, insect resistance, sterility, improvement of rooting ability, modification of lignin content and composition, increased cold tolerance, drought and salinity tolerance	Harcourt *et al.* 1995a,b Griffin 1996 McRae 1999 Edwards *et al.* 1995 Chandler 1995 Harcourt *et al.* 1996 Kyozuka *et al.* 1997 Southerton *et al.* 1998 Harcourt *et al.* 2000

3.5.3 Genetically modified eucalypts

Traits being considered for modification in eucalypts are herbicide resistance, insect resistance, sterility, improvement of rooting ability, modification of lignin content and composition, increased cold tolerance, drought and salinity tolerance (McRae 1999). Most transformation has involved marker genes and progress in adding genes of commercial significance has been slow. Species and clones from which transgenic plantlets have been recovered to date include: *E. grandis, E. camaldulensis*, *E. globulus*, *E. saligna*, *E. urophylla*, *E. dunnii* and various eucalypt hybrids *E. grandis* x *dunnii*, *E. grandis* x *camaldulensis* and *E. saligna* x *tereticornis* (McRae 1999). The only available genes of commercial interest to eucalypt growers are those for herbicide tolerance, lignin content and composition, and possibly insect tolerance (Bt toxin gene) and rooting ability (auxin gene of the Ri plasmid) (McRae 1999). Most of this work is being undertaken or tested overseas, although CSIRO is undertaking work on genetic modification of *E. camaldulensis* (Harcourt *et al.* 2000) and *E. globulus* in Australia. Work has been undertaken aimed at inserting insect resistance genes into these eucalypts (2 Bt proteins; Harcourt *et al.* 1995a; Harcourt *et al.* 2000), herbicide resistance genes (Harcourt *et al.* 2000) and is being undertaken on sterility (Southerton *et al.* 1998) and wood property genes. However, for *E. globulus* and *E. nitens* in particular, the deployment of such transgenic material would have to await the development of efficient vegetative propagation systems. No reports of genetically modified eucalypts being field tested in Australia could be found.

Griffin (1996) considered that the first genetically modified trees in commercial use are likely to be herbicide tolerant eucalypts. He considered that the only practical way of exploiting GM trees is through the fine tuning of genotypes which are already tested for the production and site adaptation and which can be mass-propagated for direct use in plantations. Assuming that GM plants are in hand in year 1, the requirement for preliminary testing would mean that operational plantings would not be started until at least 6 to 9 years later and large scale planting would occur 3 years later again (Figure 3.3).

*** 7** *No reports of GM eucalypts being field tested in Australia were found. The release of GM eucalypts in Australia is likely to be a lengthy procedure and depend upon reproductive sterility. GM* Pinus radiata *developed in New Zealand is likely to be the first GM forest tree tested in Australia.*

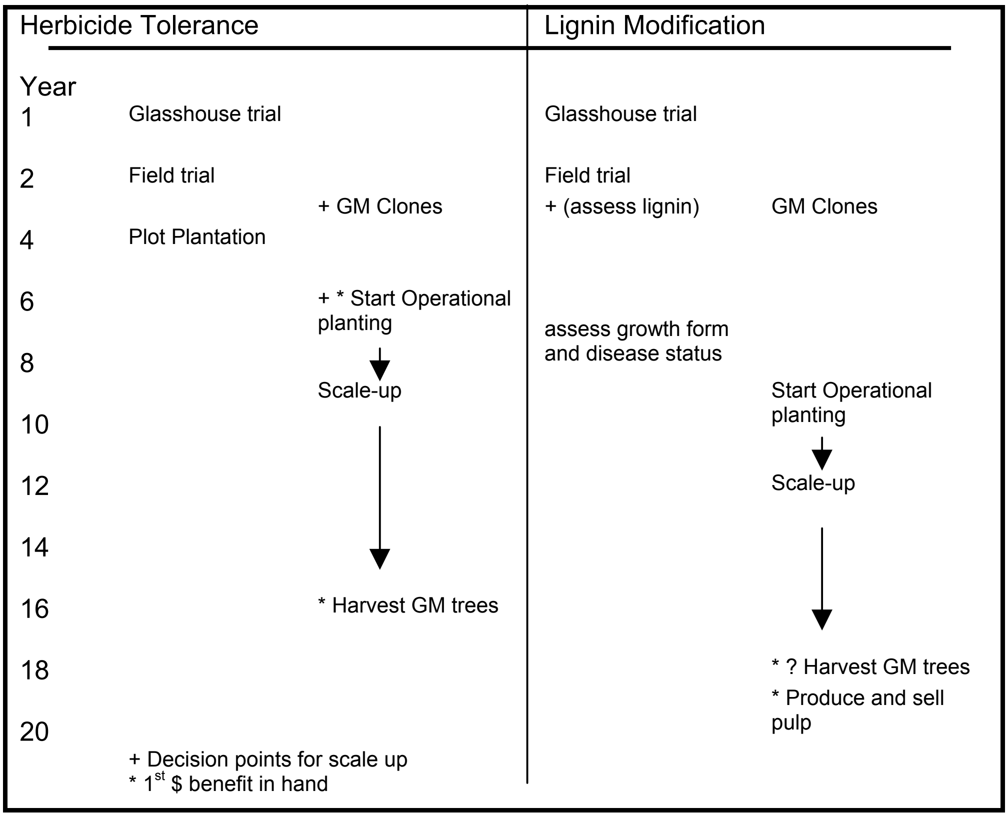

Figure 3.3 Time frame for the testing and deployment of GM eucalypts
The possible time frames for commercial exploitation of GM herbicide tolerance and lignin modification for *Eucalyptus* fibre crops grown on a 10 year rotation as given by Griffin (1996).

3.5.4 Impacts of genetically modified eucalypts on biodiversity

The use of genetically engineered or classically modified eucalypts that do not produce flowers or viable pollen in plantations to avoid genetic pollution of local eucalypts may have other unforeseen impacts on biodiversity and pollination in native vegetation. Such stands will obviously fail to provide resources for flower-feeding animals and may have secondary impacts on abundances of their predators. Accordingly, Woinarski and Cullen (1984) found lower densities of a wide range of invertebrates on many Australian plants when flowers were absent than when they were blooming. Other secondary impacts may result because flowers provide nectar and pollen sources for animals which also feed on phytophagous insects, thereby increasing their longevity and fecundity (reviewed in Price *et al.* 1980). For example, soldier beetles prey upon the eggs and larvae of chrysomelid beetles (Leon 1989; Elek 1997), while tachinid flies and braconid wasps parasitise their larvae (Greaves 1966; Tanton and Khan 1978; de Little 1982). Similarly, the larvae of the syrphid fly *Syrphus* sp. predate the psyllid *Cardiaspina albitextura* (Clark 1963). The use of genetically engineered eucalypts, which produce flowers but not pollen, will also impact on a large proportion of flower-feeding animals because many of these, such as beetles, bees and syrphid flies, are pollen feeders. Again this may have secondary impacts on their predators and prey.

Genetic engineering of plants to make them toxic to insect herbivores may harm non-target insects as well. Transgenic maize plants that express proteins from the insecticidal bacterium *Bacillus thuringiensis* contain substantial quantities of these proteins, not only in their leaves, but also in their pollen (Fearing *et al.* 1997). After anther dehiscence this pollen coats the leaves of plants growing nearby. For a large protion of its range, the host plant of the monarch butterfly *Danaus plexippus* grows in the vicinity of corn fields. Laboratory assays have now shown that when monarch larvae are reared on host leaves dusted with pollen from transformed corn, they had significantly greater mortality than those reared on leaves dusted with untransformed corn pollen (Losey *et al.* 1999).

4. Potential impacts on local biodiversity

The impacts on biodiversity resulting from planting non-local eucalypts depend largely on the existing vegetation in the area. If native vegetation is removed to allow such plantings, substantial deleterious impacts on faunal diversity are probable. In contrast, establishment of tree farms on previously cleared land would most likely provide habitat for native animals, and hence be ecologically beneficial. However, if tree farms are set up on previously cleared land adjacent to native vegetation the effects on local biodiversity are far more difficult to predict.

4.1 Scenario 1: replacement of native vegetation

4.1.1 Previous studies of biodiversity in plantations

Replacement of native vegetation with plantations is likely to impact negatively on a wide range of fauna. This is because traditional tree farms, consisting of young even-aged monocultures, provide less diverse habitats than mixed-aged multispecies native forests. Although this has rarely been examined in Australia, monocultural plantations elsewhere support fewer arthropods in the soil (Deharveng 1996 and references therein) and canopy (Chey *et al.* 1998), and fewer amphibians (Hansen *et al.* 1991), birds (Hansen *et al.* 1991; Christian *et al.* 1997; Hanowski *et al.* 1997) and mammals (Christian *et al.* 1997; but see Hansen *et al.* 1991), than native forests. Moreover, in the USA, poplar plantations carried fewer individuals and species of both birds and small mammals than did native grasslands (Christian *et al.* 1997). In Australia, bird species diversity was lower in a plantation of non-local *Eucalyptus botryoides* Smith than in adjacent natural forest dominated by *E. dives* Schauer (Woinarski 1979). Similarly, litter-inhabiting beetles were less abundant in young eucalypt plantations than adjacent mature native eucalypt forest (Bashford 1990), although such a comparison is confounded with stand age.

4.1.2 Loss of forest structural diversity

In Australia, loss of the structural diversity typical of natural mixed age forests by replacing them with even-aged stands is likely to reduce faunal diversity. Bird diversity is often correlated with the structural complexity of the habitat (e.g. Gilmore 1985). Accordingly, numerous studies have found that even-aged regrowth forests host fewer bird species and individuals than do mature forests with similar plant species compositions (e.g. Coulson and Coulson 1980; Loyn 1980; Kavanagh *et al.* 1985; Taylor *et al.* 1997; Hingston 2000). Numerous species of birds require mature trees for nesting (e.g. Mooney and Holdsworth 1991; Recher 1991), often those containing hollows (Haseler and Taylor 1993). Furthermore, the frequently used nesting materials of spider web and lichen are more abundant in mature, than regrowth, forests (Recher 1991). Removal of old trees with hollows and fissures also denies many arboreal mammals of nesting and roosting sites (Lunney *et al.* 1985; Taylor and Savva 1988; Lindenmayer *et al.* 1990b; Lunney *et al.* 1998), which is associated with declines in their populations (Braithwaite 1983a; Lunney 1987; Smith and Lindenmayer 1988; Milledge *et al.* 1991). Numerous ground-dwelling mammals also nest low in hollow standing trees or fallen logs (Dickman 1991). The absence of old trees also results in a lack of recruitment of dead wood to the ground, which is associated with declining species richness in carabid beetles (Michaels and McQuillan 1995) and declining species richness and abundance in lucanid beetles (Michaels and Bornemissza 1999) as even-aged regrowth develops. In contrast, densities of herbivorous insects are sometimes greater on young eucalypts than older ones (e.g. Greaves 1966; Ohmart *et al.* 1983). Understorey vegetation is also an important component of forest structural diversity. Small and medium-sized ground-dwelling mammals are richer in numbers of individuals and species in forests with dense understoreys (Catling and Burt 1995). Hence, replacement of native forests containing dense understoreys with plantations where understorey vegetation is discouraged by herbicide applications (e.g. Wilkinson and Neilsen 1990) is likely to adversely affect these animals.

4.1.3 Loss of plant species diversity

Lower plant species diversity in plantations than in native vegetation is also likely to impact on fauna because of the important habitat provided by plants other than eucalypts. Woinarski (1979) attributed the lower numbers of nectar, seed and fruit eating birds in a plantation of non-local *E. botryoides* to the reduced plant diversity in the plantation compared to the adjacent native forest. Furthermore, arboreal mammals were more common in Victorian montane ash forests where the basal area of *Acacia* spp. was greater (Lindenmayer *et al.* 1990a), as were sugar gliders *Petaurus breviceps* in southeastern NSW (Braithwaite *et al.* 1983b). *Allocasuarina littoralis* also provided important habitat for arboreal marsupials, particularly ringtail possums *Pseudocheirus peregrinus,* in southeastern NSW (Lunney 1987).

The absence of understorey plants and other non-eucalypt species from plantations is also likely to lower the diversity of arthropods because Woinarski and Cullen (1984) found marked differences between the compositions of arthropod communities on *Eucalyptus* species and other species in Victoria. Specifically, non-eucalypts supported more Arachnida, Coleoptera, Psocoptera, Hemiptera (excluding psyllids), Thysanoptera, Diptera, and total numbers of arthropods than did eucalypts per leaf area (Woinarski and Cullen 1984). Similarly, Hingston (1999) found that eucalypts generally supported different suites of native bees to most other plants.

However, some insect species may become more abundant in the absence of non-eucalypts. Defoliation of *Eucalyptus regnans* F. Muell. by the chrysomelid beetle *Chrysophtharta bimaculata* (Olivier) was much greater in stands where all *Acacia dealbata* Link had been removed than in mixed stands of the two species, while stands where 2.5% of *A. dealbata* saplings were retained suffered intermediate levels of herbivory (Greaves 1966). The reason for this phenomenon remains unknown, although Elliot (1990) noted that the closely related beetle *Pyrgoides orphana* defoliates *A. dealbata* during times of the year when *C. bimaculata* is dormant. It is possible that the two beetle species support the same predators and/or parasites and, hence, populations of these enemies are greater where both plants occur (P. McQuillan pers. comm.). Such indirect mutualisms have been documented in numerous other ecosystems (reviewed in Price *et al.* 1980). Indirect mutualisms between plants can also occur as a result of one plant providing resources which increase the longevity and fecundity of predators or parasitoids of another plant's herbivorous insects (reviewed in Price *et al.* 1980). These resources include nectar and pollen from flowers, as well as honeydew from sap-feeding insects. Plants growing in close proximity may also reduce the ability of each other's herbivores, or their predators or parasites, to locate their host plant. This may involve masking the host's smell or by producing odours which repel the insects associated with the other plant (reviewed in Price *et al.* 1980).

Lower diversity of eucalypt species in plantations than in native vegetation is also likely to impact on fauna. Native eucalypt forests usually comprise two or more eucalypt species, with many herbivorous insect species being restricted to one species (e.g. Wotherspoon 1998) and overall arthropod communities differing between species (Ohmart *et al.* 1983; Woinarski and Cullen 1984). Hence, the replacement of several eucalypt species with a monoculture is likely to result in less diverse insect herbivore and overall arthropod communities. The absence of particular herbivorous insects may have adverse effects on other animals which feed on them (Recher 1991). For example, pardalotes feed largely on lerp from psyllids (Woinarski 1985), and this group of insects is highly host specific (Woinarski and Cullen 1984; Wotherspoon 1998). However, this change may facilitate increases in the population sizes of herbivorous insect species which are able to feed on the cultivated species (Woinarski 1979; Stone 1991). Such high densities may encourage large numbers of leaf-gleaning insectivorous birds to colonise plantations (Woinarski 1979), and could also lead to increased populations of other predators and parasitoids.

Replacement of native eucalypt forest with another species may also affect abundances of arboreal marsupials and birds because eucalypt associations differ markedly in the numbers of these animals which they harbour (Braithwaite 1983a; Braithwaite *et al.* 1988, Braithwaite *et al.* 1989). Lunney (1987) also found that while arboreal marsupials were regularly observed in some eucalypt species, they were virtually absent from other species in the same area. In southeastern NSW, abundances and species richness of arboreal marsupials were correlated with foliar potassium, nitrogen and phosphorus levels, as well as basal areas of eucalypt species with nutrient rich foliage (Braithwaite 1983a). However, basal area of eucalypt species with low levels of potassium, nitrogen and phosphorus was negatively correlated with marsupial abundance and species richness (Braithwaite 1983a). In the same study area, bird species richness was correlated with magnesium levels in the eucalypt foliage (Braithwaite *et al.* 1989).

The change from a native forest comprising several eucalypt species to a single eucalypt species in a plantation may also have deleterious effects on animals which feed from eucalypt flowers. This is because a single species will concentrate all of its flowering within a few weeks, whereas mixed-species forests typically produce flowers over a long period because each species has a different flowering phenology (e.g. Goldingay 1990; Hingston 1997). Hence, mixed species assemblages provide floral resources all year round (Goldingay 1990). When a pollinator lives longer than the duration of a single species' flowering, other plants with different flowering phenologies are necessary for the maintenance of the pollinator population in the area (Heinrich and Raven 1972; Faegri and van der Pijl 1979; Augspurger 1980; Williams and Batzli 1982). An example of such mutualism between sequentially flowering plants that shared the same pollinator was found by (Waser and Real 1979). When drought led to poor flowering of *Delphinium nelsonii,* the population of hummingbirds, which pollinated both *D. nelsonii* and *Ipomopsis aggregata*, was adversely affected. This in turn resulted in poor seed set in the latter self-incompatible species (Waser and Real 1979). Plant associations comprising more than one eucalypt species can also involve mutual support of pollinators when they exhibit overlapping flowering phenologies. An example of this occurs in Tasmania where swift parrots, *Lathamus discolor*, forage on *E. ovata* Labill. during spring in seasons in which *E. globulus* Labill. flowering is poor (Brown 1989; Brereton 1996). Furthermore, non-local eucalypts used in plantations may not support the local flower-feeding animals. In Tasmania the flowers of the eucalypt grown most frequently in plantations, *E. nitens* (Deane and Maiden) Maiden are not visited by birds (Hingston unpubl. data) in contrast to most native eucalypts (Hingston 1997).

Similarly, replacement of mixed-species forests with monoculture plantations is likely to be detrimental to animals that gather food from under loose bark. In a study conducted in wet sclerophyll forest comprising six major eucalypt species in southeastern NSW, it was found that this floristic diversity was a major component of the habitat of the yellow-bellied glider *Petaurus australis* Shaw (Kavanagh 1987). This was because the four species that shed bark, did so at different times of the year. As a result the gliders, which fed primarily by peeling away decorticating bark in search of arthropods and honeydew, foraged on different tree species at different times of the year. Hence, Kavanagh (1987) concluded that habitats comprising only one or two eucalypt species would be unable to support yellow-bellied gliders all year round. In accordance with this, densities and species richness of arboreal marsupials were correlated with eucalypt species diversity in southeastern NSW forests (Braithwaite *et al.* 1983b). Many other animals which also use decorticating bark as a foraging substrate may also be adversely affected in the same way, including scansorial mammals such as *Antechinus* spp. (Dickman 1991) and numerous bird species (Recher *et al.* 1985; Recher 1991).

4.1.4 Fragmentation of native forest

Impacts of clearing native vegetation affect, not only the areas cleared but also, surrounding areas due to the fragmentation of habitat that this entails. Isolation of small populations may reduce pollinator abundance (Powell and Powell 1987; Jennersten 1988) and richness (Jennersten 1988; Aizen and Feinsinger 1994a), amounts of pollen transferred (Aizen and Feinsinger 1994b; Groom 1998), and/or increase the proportion of self-pollination (Jennersten 1988; Oostermeijer *et al.* 1992; Lamont *et al.*

1993; Aizen and Feinsinger 1994b; Potts and Jordan 1994). High levels of selfing and reproductive failure in small remnant populations on road verges and farmland has been documented in several eucalypt species (e.g. *E. rhodantha* - Sampson *et al.* 1996; Hopper 1997 and *E. globulus* - Hardner *et al.* 1996; Borralho and Potts 1996).

4.2 Scenario 2: replacement of farmland

Establishment of eucalypt tree farms in ecologically degraded areas, such as farmland, may benefit native fauna by providing habitat with some affinities to native vegetation. Phytophagous insects can be quite common in eucalypt plantations in Australia (Woinarski 1979). Fallen leaves also provide food for detritivores. These can form the basis of food chains involving predaceous arthropods and insectivorous vertebrates. In the USA, birds were more abundant in poplar plantations than in cropping land (Christian *et al.* 1997; Hanowski *et al.* 1997) or pasture (Christian *et al.* 1997). However, these plantations supported no more small mammal individuals than did cropping land and sometimes fewer individuals than did pasture (Christian *et al.* 1997). Furthermore, some species of birds were less common in plantations than in row crops and/or pasture (Hanowski *et al.* 1997).

4.3 Scenario 3: establishment adjacent to native vegetation

4.3.1 Direct effects on biodiversity in adjacent vegetation

Planting non-local eucalypts near native vegetation can affect densities of phytophagous insects on the native eucalypts if they can also feed on the introduced species. In northern NSW, planting non-local *E. dunnii* Maiden attracted the Christmas beetle *Anoplognathus chloropyrus* away from the native *E. grandis* Hill ex Maiden (Carne *et al.* 1974). However, in Tasmania widespread establishment of the non-indigenous *E. nitens* in plantations appears to have facilitated increased abundances of *Chrysophtharta bimaculata* in native forest. This beetle has exhibited dramatic increases in abundance as the area of *E. nitens* plantation has increased (Stone 1991). This may be due to higher larval survival and growth rates in the absence of predators and parasites on leaves of *E. nitens* than on leaves of *E. regnans* (Elek 1997), the native species upon which they grow fastest (Greaves 1966). Furthermore, the larvae developing more rapidly on leaves of *E. nitens* than those of native species (Elek 1997; see also Greaves 1966) reduces the amount of time available to predators and parasites to control their populations (Greaves 1966). Increased abundances of this beetle impact particularly heavily on the native hosts, *E. regnans* and *E. delegatensis* R. Baker, because females prefer to oviposit on these species than *E. nitens* (Elek 1997). Increases in the population sizes of herbivorous insect species that are able to feed on the cultivated species (e.g. Woinarski 1979; Stone 1991) may also alter abundances of their predators and parasitoids in nearby native vegetation. If the predators and parasitoids were attracted away from native vegetation to the greater food availability in the plantation, their abundances in native vegetation would decline. However, if the greater food availability in the plantation facilitated an increase in the overall population size of the predators and parasitoids this could translate to greater numbers occurring in the adjacent native forest.

4.3.2 The impact of hybridisation on biodiversity

Hybridisation between non-local eucalypts in plantations and local eucalypts in adjacent native forest may alter the abundance of herbivorous insects and pathogenic fungi. In the only detailed study of a eucalypt hybrid zone to date, it was shown that the hybrid zone between *E. amygdalina* Labill. and *E. risdonii* Hook. f. supported more insect and fungal taxa than adjacent parent populations (Whitham *et al.* 1994). Hybrid plants also supported greater numbers of insect taxa than pure parental types within the hybrid zone, a trend also detected in a planting of these same species and hybrids in a randomized block design (Dungey *et al.* 2000). Hybrids between other species have also been reported as more susceptible to fungal attack than their parental species when grown in the same trial (Dungey *et al.* 1995, 1997). Hence, this phenomenon has a genetic basis (Whitham *et al.* 1999). This may be due to the breakup of coadapted gene complexes following genetic recombination in advanced hybrid generations, rendering hybrids more vulnerable to insect attack (Whitham *et al.* 1994). However, in some cases the F_1 hybrids themselves may be more susceptible to herbivores than their parental species (reviewed in Fritz 1999 and Whitham *et al.* 1999; Dungey *et al.* 2000).

Floate and Whitham (1993) proposed a model by which hybridisation between plants could facilitate evolutionary shift of herbivorous insects from one species to the other. According to this model, hybrids with intermediate characteristics act as evolutionary 'stepping-stones' allowing a gradual accumulation of the mutations in the insect necessary for it to expand its feeding niche onto the other species. Hence, the greater the introgression between species the easier it becomes for insects to evolve these adaptations. In support of their argument, Floate and Whitham (1993) cited the case of hybridisation between *Populus angustifolia* and *P. fremontii.* In this case, monophagous gall-forming insects that fed on *P. angustifolia* were also recorded from F1 hybrids and backcrosses to *P. angustifolia*, but not from *P. fremontii* with which no backcrossing occurred. In contrast, none of the gall-forming insects specific to *P. fremontii* were recorded from hybrids. This hypothesis may also be applicable to the predators and parasites of these herbivores, as well as plant parasites and pathogens, and possibly even pollinators (Floate and Whitham 1993). However, Pilson (1999) was critical of this hypothesis on the basis of its dependence on additive inheritance of genes controlling host recognition and survival by herbivores.

4.3.3 Impact of plantation eucalypts on pollination in native vegetation

It is difficult to predict the impact of establishment of stands of non-local eucalypts on pollination in nearby native forest because the relationship between plants that share floral visitors may involve competition or mutualism. Species whose flowering phenologies overlap those of the introduced eucalypt may receive fewer visits by pollinators if these animals feed from flowers of the non-local species instead of the native species (Free 1968; Green and Bohart 1975; Thomson 1978; Campbell and Motten 1985; Rathcke 1988). However, the provision of additional floral resources by an introduced eucalypt may enhance pollinator visitation rates to native species by increasing the pool of attraction in the area (Thomson 1978, 1981; Campbell and Motten 1985). Furthermore, as local flowering intensity of eucalypts varies enormously between years (Brown 1989; Moncur 1993; Moncur *et al.* 1994b; Brereton 1996), establishment of another species with similar flowering phenologies may maintain the population sizes of eucalypt pollinators during years when flowering of the native species is poor.

Reproductive success may also be adversely affected in synchronously flowering co-occurring species if pollen is transferred between species as a consequence of a lack of pollinator constancy (Waser 1978). This may involve reduced male fitness through loss of pollen via transfer to stigmas of other plant species (Campbell and Motten 1985) or lower female fitness through the clogging of the stigma with the pollen of other plant species (Stucky 1985; Galen and Gregory 1989). Interception of pollen by other plant species also reduces the average distance of pollen transfer to conspecific stigmas (Campbell 1985).

5. A framework for risk management

A framework for the management of genetic pollution from farm forestry with eucalypt species and hybrids is detailed below. Where possible general guidelines that will help minimise this risk are given based on available information. However, research is clearly required to fine-tune these guidelines (see Section 6).

Risk assessment will need to integrate information on the probability of an event occuring with information on the effect of the event if it does occur. The probability of genetic pollution occuring will depend upon the likelihood of hybrid formation and the fitness of the F_1 and advanced generation hybrids relative to the native species. The consequences and acceptability of any given level of risk will mainly depend upon the conservation value of the adjacent eucalypt forest ecosystem and eucalypt gene pools.

The biological framework for assessing the risk of genetic pollution is given in Figure 5.1 (see also Drake 1980) which is based on the classification of barriers to gene flow in plants detailed in Table 5.1. Four general factors act to influence and/or prevent the success of hybridisation and gene flow, namely geographic and ecological isolation and reproductive and post-zygotic barriers (Levin 1978; Table 5.1). Hybridisation and gene flow between previously isolated populations that differ in their genetic structure will only occur if they are anatomically, physiologically and genetically compatible. If hybrids are produced from successful interbreeding then all the stages of development starting from the zygote through to reproductive maturity of the hybrid, have to be successful. Combined with this, later generation hybrid break-down resulting in reduced fitness of F_2 or backcrossed progenies can reduce the potential for introgression.

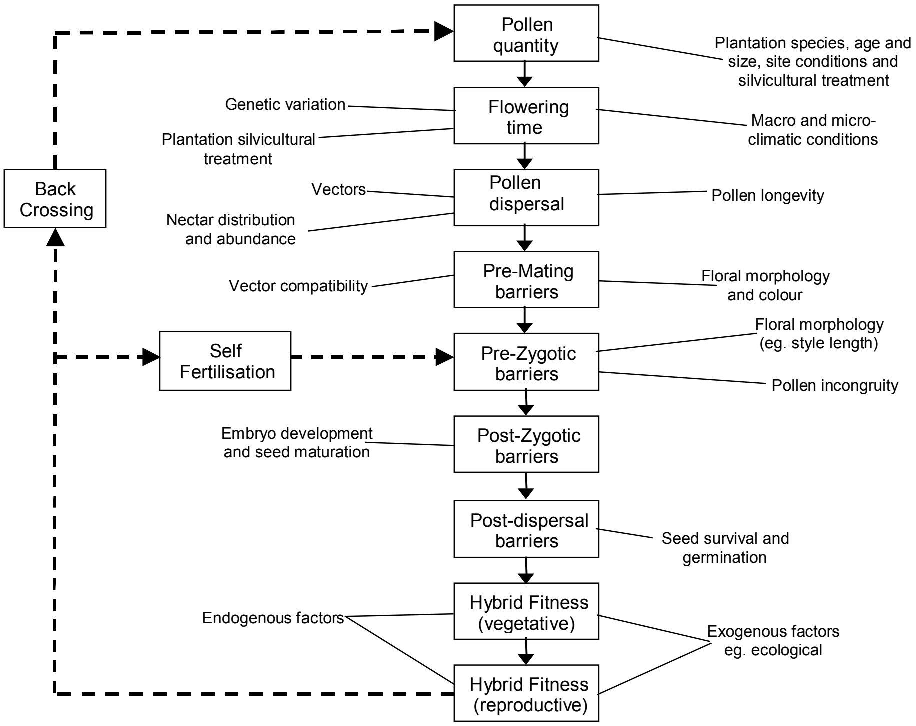

Figure 5.1 Framework for assessing the risk of genetic pollution

Table 5.1 Classification of isolating mechanisms in plants.
Gene flow between two taxa can be arrested at any of these stages (from Levin 1978).

Spatial
1. Ecological

Reproductive
2. Temporal divergence
    (a) Seasonal
    (b) Diurnal
3. Floral divergence
    (a) Ethological
    (b) Mechanical

Premating

Postmating

4. Reproductive mode
5. Cross-incompatibility
    (a) Pollen-pistil *Prezygotic*

    (b) Seed *Postzygotic*
6. F_1 hybrid inviability or weakness
7. F_1 hybrid floral isolation
8. F_1 hybrid sterility
9. Hybrid breakdown

5.1 Identification of conservation values

The first element in risk assessment should be the identification of the conservation value of eucalypt forest ecosystems and gene pools likely to be affected by pollen-mediated gene flow from eucalypt plantings. A key element in such assessment is the presence of endangered or threatened species in the vicinity. Eucalypt species currently on the Endangered Species Protection Act 1992, Schedule 1 are listed in Appendix 2. However, as the current state of eucalypt taxonomy is continually changing and many new taxa are being discovered or described as gene pools are more fully explored, a boarder conservative approach is required. At the gene pool level, such an approach should account for natural patterns of intraspecific genetic or ecological diversity, and biologically significant areas of natural hybridisation and intergradation (Whitham *et al.* 1991; Hopper 1997). Moritz (1999) argues that the goal of conservation should be to conserve ecological and evolutionary processes, rather than to preserve specific phenotypic variants which are the products of those processes. In this respect it was suggested that we should seek to conserve historically isolated, and thus independently evolving, sets of populations (i.e. Evolutionarily Significant Units). This can require manipulation of the component 'Management Units', some of which may be phenotypically distinct. It was suggested that mixing within 'Management Units' might allow augmentation of remnant populations that are showing signs of inbreeding depression or increased fragmentation. The racial classification of *E. globulus* ssp. *globulus* (Dutkowski and Potts 1999) would provide an initial framework for such management units for that species. The conservation value and management of fragmented forest remnants in the rural landscape is of special relevance to farm forestry (e.g. Prober and Brown 1994; Byrne and Macdonald 2000) (see 3.3.2). Such fragments are often of high conservation value and a living record of eucalypt distributions and variation patterns prior to European settlement.

5.2 Pollen quantity: 'Source vs sink'

5.2.1 Population size

There are several reports of hybridisation rates increasing with increasing rarity in forest trees, suggesting that as the scale of planting increases the magnitude of gene flow into native forest will increase (see Gliddon 1994). For example, gene exchange between *Nothofagus nervosa* and *N. obliqua* in southwest Argentina appeared limited to those special cases where *N. nervosa* individuals were rather isolated and surrounded by many *N. obliqua* trees (Gallo *et al.* 1997). The purity of remnant cork oak (*Quercus suber*) in Portugal and Spain is threatened by hybridisation with the surrounding more common holm oak (*Q. ilex*) (Varela 1995). Such pollen swamping has also been reported in *Eucalyptus* (Potts 1990; Potts and Wiltshire 1997). *Eucalyptus risdonii* and *E. amygdalina* are two closely related species of eucalypts that hybridise naturally (Potts and Reid 1988). Levels of hybridisation at the boundary of large stands of the two species average 3%, but in small patches this increases to more than 14% with some individuals exceeding 75% (Potts and Wiltshire 1997). Of the 238 endangered taxa declared in 1989 in southwestern Australia, 176 are woody long-lived perennials such as mallee eucalypts (Hopper 1997). In several of these taxa, significant hybridisation has been detected. High levels of interspecific hybridisation (up to 47% of the seeds assayed, with no mature hybrids in populations) were detected in some small populations of the rare clonal mallee, *Eucalyptus argutifolia* using isozyme markers (Kennington and James 1997). The increased proportion of hybrids within smaller populations, would enhance the potential for interspecific gene flow, because of the greater probabilities of the hybrids back-crossing with the rarer species. Eucalypts exhibit marked inbreeding depression (see Potts and Wiltshire 1997). Increased inbreeding in small populations (Potts and Jordan 1994; Borralho and Potts 1996) would therefore be also expected to increase the relative fitness of the hybrids compared to the pure species seedling with which they would be competing (Lopez *et al.* 2000b).

* 8 *Isolation distances should be greater as the size of the 'source' population increases relative to the 'sink' population.*

5.2.2 Age to first flowering

The age of first flowering under plantation conditions varies markedly between and within species (reviewed in Eldridge *et al.* 1993 and House 1997; Table 5.2) and depending on rotation age will determine the interval over which the plantation can potentially produce pollen. The age of first flowering can be affected by environmental and genetic factors and there is the opportunity to delay the onset of flowering in plantations to minimise the risk of genetic pollution. Within *E. globulus*, for example, there is a large amount of genetic variation in the species for the age to first flowering. Some families and localities rarely flower under normal plantation conditions whereas others may flower in the first 2-3 years (Chambers *et al.* 1997; Dutkowski and Potts 1999). Occasional precocious flowering may occur in seedlings in the nursery in many species (e.g. *E. grandis*, see Eldridge *et al.* 1993) which is believed to be under strong genetic control. In the case of *E. globulus*, seedlings of the precocious flowering Wilsons Promontory race (Lighthouse) have been observed with flower buds in their first year in the plantation (Potts unpubl. data). Within populations, the onset of first flowering is genetically independent of the transition to adult foliage (*E. globulus* Jordan *et al.* 1999; *E. risdonii-tenuiramis* Wiltshire *et al.* 1998) and growth and wood density (Chambers *et al.* 1997) which means delayed flowering can be selected without compromising economic traits. Paclobutrazol is a chemical widely used to enhance and accelerate flowering in eucalypts (Moncur *et al.* 1994b; Moncur and Sunil 1998). This chemical could be used to allow breeding and deployment from plants selected for delayed onset of flowering or reduced flower abundance.

* 9 *The timing of the onset of first flowering and flower abundance can be genetically manipulated relatively simply to reduce the risk of genetic pollution.*

Table 5.2 Age of first flowering for the major plantation eucalypts.
Reports of the age of first flowering or age of the onset of first general flowering in plantations for the major plantation eucalypt species.

Species	Age of first flowering	Reference
Temperate species		
E. globulus ssp. *globulus*	May not flower heavily, even at wide spacing until 7-10 years	Eldridge *et al.* 1993
rotation age: pulpwood 10-12 years	Only 10-15% of trees reproductive by age 4 years in Tasmanian plantations, considerable genetic variation between localities and families	Chambers *et al.* 1997 Dutkowski and Potts 1999
	Exposed coastal cliff top populations are precocious	Jordan *et al.* 2000
E. nitens	May not flower heavily, even at wide spacing, until 7-10 years	Eldridge *et al.* 1993
rotation age: pulpwood 12-17 years	Shy flowerer, with a period of at least 5 years usually elapsing before flower buds are initiated; it flowers infrequently and bears few seeds.	Moncur *et al.* 1994a
	Some first flowering may occur at age 3 years but most occurs at age 5	Wayne Tibbits pers. com.
	1-2% of trees flowering by age 3.5 years 25-44% of trees flowering by age 5 years in 3 Tasmanian trials	Dutkowski and Williams (unpubl data) CRCSPF
Tropical and subtropical species		
C. variegata	3-4 years	Nikles *et al.* 2000
E. grandis	First flowering in plantations generally occurs at 2-3 years	Eldridge *et al.* 1993
E. pellita	Sometimes 12 months, normally 2-3 years	David Lee (pers. com.) QFRI
E. pilularis	2 years at 1 site, abnormally early	David Lee (pers. com.) QFRI com.)
E. cloeziana	3 years (but provenance variation)	David Lee (pers. com.) QFRI
E. dunnii	Slow to reach flowering age, with only a few in flower at 10 years 7-10 years	Graca (1987) cited in Eldridge *et al.* 1993 David Lee (pers. com.) QFRI

Table 5.2 Age of first flowering for the major plantation eucalypts. *cont.*

Dry land species

E. cladocalyx	unknown	
E. occidentalis	unknown	
E. camaldulensis	Precocious flowering in seedlings reported	see House 1997
	8.5% at age 9 yr, Wellington catchment, WA	Richard Mazanec (pers. com.) CALM
E. sideroxylon/tricarpa	<0.2% at age 7 yr, Wellington catchment, WA	Richard Mazanec (pers. com.) CALM
E. kochii	c. 4 yr, but will be harvested for first oil harvest at 4 years, coppice regrowth harvested every 2 years	M. Byrne (pers. com.) CALM
E. horistes	c. 4 yr, but will be harvested for first oil harvest at 4 years, coppice regrowth harvested every 2 years	M. Byrne (pers. com.) CALM
E. polybractea	unknown	

5.2.3 Flowering abundance

In addition to genetic effects, environmental and silvicultural factors are important in determining the intensity of flowering in eucalypts (Eldridge *et al.* 1993; Moncur and Hasan 1994; Moncur *et al.* 1994a; Moncur *et al.* 1994b; House 1997). A typical pattern in pulpwood plantations is for flower bud crops to occur at or just after canopy closure and then these are substantially reduced in later years when trees are under intense competition. Flower bud abundance is often site dependent and there are numerous examples where sites that are within the normal planting zone for a species are not necessarily sites where good flowering may occur. For example, Moncur *et al.* (1994a) notes that the altitudinal range of most plantings of *E. nitens* in Tasmania is outside that for optimal flower production. Environmental conditions appeared more favorable for flower and seed production at low altitudes where maximum and minimum temperatures were higher and rainfall lower during the induction period, than at higher altitudes. Sites, which are good for growth, are not necessarily good for flower initiation. It was also noted that spacing is an important factor in determining flowering intensity. For example, widely spaced *E. nitens* trees with limited competition produce significantly more flowers (even on a per hectare basis) than trees that were closely spaced (Moncur *et al.* 1994a; Williams 1999). Indeed, Moncur (1994a) indicates that there is a positive correlation between flower buds produced and light interception. This is consistent with the general observation of greater flowering on plantation edges. Indeed, poor flowering in plantations of *E. globulus* and *E. nitens* has for a long time delayed progress in breeding and deployment programs (Moncur and Sunil 1998). *E. globulus* is renowned for its poor flowering in many plantation sites, particularly in Western Australia. Application of nitrogen fertiliser has also been shown to increase flower bud density in *E. nitens* (Williams 1999). In *E. dunnii* plantings in Brazil, Graca (1987) recorded that flowering was increased at higher latitudes and lower average temperatures in the coldest month. Stands that were thinned early or trees at stand edges also flowered more frequently than those thinned late or in the middle of the stand. Flowering abundance in most species will therefore be expected to decrease with the high stocking rates used for pulpwood compared to sawlog regimes.

* 10 *Silvicultural regimes used in farm forestry such as increased spacing between trees required in drier regions, plantings with a high edge to area ratio and thinning for sawlog production may enhance flower and hence pollen production and increase the risk of genetic pollution***.**

* 11 *Flowers are often more abundant on plantation edges and their abundance could be reduced by surrounding plantations with guard rows of reproductively inert stock.*

5.2.4 Male sterility

While considerable effort is focusing on the genetic engineering of sterility in forest trees, including eucalypts (see Table 3.4), there is the possibility of exploiting naturally occurring male sterility to reduce the risk of genetic pollution. There are several reports of male sterile eucalypts in natural populations (see Potts and Wiltshire 1997). For example, Ellis and Sedgley (1993) report that 57% of *E. leucoxylon* trees examined were male sterile. There are no reports involving the main plantation species in Australia nor has a genetic basis to this sterility been demonstrated in most cases. Nevertheless, in Brazil partial male sterility appears to be maintained after grafting and has been exploited for production of F_1 hybrid seed (Campinhos *et al.* 1998).

5.3 Divergence in season of flowering

Seasonal differences in flowering time are one of the major pre-zygotic barriers to gene flow within *Eucalyptus* (Pryor 1976; Drake 1980). Exactly how divergent flowering times must be before gene flow is reduced is unclear at present. Nevertheless, Adams *et al.* (1992) reported that genetically based differences in peak flowering time between Tasmanian and Victorian provenances of *E. regnans* of only 2 weeks appeared to reduce inter-provenance crossing in a seed orchard to only 65% of that expected under random mating. Gene flow was also markedly asymmetric owing to the protandrous flower development of most eucalypts that favours pollen flow from late- to early-flowering trees.

* 12 *Differences in flowering time will be a major barrier to gene flow between plantation and native forest eucalypts.*

* 13 *Because pollen is usually shed before the eucalypt stigma becomes receptive, later flowering trees are more likely to pollinate early flowering trees than visa versa.*

Generalised flowering times of the eucalypts can be found in most regional and national taxonomic works on eucalypts (e.g. Boland *et al.* 1980; Boland *et al.* 1985; Brooker and Kleinig 1996; see also House 1997; Potts and Wiltshire 1997; Keatley and Hudson 1998 for specific references). Species within the genus show great variation in flowering time. Some broad taxonomic trends have been reported. Noble (1989)'s review of species in Boland (1980) suggested that in general *Monocalyptus* species tended to flower in spring (48%) whereas *Symphyomyrtus* species tended to flower in summer (45%). At a more local level, the Tasmanian peppermint species (Series *Piperitae*) tend to be spring flowering whereas the ash species (Series *Oblique*) were autumn flowering (Potts and Reid 1983). In a study of 51 species, Keatley and Hundson (1998) found species with large buds or fruits, or large umbel volumes tended to flower earlier in the growing season. They also suggested that the *Symphyomyrtus* sections (*Adnataria*, *Bisectaria* and *Maidenaria*) had discernable bud development and flowering times. Generalised flowering times of the major plantation species are given in Table 5.3. However, flowering within eucalypt species may be highly variable and influenced by numerous factors (see Eldridge *et al.* 1993; House 1997; Potts and Wiltshire 1997).

Key points are summarised below.

(i) Although the peak flowering may be regular in some species, others can flower intermittently over the greater part of the year and sporadic out-of-season flowering can occur (see examples in House 1997)

(ii) Flowering time may vary from stand to stand, and tree to tree within stands of the one species. For example, Pook *et al.* (1997) only observed synchronous production and flowering of buds on all trees in a *Corymbia maculata* stand once in 15 years. There is some suggestion that younger trees flower earlier than older ones (House 1997).

(iii) Individual trees may flower over considerable time (e.g. *E. globulus* 37 days average - Gore and Potts 1995; *E. regnans* 43 days average - Griffin 1980; *E. urnigera* up to 100 days - Savva *et al.* 1988a).

(iv) Heavy and light flowering years occur in many species and in cases individual trees may not be synchronised in this respect. Species such as *C. maculata* may only flower heavily every 4 to 10 years depending on environmental conditions (see House 1997).

(v) Flowering is usually delayed at higher elevations and appears to be related to the heat summation. Moncur *et al.* (1994a) note that the flowering time of *E. nitens* was delayed by 21 days going from 40 to 720 m altitude. They also noted that trees with larger bud crops tended to flower earlier and for longer. In *E. urnigera*, a low altitude population flowered over 3 months earlier than a high altitude population on the same mountain (Savva *et al.* 1988a). Local site conditions can cause differences in flowering between sub-populations.

(vi) Within stands/sites, variation in flowering time can be under strong genetic control (e.g. *E. globulus* Gore and Potts 1995) and consistent from year to year (Griffin 1980).

(vii) There is often large genetic based variation in flowering time within species. For example in common environment trials, western and mainland races of *E. globulus* flower much later than races from eastern Tasmania and the Furneaux group (Gore and Potts 1995). *E. nitens* from the Torrongo provenance flowers slightly later than the closely related *E. denticulata* on the same site.

(viii) Interspecific hybrids tend to exhibit flowering times intermediate between their parental species (Pilipenka 1969; Potts and Reid 1985; Lopez *et al.* 2000a), although there are exceptions (e.g. *E. ovata* x *globulus* Lopez *et al.* 2000a).

* 14 *Flowering time can be markedly influenced by site and seasonal effects requiring generalised flowering information to be supplemented with local observation. Nevertheless, flowering time is also under strong genetic control and there is often large genetic based variation within the plantation species that could be exploited to minimise flowering overlap with native provenances or species.*

Table 5.3 Flowering season of the major plantation eucalypts.
Reports of flowering time of the major plantation eucalypt species in *native stands* or in Australian plantations. Information on flower bud size, number of buds per umbel and flower colour is compiled from Brooker and Kleinig (1996).

Species	Flowering time	Reference
Temperate species		
E. globulus ssp. *globulus*	*Sept-Dec*	Boland *et al.* 1985
Bud width 1.8 cm, 1(3 rare)/umbel	*Sept-Dec*	Williams and Potts 1996
White flowers	*May-Jan*	P. Gore (pers. com.)
E. nitens	*Jan-Mar*	Boland *et al.* 1985
Bud width 0.3 cm, 7/umbel	*Jan-Mar* (Myrtle Bank, Tas.)	Tibbits 1989
White flowers	*Dec-Feb* (Huntsman, Tas.)	Barbour unpubl. 1999
Tropical and subtropical species		
E. grandis Bud width 0.5 cm, >7/umbel White flowers	*Apr-Aug*	Boland *et al.* 1985
E. pellita Bud width 1.2 cm, >7/umbel White flowers	*Dec-Feb*	Boland *et al.* 1985
E. pilularis Bud width 0.5 cm, 7-15/umbel White flowers	*Sept-Mar*	Boland *et al.* 1985 Florence 1964
E. cloeziana Bud width 0.4 cm, 7/umbel White flowers	*Nov-Feb*	Boland *et al.* 1985
E. dunnii	*Mar-May*	Boland *et al.* 1985
Corymbia citriodora	*June-Nov*	Boland *et al.* 1985
Bud width 0.6 cm, 3/umbel Creamy flowers	*Jan-Apr(-June)*	Hill and Johnson 1995
Corymbia henryi	*Erratic,* *Mar, July-Sep, Nov-Dec* *Prolific flowering only occurs at intervals of several years*	Hill and Johnson 1995
Corymbia maculata	*May-Sept*	Boland *et al.* 1985
Bud width 0.7 cm, 3/umbel White to cream flowers	*Erratic, May-June, Aug-Sept* *Prolific flowering only occurs at intervals of several years*	Hill and Johnson 1995
Corymbia variegata	Oct-Nov	David Lee (pers. com.)
	Jan, Apr	Hill and Johnson 1995

cont.

Dry land species		
E. cladocalyx	*Jan-Apr*	Boland *et al.* 1985
E. occidentalis	*Apr-May*	Boland *et al.* 1985
Bud width 0.7 cm, 7 (9 rare)/umbel White flowers	*Mar-May, sometimes to Aug*	Chippendale 1973
E. camaldulensis	*Dec-Feb*	Boland *et al.* 1985
Bud width 0.6m, 7-11/umbel White flowers	*July-Feb*	Brooker and Kleinig 1996
E. sideroxylon	*May-Oct*	Boland *et al.* 1985
Bud width 0.5m, 7/umbel White, pink, red or pale yellow	*May-Nov*	Brooker and Kleinig 1996
E. tricarpa		
E. kochii	*Sept-Jan*	Chippendale 1973
E. horistes		
E. polybractea	*Mar-June*	Boland *et al.* 1985

5.4 Pollen dispersal

5.4.1 General

The distance and levels of pollen-mediated gene flow are a major component in assessing the risk of genetic pollution. However, even for well studied crop plants data on isolation with distance is highly variable even within a single crop and there is often insufficient data in the literature to allow reasonably confident predictions to be made of the levels of contamination (Gliddon 1999).

Studies of pollen-mediated gene flow in plants almost universally describe a highly leptokurtic distribution of pollen from a source (reviewed by Levin and Kerster 1974; Levin 1981) (see also Figure 5.2). However, it is important to note that, pollen-mediated gene flow is one of the least well understood parameters of plant populations (Levin 1981; Ellstrand and Marshall 1985), although this could change rapidly with the advent of molecular marker technologies. Pollen-mediated gene flow is a fluid parameter and there is a clear difference between pollen dispersal and realised gene flow (Levin 1981). Little is known about variation in pollen dispersal capabilities among individuals and populations and how this changes through time and space, particularly in forest trees. For example, Cambell *et al.* (1989) showed that gene flow distances change over 3 fold among populations and years and shifted over the season within a given population and at an individual level. Dispersal distances were also affected by floral morphology. In radish, the rate of immigration has also been shown to vary over seasons (Ellstrand *et al.* 1989) and to be affected by the spatial distribution of plants (Ellstrand and Marshall 1985). In animal pollinated plants, factors such as pollen 'carryover' and the disproportionate genetic effects of low-frequency long-distance pollen dispersal are important. Other intrinsic factors affecting pollen-mediated gene flow include: the shape, size and density of both donor and recipient populations; the height of plants and characteristics of intervening vegetation; as well as the spatial and temporal dynamics of seed productions, breeding system (degree of self-incompatibility) and life history (summarised in Raybould and Gray 1993).

Pollination mechanisms are a major determinant of gene flow with levels of gene flow increasing through self, animal and wind pollinated species (Govindaraju 1988). A comparison of 14 gymnosperm and 7 angiosperm forest tree species (including 3 eucalypt taxa *E. caesia* ssp. *magna*, *ssp. caesia* and *E. pauciflora*) showed high levels of total gene flow among gymnosperms while levels varied from high to low in the angiosperm trees (Govindaraju 1989). High levels of long distance gene flow were found in wind-pollinated gymnosperms and oaks. By comparing population differentiation for nuclear and maternally inherited markers for the 6 wind pollinated forest tree species, Ennos (1994), estimated rates of pollen migration far surpass estimated rates of seed dispersal, particularly in the oaks. This would also appear to be the case for the animal pollinated eucalypts, *E. nitens* (Byrne and Moran 1994; Byrne *et al.* 1998) and *E. kochii* (Byrne 1999; Byrne and Macdonald 2000). On average, Adams (1992) suggests that insect–mediated pollen dispersal may not be much greater than the mean distance between nearest flowering trees. However, long distance dispersal may occur as several studies have shown that the proportion of detected immigrants into a stand was unrelated to the distance mother trees were from the edge of the study plot (Adams 1992; see also Barbour *et al.* 2000).

The level of pollen-mediated gene flow in natural populations and crop/weed complexes is proving much more extensive than previously believed (e.g. Wilson 1990; Raybould and Gray 1994). High levels of long-distance pollination have recently been revealed in several wind- and animal-pollinated forest tree species. For example, paternity studies indicated a *Pinus flexis* population received 1-7% pollen immigration from populations greater than 2 km away (Schuster and Mitton 2000). Similarly, in a paternity analysis of a stand of 62 adult bur oaks (*Quercus macrocarpa*), Dow and Ashley (1998) found 57% of acorns from a small stand of bur oak were pollinated from trees outside the stand and the average within-stand pollination distance was 75m. In the case of a 5.8 ha mixed oak stand (*Q. robur* and *Q. petraea*), Streiff *et al.* (1999) found 65-69% of offspring were pollinated by male parents from outside the study site. Within the stand there was an excess of nearby matings and the average pollen dispersal curve was fitted to a negative exponential curve. However, extrapolation of this curve was insufficient to explain the level of long-distance pollination events. Strong directionality to pollen dispersal has been reported in wind-pollinated species (*Quercus* - Streiff *et al.* 1999; *Pinus* - Burczyk *et al.* 1996; *Pseudotsuga* - Burczyk and Prat 1997) and male mating success increased with tree size (Burczyk *et al.* 1996). In the case of animal pollinated species, paternity analyses revealed that 90-100% of the progeny from an isolated patch of a Neo-tropical tree species (*Spondias mombin*) were derived from the main population 800-1000m away (Nason and Hamrick 1997). This tree species was pollinated by a variety of generalist insects. By comparison monoecious, *Ficus* species were rarer in the forest and pollinated by species-specific wasps. In this extreme case, pollen dispersal distances of routinely 6-14km were recorded (Nason and Hamrick 1997). Plant density affects pollen dispersal in insect-pollinated species, with greater clumping reducing pollen-mediated gene flow distances (Stacy *et al.* 1996). Data has suggested that fragmentation of the wind pollinated *Acer saccharum* forests has also resulted in greater rates of gene flow than pre-fragmentation (Fore *et al.* 1992), and this may well also apply to animal pollinated species.

* 15 *To predict the rate of introgression and define buffer distances it is essential to characterise the frequency distribution of pollen and seed dispersal distances under field conditions.*

5.4.2 Pollinator movements

The extent of dispersal of pollen from planted non-local eucalypts to native stands is obviously influenced by the foraging movements of pollinators. Eucalypt pollination is usually undertaken by active, generally non-specific pollinating vectors such as birds, insects, marsupials and mammals (reviewed in Ford *et al.* 1979; Eldridge *et al.* 1993; House 1997). Understanding the factors affecting the movements of these pollinators is an important part of understanding the patterns of dispersal of pollen in eucalypt forests (see Levin 1981; Handel 1983). Many Australian honeyeater birds defend nectar resources (Ford and Paton 1982; Paton 1993), including flowering eucalypts (Ford 1979; Paton 1980; Franklin *et al.* 1989),which results in very localised foraging movements. Paton and Ford (1983; 1985) found that the territories of both New Holland honeyeaters and red wattlebirds were restricted to parts of individual trees of *E. leucoxylon* F. Muell. and, hence, outcrossing only occurred when an intruder entered the territory to feed or a territory holder returned after feeding on flowers from another tree outside its territory. However, territory intrusions were common; averaging over 24 per hour (Paton 1985). As some of these intruding birds were transients to the area (Paton 1985), they may have travelled large distances in a short period of time. Similarly, although the average distances moved between trees by honeyeaters were only slightly greater than nearest neighbours on *E. stoatei* (Hopper and Moran 1981) and *E. urnigera* (Savva *et al.* 1988b), occasional long intertree flights were noted. In *E. stoatei* one honeyeater was observed flying 50 m between trees (Hopper and Moran 1981), while in *E. urnigera* long distance flights of over 30 m accounted for 6-9% of all intertree movements (Savva *et al.* 1988b).

The patterns of movement between trees by honeyeaters vary between and within species as well as over time for individuals. The proportions of intertree movements on *Banksia menziesii* to nearest neighbours was greater for larger than for smaller species of honeyeater, ranging from 66% in little wattlebirds to 38% in western spinebills (Ramsey 1989). This was partly due to the smaller species being chased by larger species, leading to the former making long escape flights (Ramsey 1989). Individual birds also differ in the size of their feeding territories on *Banksia* spp., both interspecifically (Paton and Ford 1983) and intraspecifically (Paton and Ford 1983; Newland and Wooller 1985). The sizes of these individual territories may also vary over the course of a flowering season as floral abundance changes (Paton and Ford 1983).

It is generally believed that birds move more widely while foraging on flowers than do insects (Ford *et al.* 1979; Eldridge *et al.* 1993; Paton 1993). For example, Paton (1993) observed honeybees visiting a total of 4600 flowers of *Callistemon rugulosus* on plants separated by a minimum of only 3 m for a total of 9.9 hours without recording an individual moving between plants. In fact each honeybee restricted its foraging to a small section within a particular bush over several days (Paton 1997). In contrast, during a similar amount of time observing New Holland honeyeaters foraging at the same plants, interplant movements averaged 7.3 per hour and one every 400 flowers visited (Paton 1993). Individual honeybees are also known to restrict their foraging to small patches of herbaceous plants for extended periods of up to 16 days (Butler *et al.* 1943), and to single plants of *Eucalyptus grandis* for long periods (Hodgson 1976). Similarly, beetles and a species of syrphid fly have been observed restricting their foraging to individual bushes of *Thryptomene calycina* for long periods (Beardsell *et al.* 1993). However, large blowflies frequently flew between the same bushes (Beardsell *et al.* 1993). Furthermore, small insects are known to consistently transport pollen between Panamanian tropical rainforest trees separated by several hundred metres (Stacy *et al.* 1996), and solitary bees have also been recorded travelling up to 1200 m within two hours between conspecific trees in Costa Rican dry forest (Frankie *et al.* 1976).

As for birds, the movement patterns of flower-feeding insects are highly variable. Janzen (1971) found that euglossine bees could cross 5 km of open water to feed, whereas Powell and Powell (1987) found that bees in the same family would not cross forest clearings of 100 m. Similarly Dafni and Shmida (1996) found that bumblebees could forage up to 2 km from their nest, Osborne *et al.* (1999) recorded the same species foraging at least 610 m from their nest, but Bowers (1985) found that workers of another species foraging in a meadow never entered another meadow 400 m away.

The effect of pollinator movements on the extent of dispersal of pollen from planted non-local eucalypts to native stands will be greatly modified by the degree of pollen carryover, where pollen deposited on the pollinator's body at a flower is then transferred to a number of flowers visited subsequently (Rasmussen and Brodsgaard 1992). Although most pollen is usually deposited on the first few flowers visited, pollen deposition curves are typically characterised by long tails indicating that pollen may be transferred to flowers visited some time later (Thomson and Plowright 1980; Morris *et al.* 1994; Cresswell *et al.* 1995). These pollen deposition curves differ between pollinator species (Campbell 1985). Little is known of these pollen deposition curves in *Eucalyptus,* but they are likely to have tails at the longer end of the scale because of the usually open, unspecialised floral morphology, and the large quantities of pollen produced in this genus. These floral characters are likely to result in pollen being scattered over large areas of the pollinator's body, and haphazard deposition of this pollen on stigmas. Consequently, large quantities of pollen may accumulate on animals, with only small patches being wiped off when a stigma is contacted. Large quantities of *Eucalyptus* pollen have been found on birds that were mistnetted near flowering *E. globulus.* An average of 13547 grains (range 2949 - 33073) were carried in the first 22 mm from the bill tip of swift parrots, and an average of 4419 grains (range 215 - 32474) in the first 22 mm of honeyeaters (Hingston unpubl.). Hence, *Eucalyptus* pollen is likely to be carried for long periods of time. Eucalypt pollen may adhere to strong flying insects for up to 8 days under field conditions (A.R. Griffin pers. comm. cited in Ashton and Sandiford 1988), causing Ashton (1988) to suggest insects may be important in long distance pollination over several kilometers.

Another factor influencing the extent of dispersal of pollen from planted non-local eucalypts to native stands is the potential for pollen transfer between animals. Free and Williams (1972) found pollen in the corbiculae of honey bees from plant species which they were not foraging on, suggesting that pollen may be transferred between individuals whilst in the hive. This was confirmed by DeGrandi-Hoffman *et al.* (1986) who found that individual honey bees confined to within the hive accumulated sufficient pollen from their forager hivemates within 3-4 h to pollinate apples (*Malus domestica* L. Borkh.). As a result, stigmas could conceivably receive pollen from flowers twice the foraging range of honeybees away (Free and Williams 1972). This distance could be as much as 40 km, as pollen from plants 20 km away has been discovered in honey bee hives (Schwarz and Hurst 1997). Although it has never been demonstrated, Heinrich (1975) speculated that pollen might also be transferred between animals at flowers.

The other factor influencing pollen dispersal is the period of time over which pollen can remain viable in the field. This is a completely unknown factor. If pollen remains on an animal for a very long period (i.e. pollen carryover is high) or pollen is transferred between animals, and this pollen remains viable for a long time, pollination may occur over vast distances. Such long distance pollen dispersal may occur as a result of the frequently documented nomadic or migratory movements of flower-feeding birds (Christensen 1971; Ford *et al.* 1979; Paton and Ford 1983; Newland and Wooller 1985; Franklin *et al.* 1989; Ramsey 1989; Brereton 1997). There is clear opportunity for long-distance pollen dispersal with the seasonal movement of many honeyeaters as they track the changing nectar resources across southeastern Australia (e.g. McGoldrick and Macnally 1998). Flying-foxes are also noted as tracking mass flowering in the eucalypts such as *Corymbia maculata* and their seasonal movements within NSW and tropical Australia may extend as far as 800km. Long distance movements of flower-feeding insects are obviously much harder to document, but this has also been found. In Kansas, Michener (1953) captured a leafcutter bee *Megachile brevis* approximately 9 km from the place where he had marked it two weeks earlier. A specific discussion of the various floral visitors of eucalypts to disperse pollen over long distances is given in House (1997).

5.4.3 Pollen dispersal in *Eucalyptus*

Eucalypts have a mixed-mating system with high levels of outcrossing. Direct estimates of pollen-mediated gene flow have been made in natural forests using interspecific F_1 hybrids as genetic markers (Pryor 1976; Potts and Reid 1988; Potts and Reid 1990; Barbour *et al.* 2000), and in seed orchards using radio-labelled pollen (Pacheco *et al.* 1986) and allozyme based paternity analysis (Sedgley and Griffin 1989 p. 237; Adams 1992; Eldridge *et al.* 1993; Junghans *et al.* 1998; Campinhos *et al.* 1998) (Table 5.4).

The data on pollen-mediated dispersal in eucalypts is sparse and quite variable and no large-scale paternity studies have been reported to date. Nevertheless, there is circumstantial evidence to suggest that in many cases, pollen dispersal is still relatively restricted at the local level, but that the pollen dispersal curve is highly leptokurtic (e.g. Barber 1965) and variable. For example, many studies suggest that most pollen is distributed in relatively close proximity to a source (<200m; e.g. Pryor 1976; Potts and Reid 1988; Sampson *et al.* 1989; Sedgley and Griffin 1989; Peters *et al.* 1990). However, isolated mature hybrids have been found in native stands regularly up to 1km from a boundary (Ashton 1981; Potts and Reid 1983; Potts and Reid 1988) and there are reports of possible rare long distance dispersal (<6km; Ashton and Sandiford 1988; Potts 1990) and relatively high levels of gene flow across barriers (400-800m; Campinhos *et al.* 1998; Junghans *et al.* 1998). While it is difficult to assess exactly how far the tail of the pollen dispersal curve extends in eucalypts, it is likely to be long, particularly where bird pollination is involved, suggesting ample opportunity for rare long-distance pollen-mediated gene flow. In the extreme case, Ashton (1973) has reported isolated gum-topped stringybarks in the Trentham forest that could be the result of hybridisation between the surrounding *E. obliqua* and *E. regnans*. Hybrids between these two species are common along their boundaries (Ashton 1981), but in this case the intermediate trees are more than 25km from the nearest *E. regnans*. Molecular markers would be needed to verify whether these trees have resulted from long distance dispersal. Long-distant gene flow is also implied by estimates of gene flow between populations within species derived from population genetic data using theoretical approaches based on the private allele or Fst methods. Such indirect estimates of the mean number of migrants exchanged between populations (N_m) have been made in several eucalypts and range from 0.78 to 360, with most above one (see Govindaraju 1989; Moran 1992; Potts and Wiltshire 1997). However, unless nuclear and cpDNA data is compared, these measures do not differentiate pollen from seed dispersal (Ennos 1994).

The difference between the various sources of information lies in focusing on the peak or mean pollen-dispersal distances instead of the tail of the potentially leptokurtic dispersal curve. This tail must be summed over numerous point sources (Ellstrand 1992a), and through time may account for considerable levels of hybridisation (Arnold 1992). Major differences in dispersal may also occur in a continuous as opposed to fragmented population structure and immigration levels will be related to the relative size of the ‘source’ and ‘sink’ population.

Table 5.4 Reports of pollen dispersal in eucalypts.

Species	**Distance**	**Comments**
E. urnigera x *E. ovata*	c. 5km	A single F_1 hybrid with the lowland *E. ovata* was found in open pollinated seed of *E. urnigera* collected from a mountain top (Potts 1990)
E. saligna	> 300m	Tracking of radio-active pollen through a seed orchard revealed that bees were carrying pollen up to at least 300m from a source (Pacheco *et al.* 1986). Greatest activity was 100m from the hive.
E. rhodantha	<170m	At the local level, gene flow was not sufficient to remove genetic differences between sub-populations separated by only 170m (Sampson *et al.* 1989)
E. pulverulenta	250m	2 out of 74 (3%) open-pollinated progeny from an isolated homozygous tree 250m from the edge of the nearest stand were heterozygous for the more common allele, whereas heterozygotes occurred in 25 to 65% of progeny from five other homozygotes within the stand. Suggested 250m was close to the limit of the pollen dispersal range (Peters *et al.* 1990).
E. robertsonii x *E. fastigata*	<40m	Comparison of F_1 hybrids between synchronously flowering species pairs showed a rapid drop-off in dispersal by 40m (Fig 6.2) (Pryor 1976).
E. amygdalina x *E. risdonii*	> 500m	F_1 hybrids with *E. risdonii* detected in open-pollinated seed of *E. amygdalina* dropped from 2.8% at the boundary to 1.3% at 50m and 0.1% by 500m across continuous forest (Potts and Reid 1988)
E. ovata x *E. nitens*	c. 300m	*E. ovata* x *nitens* F_1 hybrids were detected in open-pollinated seed collected from remnant *E. ovata* trees within 300m of an *E. nitens* plantation. While hybrids were detected at the furthest distance (<0.5%), high frequencies (5-16%) were only found in trees sampled within 150m of the trial (Barbour *et al.* 2000). New sampling of *E. ovata* trees overlapping the flowering of *E. nitens* has shown average levels of c. 4% in a small patch of *E. ovata* 300m within native forest (Barbour unpubl. data). Up to 47% hybrids were found in an isolated, remnant tree within 30 m from the nearest flowering *E. nitens*
E. kochii	c. 500m	A single microsatellite locus indicates substantial levels of immigration into isolated, remnant roadside patches (M. Byrne unpubl. data)

E. regnans	42 m	Mean pollen dispersal distance in an *E. regnans* seed orchard using paternity analysis (T. Adams, R. Griffin and G. Moran; cited in Sedgley and Griffin 1989 p. 237; Adams 1992)
E. grandis x *E. urophylla*	400m & 800m	Minimum estimates of contamination of *E. grandis* clones in a Brazilian seed orchard separated by 400m (Campinhos *et al.* 1998) and 800m (Junghans *et al.* 1998) of native forest from commercial eucalypt plantation were 14.2% (20.2% of outcrosses) and 2.8%.
E pulchella x *E. obliqua*	>100m	putative natural F_1 hybrid believed to be derived from pollen dispersal into the range of *E. pulchella* (Potts and Reid 1983)
E. macrorhyncha x *E. regnans*	6km?	Mature natural hybrids believed to be the product of long-distance pollen dispersal reported up to 6 km from a pollen source (Ashton and Sandiford 1988). Needs verification with markers.

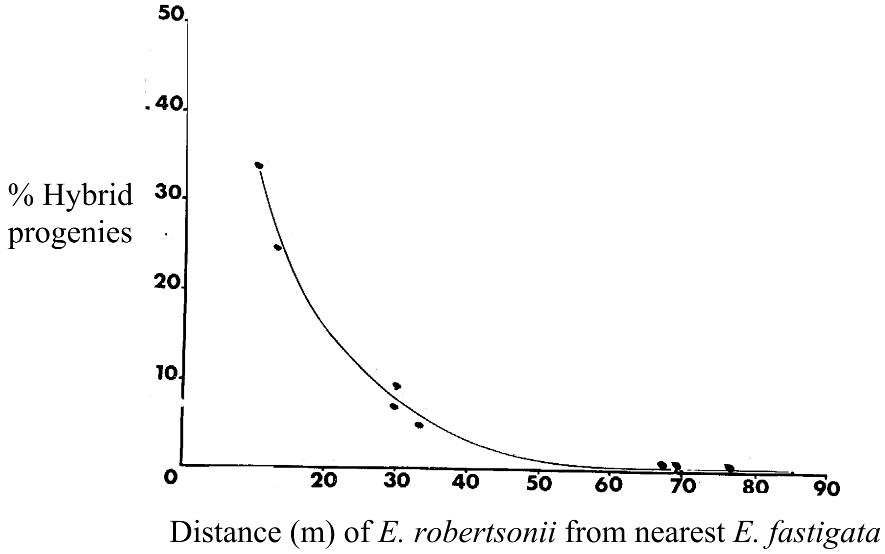

Figure 5.2 Dispersal of *E. robertsonii* pollen with distance.
The distance of pollen travel between synchronously flowering pairs of trees as revealed by the percentage of hybrid progeny in seed lots of *E. robertsonii* contaminated by pollen from *E. fastigata* (adapted from Pryor 1976). Most pollen is likely to be distributed close to a source but distances will in part depend upon the spatial distribution of the flowering resource. However the tail of the distribution may be more extensive than portrayed in this figure (see Table 5.4) and the importance of these longer distance dispersal events will be dependent on numerous factors including the relative size of the 'source' population.

5.4.4 Isolation distances

In crop plants, experiments have lead to specific recommendations of minimal isolation distances for maintaining varietal purity (Levin and Kerster 1974; Raybould and Gray 1993). The average isolation distance for self fertilising species is c. 300m and that in primary outcrossing species is 800 m, although some of these distances may allow contamination of up to 10% (Raybould and Gray 1993). In the case of seed orchards of insect pollinated eucalypts, buffer zones of the order of 100-200m planted with non-interbreeding trees have been suggested as realistic (see Eldridge *et al.* 1993). However, this distance does not accord with the contamination levels detected by Campinhos *et al.* (1998). As noted by Ellstrand (1992a), gene flow may be so highly idiosyncratic from species to species and place to place that it is difficult to make generalisations. For example, in insect pollinated crop plants, studies of gene flow between populations or patches of plants using allozyme markers and various forms of paternity exclusion analyses demonstrate:

(i) considerable variation in gene flow between different patches not necessarily directly related to interpatch distance;

(ii) occasionally high amounts of gene flow between patches; and

(iii) gene flow occasionally occurring over very long distances (Raybould and Gray 1993).

Models predict that the influence of isolation corridors (or plant patches) on the spread of genes can be dramatic and a favoured gene's invasion can be substantially delayed by such barriers (Manasse and Kareiva 1991). However, such models do not account for the impact of such barriers modifying pollinator behaviour.

In eucalypts, such distances will vary with numerous factors affecting pollinator movements (see House 1997) and the acceptable level of contamination will depend upon conservation values and probability of survival after dispersal. While the patterns and distance of pollen-mediated dispersal in eucalypts is clearly a high priority research area, several guidelines to minimise the risk of genetic pollution would include:

* 16 *Within a continuous native forest abutting a plantation and with synchronous flowering, pollen immigration should be dramatically reduced by c. 1km from a source of exotic pollen.*

* 17 *Isolation distances should be greater for bird-pollinated than insect pollinated species.*

* 18 *Isolation distances should be greater for a patchy as opposed to spatially continuous flowering resource.*

* 19 *With a high conservation value, high risk situation (i.e. high probability of gene flow, large source population) a conservative approach should be adopted until further research is undertaken on pollen dispersal distances.*

5.5 Other pre-mating barriers

The manner in which the large variety of floral syndromes found in eucalypts may impact on their pollination ecology is reviewed by Griffin (1982) and House (1997). The majority of eucalypts have small white or cream flowers grouped into large conflorescences, which are mainly visited by a range of insects, birds and bats. However, species, particularly in Western Australia, have large coloured flowers, which would appear to be adapted specifically to bird or mammal pollination. The full extent to which divergence in these floral syndromes in the genus contributes to additional post-mating reproductive isolation through attracting different communities of flower visitors or affecting the pollination efficiency of different components of this community is unclear at present. Nevertheless, the extensive overlap in flower visitor profiles between *Eucalyptus* species (see House 1997) suggests that pollinators will not provide marked pre-mating barriers between species. Although small-flowered species visited exclusively by insects will not receive pollen from larger-flowered species via birds, the frequent visits to larger flowered species by insects are likely to facilitate such transport. The frequency of reverse transport of pollen, from small-flowered to large flowered species, by shared insect visitors will be determined by the frequency with which insects contact their stigmas. Hingston and Potts (1998a) noted that foraging insects often failed to contact the stigmas of the large flowers of *E. globulus*. However, subsequent research has shown that the frequency of stigma contact by insects in this species differs greatly between individual trees. For example, the percentage of flower visits by honeybees that result in stigma contact range from 9.3 to 82.4% (Hingston unpubl.). Occasionally, large-flowered species have floral structures which prevent insects accessing the stigmas, such as in *E. stoatei* (Hopper and Moran 1981). Hence, this species is probably reproductively isolated from exclusively insect-pollinated conspecifics via this pre-mating barrier.

5.6 Pre-zygotic barriers (crossability)

Controlled crossing has demonstrated two major pre-zygotic barriers to hybridisation in the genus. 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 (Gore *et al.* 1990). Even when the large flowered species is used as the pollen parent, seed set may be markedly reduced compared to intraspecific crosses (Gore *et al.* 1990; Potts *et al.* 1992). This is possibly due to pollen tubes 'overshooting ' the ovules of the small-flowered species. The structural barrier is a major problem for producing F_1 hybrids with *E. globulus* ssp. *globulus* which has a much larger flower than many of the species that breeders wish to cross with it (e.g. *E. gunnii*, *E. camaldulensis*, *E. nitens*, *E. grandis*, *E. dunnii*). Exactly how different in size, flowers/styles must be before this structural barrier causes a significant reduction in seed set is unclear at present. No seed is obtained when *E. nitens* pollen is directly applied to *E. globulus* ssp. *globulus* females but the cross is successful using F_1 hybrid pollen. However, seedset was slightly reduced when *E. nitens* pollen was applied to the F_1 females compared with pollinations with either *E. globulus* or unrelated F_1's (Potts *et al.* 2000). Flower/style size is inherited in an intermediate manner, although biased towards the small flowered species (*E. camaldulensis* x *globulus* McComb *et al.* 2000; *E. nitens* x *globulus* Tilyard *et al.* 2000). This means that once F_1's are formed this physical barrier between two species will be rapidly broken down.

The second barrier is physiological (incongruity) and results in pollen tube abnormalities and pollen tube arrest in the pistil, the frequency of which has been shown to increase with increasing taxonomic distance between the parents (Ellis 1991) (Figure 5.3). The key studies that compare the crossability of a broad range of taxa are Ellis *et al.* (1991) and Tibbits (2000). In all studies reported to date, interspecific crosses have been undertaken in the absence of competition with intraspecific crosses. Mixed pollinations (Carney *et al.* 1996) are likely to result in this physiological barrier being accentuated.

* 20 *The probability of successful hybrid seed set will be reduced with increasing difference in flower size and increasing taxonomic distance between two species.*

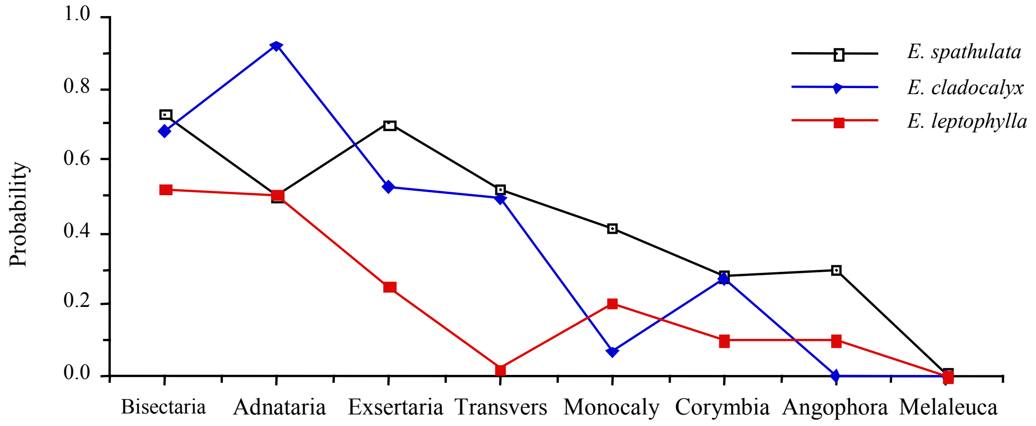

Figure 5.3 The effect of taxonmic distance between parents on the probability of cross success. The effect of taxonomic distance on the probability of pollen tubes reaching the base of the style in the three species from the subgenus *Symphyomyrtus* section *Bisectaria* (from Ellis *et al.* 1991). Seedlings only survived from crosses within the *Bisectaria* and 2 of the 5 intersectional cross types with the *Adnataria* (*E. spathulata* x *E. viridis*; *E. cladocalyx* x *viridis*; Ellis 1991). The three inviable intersectional cross types (*E. spathulata* x *lansdowneana*, *E. leptophylla* x *lansdowneana* and *E. leptophylla* x *melliodora*, all had good germination rates, produced healthy cotyledons but all seedlings withered before the production of the first leaf pair.

5.7 Hybrid fitness (post-zygotic barriers)

5.7.1 General

The fact that interspecific matings and even seed occurs from these matings does not necessarily mean that hybrids will survive and introgression will occur (e.g. Ellis 1991; Kennington and James 1997). Unfavorable genomic interactions may result in reduced hybrid fitness (Rieseberg *et al.* 1996; Wu and Li 1999). If the species is rare, the burden of producing such unfit offspring may markedly lower the reproductive output of the population and lead to extinction (Rhymer and Simberloff 1996). However, in most eucalypts this is unlikely to be a major problem as seed output far exceeds the regeneration capacity of the site and intense post-dispersal competition and selection results in only the most competitive progenies surviving to reproductive maturity (Hardner and Potts 1997). Exceptions will be where pollen swamping is extremely high, reproductive output per individual is very low or the population is already subject to the deleterious effects of inbreeding.

In a general review of studies of hybrid fitness, Arnold and Hodges (1995; Arnold *et al.* 1999) found that hybrid types (e.g. F_1, F_2, BC_1) may vary widely in fitness and that hybrids in general may have lower, equivalent or greater fitness than parental types. They argue that a general pattern of reduced hybrid fitness is not supported by the available data. However, Day and Schluter (1995) consider that studies reported in the literature may be biased towards combinations where hybrids are already relatively common. This is certainly the case in eucalypt breeding where it is the successful hybrid combinations which dominate the literature (Venkatesh and Sharma 1977; Campinhos and Ikemori 1977; Martin 1989 c.f. Pilipenka 1969; Griffin *et al.* 1988). Hybridisation sometimes leads to populations of lower fitness in first or latter generations and occasionally the decline in adaptation to the local environment may be dramatic. In other situations hybrids may be better adapted to the local conditions, although this may only be transitory and not reflect the long-term site environment. The relative fitness of hybrids and their parental taxa may be habitat dependent (i.e. dependent on exogenous selection) (Martin 1989; Nikles and Griffin 1992; Emms and Arnold 1997; Arnold 1997;

Potts *et al.* 2000) or determined by endogenous factors such as genomic incompatibilities which result in hybrids being less fit than parent taxa in all environments (Levin 1978; Emms and Arnold 1997; Arnold 1997). A key element determining the rate of introgression of genes is the relative fitness of hybrid plants in native environments (Manasse and Kareiva 1991). However, it is difficult to say at this stage what level of reduced hybrid fitness is required to prevent introgression. Arnold *et al.* (1999) argue that there are numerous examples in nature which demonstrate that extremely low fertility or viability of early-generation hybrids (e.g. F_1, F_2, BC_1) does not necessarily prevent extensive gene flow.

5.7.2 Eucalypt F_1 hybrids

There are only a few reports of F_1 hybrid seed exhibiting reduced germination potential (e.g. *E. gunnii x globulus* Potts *et al.* 1992). In most cases if viable hybrid seed is produced germination is as successful as the intraspecific seed (Ellis 1991; Lopez *et al.* 2000b). However, hybrid inviability may be rapidly manifested thereafter as failure to develop seedling leaves (Figure 5.3), or seedling abnormalities and dwarfism (e.g. Potts *et al.* 1992; Lopez *et al.* 2000b; Griffin *et al.* 2000). For example, following extensive manipulated crossing undertaken in the USSR in the 1940's, Pilipenka (1969) reported that F_1's produced various proportions of dwarfs that died in the first 4-6 years and only a few reached the age of 10-12 years. The dwarfs were plants with severely retarded growth and development that often remained constantly in the juvenile phase, with reduced vegetative organs and rarely flowers. It was also noted that many interspecific hybrids have greater vigour compared to their parents in the early periods of their life, but this decreases at later ages (Pilipenka 1969). High levels of such inviability in F_1 hybrids have subsequently been reported for numerous cross types (e.g. *E. nitens* x *globulus* Potts *et al.* 1992; *E. grandis* x *nitens* Shelbourne *et al.* 1999). de Assis (2000) noted that high levels of abnormal phenotypes which were of poor vigour were common in artificial eucalypt F_1 hybrids. These abnormal plants arose up to 2 years after field planting, after which phenotypes stabilised and normal plants were no longer likely to develop abnormalities. He noted that *E. dunnii* x *E. grandis* and *E. dunnii* x *urophylla* F_1 hybrids had fewer abnormalities than their reciprocals, suggesting some type of maternal effect in their expression.

As with crossability, there is mounting evidence that, at least within *Symphyomyrtus*, the fitness of the F_1 hybrids decreases with increasing taxonomic distance between species (Pryor 1957; Pilipenka 1969; Cauvin *et al.* 1987; Griffin *et al.* 1988; Ellis 1991; Potts *et al.* 2000). Successful intersectional F_1 crosses have been produced within *Symphyomyrtus.* However, the frequency of hybrid inviability in such wide crosses is often high and only after very intensive selection have suitable hybrids been found for use in forestry (e.g. *E. camaldulensis* x *globulus* McComb *et al.* 2000; *E. grandis x globulus* Griffin *et al.* 2000; see 3.2.2). Indeed a feature of many eucalypt F_1 hybrid families which exhibit abnormal dwarf seedlings is that remaining full-sib seedlings of normal phenotypes are often vigorous and, on average, frequently exhibit early growth rates comparable or intermediate between parental types (Tibbits 1988; Volker 1995; Potts *et al.* 2000). Within species, crossability and F_1 hybrid viability has been shown to vary with parental provenance and even individual trees (Volker 1995; Griffin *et al.* 2000; de Assis 2000; McComb *et al.* 2000). However, at present this variability in hybridisation potential cannot be predicted.

In most cases, survival and growth must be used as surrogates for lifetime fitness estimates. Further, many of the artificial hybrid combinations are usually tested in relatively non-competitive plantation environments that may not be indicative of their fitness under strong competition with parental or other pure species types in native habitats. In addition, early performance can give a biased impression of lifetime fitness and it is often argued that hybrids tend to only survive in youthful habitats and early stages of succession (Pryor 1953; Pryor 1976). An example is provided by the interseries cross between *E. ovata* and *E. globulus* where high mortality of the F_1 hybrid commenced at age 4 years (Figure 5.4). Nevertheless, such trials are likely to over estimate hybrid fitness and thus poor fitness in the greenhouse and field trials should reflect even poorer performance in the wild e hybrids will be subject to direct, intense competition.

%
survival

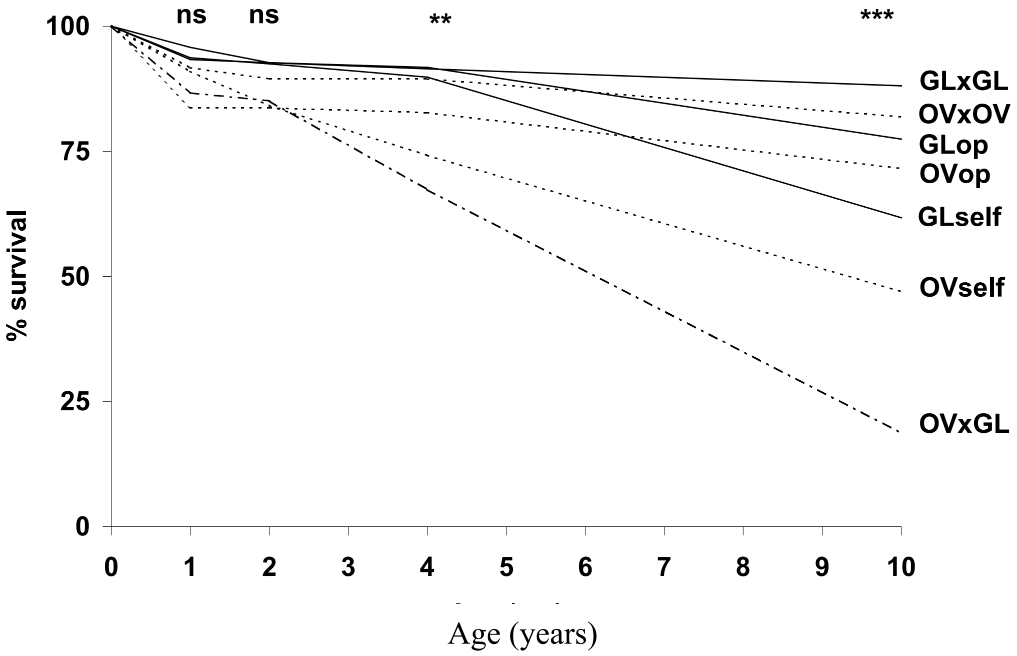

Figure 5.4 Later age F_1 hybrid inviability in eucalypts
The survival of interseries F_1 hybrids (*E. ovata* x *globulus*) in a field in NW Tasmania over a 10 year period was markedly reduced compared to open-pollinated and outcrossed progenies of the pure species. The graph shows the percentage survival at 1, 2, 4 and 10 years after planting in the field of *E. globulus* (GL) and *E. ovata* (OV) progenies derived from self pollination (self), natural open-pollination (op), intra-specific outcrossing (GLxGL or OVxOV) and interspecific hybridisation of *E. ovata* x *E. globulus* (OVxGL). The poor fitness of the hybrids was reflected in significantly lower survival from age 4 years onwards and by year 10, only 19% of the F_1's planted were still alive compared with 88% and 82% of the *E. globulus* and *E. ovata* outcrosses respectively. (adapted from Lopez *et al.* 2000b)

*21 *The probability of F_1 hybrid inviability will generally increase with increasing taxonomic distance between the parent species.*

Even if hybrids survive to later ages in nature, the probability of introgression will depend upon their reproductive output. There are few studies in *Eucalyptus* where the reproductive fitness of eucalypt hybrids has been quantified in natural environments (Drake 1975; Drake 1978; Drake 1980; Drake 1981a; Drake 1981b; Potts 1986; Morrow *et al.* 1994). In most cases reported mature hybrids do flower and produce seed crops in native stands. However, in the few cases examined, the reproductive output of hybrid types resembling F_1's have shown reduced output relative to parental types. Nevertheless, in the only case separating advanced generation hybrid types, the backcross type phenotypes had reproductive fitness greater than one but not the other parental type (Potts 1986). A generalised model for assessment of the reproductive success of eucalypt hybrids has been developed by Drake (1981b; 1981a). This model has already been applied to predict the evolutionary potential of natural hybrids and is equally relevant to pollen as well as seed output (Figure 5.5). However, it is the final parameters of this model - estimates of lifetime seed and pollen output of the hybrids that determine their evolutionary potential (Potts 1986) and the potential for introgression.

* 22 *While interspecific F_1 hybrids may survive to maturity in the wild, their reproductive output may be reduced compared to parental types.*

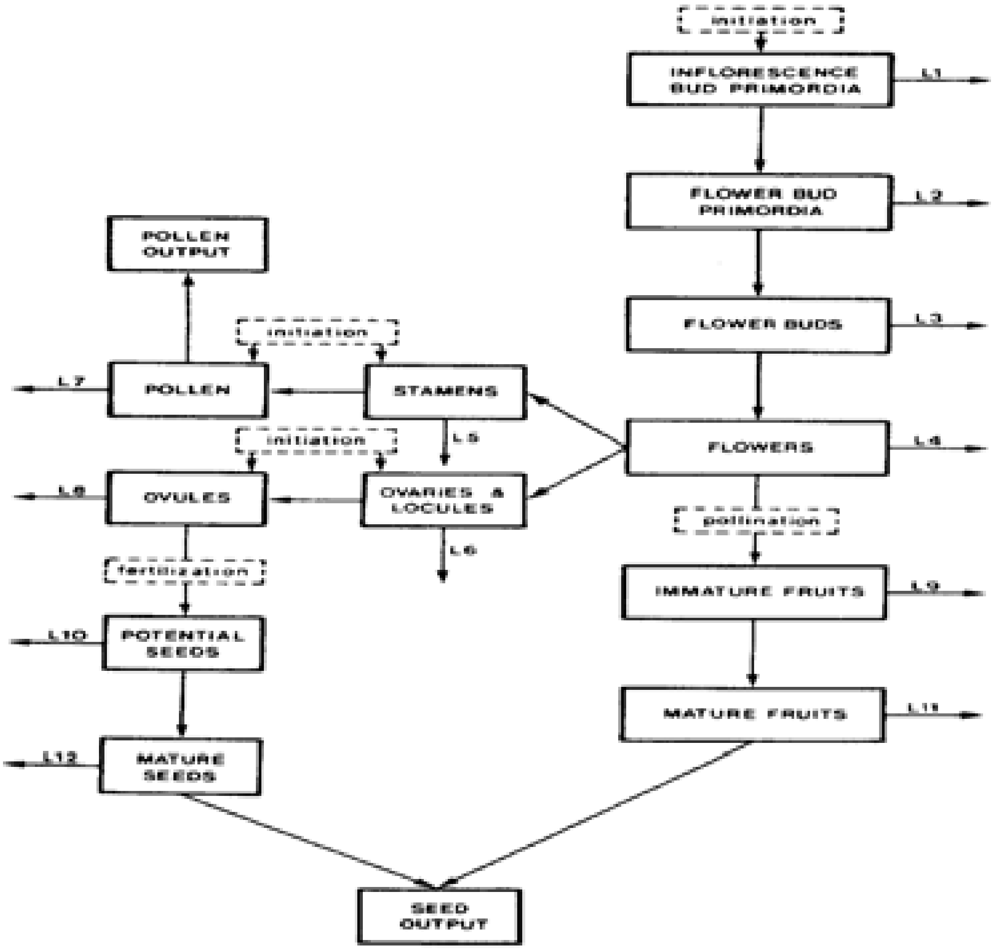

Figure 5.5 Generalised reproductive output model for eucalypts.
The generalised seed output model used by Drake (1981a) to quantify the relative reproductive success of two eucalypt hybrid systems. (Reproduced with permission of CSIRO Publishing, from Drake DW [1981] Australian Journal of Botany Vol. 29, fig. 1, p. 27)

5.7.3 Advanced generation hybrids

Barriers to hybridisation may extend beyond the F_1 generation. Recombination and segregation in the F_2 or backcross-generations may result in advanced generation hybrid breakdown (outbreeding depression) which may result from chromosomal differences, genomic incompatibility or disruption of gene complexes. For example, in controlled crosses between *E. grandis* and *E. pulverulenta*, Paton (1981) reported lower nursery survival of F_1, backcrosses, and F_2 progenies, compared with parental progenies. However, it is important to differentiate advanced generation hybrid breakdown from the effects of inbreeding that are often confounded in advanced generation hybrids. Nevertheless, using unrelated *E. nitens* x *globulus* crosses, outbreeding depression in growth and survival extending across the F_1 and F_2 generations has been recently demonstrated (Potts *et al.* 2000; Figure 5.6), clearly indicating greater average fitness of the parental species in two quite different test environments. This depression in average vigour also extended to the BC_1 generations but was not significant at 4 years of age. Other reports of advanced generation hybrid breakdown in eucalypt hybrids are detailed in Section 3.2.2. This may be a strong barrier to introgression in some instances, with Pilipenka (1969) reporting that dwarfs may represent 90-95% of some advanced generation hybrid combinations.

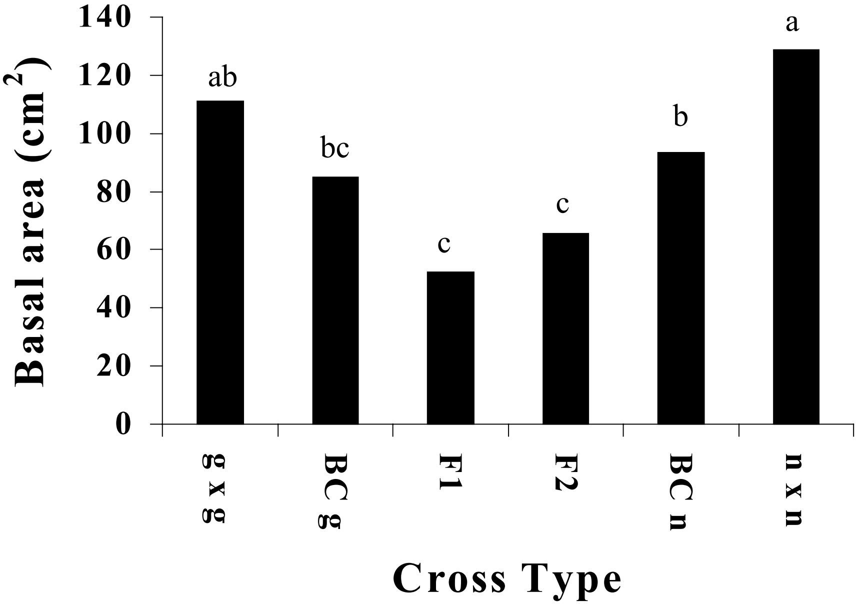

Figure 5.6 Inviability in F_1 and advanced generation eucalypt hybrids.
The mean basal area per planted seedling (treating deaths as zero) for *E. nitens* x *globulus* hybrids and pure species controls in a trial in northwestern Tasmania at age 4 years. Cross types correspond to *E. globulus* (g x g) or *E. nitens* (n x n) outcrosses, backcrosses of the F_1 hybrids to *E. globulus* (BCg) or *E. nitens* (BCn), F_1 and outcrossed F_2 hybrids (from Potts *et al.* 2000). Common letters indicate means which are not significantly different at the $P<0.05$ level.

5.8 Guide lines based on taxonomic relationship

Rhymer and Simberloff (1996) consider that the degree of genetic differentiation of the parental taxa can provide a good indication of the likelihood of crossability problems or outbreeding depression, and eucalypts are clearly no exception. An indication of the probability of successful hybridisation between a plantation species and adjacent native species can therefore be made from the taxonomic similarity of the two species. In addition, specific recorded natural and artificial/spontaneous hybrids of the main species likely to be used in farm forestry are given in Appendix 1. Broad taxonomic guidelines for assessing the risk of genetic pollution are detailed below.

5.8.1 Different subgenera

* 23 *There is no risk of hybridisation when the two species involved are from different subgenera.*

The only exception is *E. cloeziana* from the monotypic subgenus *Idiogenes* that may hybridise with some species of the closely related subgenus *Monocalyptus*. There also appears to be inconsistencies between the two P&J subgenera *Corymbia* and *Blakella* which have now been grouped in the genus *Corymbia* and their taxonomic classification re-assessed (Hill and Johnson 1995; Brooker 2000; see also Steane *et al.* 1999). Most of the plantation species are from the subgenus *Symphyomyrtus*. The only manipulated intersubgeneric hybrids reported to date have involved the closely related subgenus *Telocalyptus* (*E. deglupta*) and the *Symphyomyrtus*. However, when seedlings have been obtained, these have been dwarfs (e.g. *E. urophylla* x *deglupta* or *E. pellita* x *E. deglupta*; Vigneron and Bouvet

2000; see also Griffin *et al.* 1988). However, molecular data suggests that the taxonomic status of *Telocalyptus* requires re-assessment (see Steane *et al.* 1999). The main barrier to hybridisation between the major subgenera appears to be physiological and results from the arrest of pollen tube development in the style (Ellis *et al.* 1991). The hybrid combinations involving the new minor subgenera define by Brooker (2000) have yet to be examined.

5.8.2 Different sections

* 24 *There is a reduced probability of introgression if adjacent species are from different sections within* Symphyomyrtus.

An overview of the phylogeny and distribution of the *Symphyomyrtus* P&J sections is given in Potts and Pederick (2000) and is summarised as follows. The subgenus *Symphyomyrtus* is the largest and most widely distributed subgenus and includes more than 300 species in six major sections (Table 2.1; Figure 5.7). Most species used in plantation forestry, particularly outside Australia are from the sections *Maidenaria* (e.g. *E. globulus*, *E. nitens*), *Exsertaria* (e.g. *E. camaldulensis*, *E. tereticornis*) and *Transversaria* (e.g. *E. saligna, E. grandis, E. urophylla*) (Eldridge *et al.* 1993). Within *Symphyomyrtus*, the section *Adnataria* is widespread, but predominates in the subtropics. The sections *Bisectaria* and *Dumaria* are centred on the southwest of Australia and include many species of mallee habit. *Bisectaria* is the more diverse and includes species of moister forest sites. Its species dominate or co-dominate eucalypt communities in a large portion of the medium-dry parts of southwestern Australia. The section *Exsertaria* includes mainly tropical and eastern species and, with the exception of *E. rudis*, is absent from the southwest of Australia. The species of the southwest of Western Australia, particularly from the wetter zones, are very distinct from those of the eastern half of the continent. Only a few dry country mallee species of the *Symphyomyrtus* sections *Bisectaria* and *Dumaria* transgress this disjunction today. The main subgenera are represented in both areas but the proportion of species in each, and sections represented, differs. The *Bisectaria*, for example, is predominantly a western section, and only three extant species occur in eastern Australia (*E. pachycalyx*, *E. squamosa* and *E. bakeri*).

The records of natural and manipulated intersectional hybrids reported in Griffin *et al.* (1988; see Appendix 3) are summarised in Figures 5.8, 5.9 and 5.10. The situation with other subgenera is less clear (e.g. genus *Corymbia* Hill and Johnson 1995). While this matrix requires updating with reports from the last 12 years, hybrid records for the main plantation species based on a limited survey have been included in Appendix 1 and new records of manipulated and artificial hybrids integrated with those of Griffin *et al.* (1988). The records of manipulated hybrids are dominated by interest in the key *Transversaria*, *Maidenaria* and *Exertaria* species in forestry internationally and work being undertaken by Prof. M. Sedgleys' research group at the Waite Agricultural Research Institute (Univ. Adelaide) where eucalypt hybrids are being bred for the floriculture industry. The latter work mainly focuses on *Bisectaria* species. While intersectional F_1 hybrids involving *Symphyomyrtus* species are being widely generated and tested, they generally suffer from poor seed set and high levels of inviability (e.g. McComb *et al.* 2000; Griffin *et al.* 2000). This would suggest that they would be unlikely to survive to reproductive age in a competitive forest environment. General conclusions are given below.

Table 5.5 Major sections with the subgenus *Symphyomyrtus*
The table indicates the alignment of Pryor and Johnson's (1971) sections of *Symphyomyrtus* with those of Brooker (2000).

P&J	P&J	Brookers'	Brookers'	Common name

Code	Section	Subgenera	Section	
SB	*Equatoria*	*Minuti-fructus*	*Domesticae*	*E. brachyandra*
SS	*Howittiannae (Telocalyptus)*			*E. raveretiana* *E. howittiana*
			Equatoria	*E. deglupta*
SD	*Tingleria*	*Cruciformes*		*E. guilfoylei*
SE	*Transversaria*	*Symphyomyrtus*	*Inclusae*	*E. diversicolor*
			Latoangulatae	eastern blue gums, red mahoganies, grey gums
			Similares	*E. longifolia*
			Incognitae	*E. cosmophylla* *E. paludicola*
SI	*Bisectaria*	*Symphyomyrtus*	*Bolites*	*E. gomphocephala*
			Sejunctae	*E. cladocalyx*
			Bisectaria	mallees and gums
SL	*Dumaria*		*Dumaria*	mallees
SN	*Exsertaria*	*Symphyomyrtus*	*Racemus*	*E. michaeliana*
			Liberivalvae	*E. bancroftii* etc
			Exertaria	*E. exerta* - northern and eastern red gums
			Platysperma	*E. brevifolia* + 5 others
			Pumilio	*E. pumila*
SP	*Maidenaria*	*Symphyomyrtus*	*Maidenaria*	gums
SQ	*Umbra-warrenses*	*Symphyomyrtus*	*Platysperma*	*E. umbrawarrensis*
SU	*Adnataria*		*Adnataria*	Boxes and iron barks
SW	*Sebaria*	*Alveolata*		*E. microcorys*

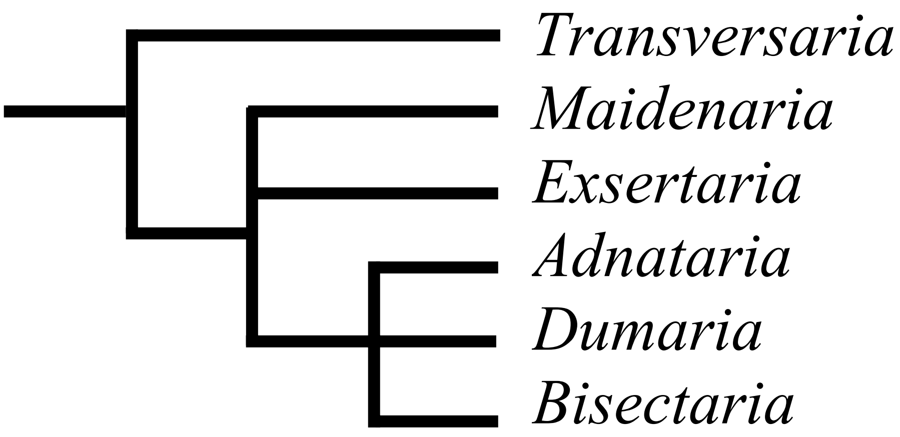

Figure 5.7 Phylogeny of the major *Symphyomyrtus* sections
Phylogeny of the major sections of the *Symphyomyrtus* as proposed by Chappill and Ladiges (1996) (modified from Ladiges 1997). Pryor and Johnson (1981) suggest that the sections *Transversaria* and *Bisectaria* are sister sections, however this is not consistent with artificial hybridisation experiments (Ellis *et al.* 1991) nor some cladistic analyses (Sale *et al.* 1993; Chappill and Ladiges 1996; Steane *et al.* 1999). Recent molecular data suggests that the *Exertaria* may be more closely related to *Transversaria*, and both have closest affinities to *Maidenaria* (Steane unpubl. data), which is consistent with the greater frequency of inter-sectional hybrids (Figure **5.8**).

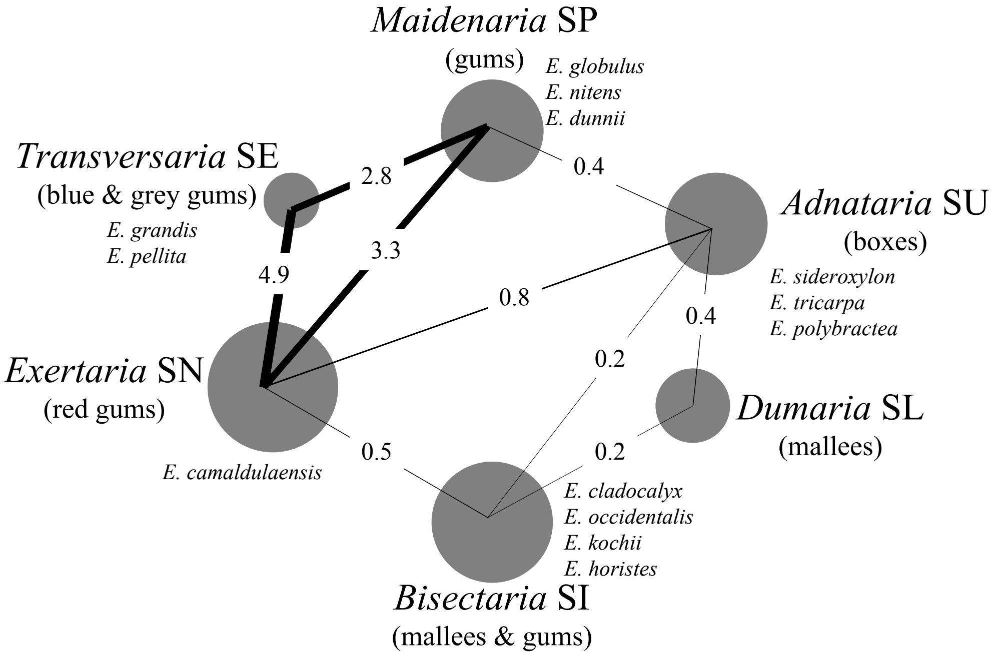

Figure 5.8 Natural inter-sectional hybridisation in *Symphyomyrtus*.
Occurrence of natural inter-sectional hybrids within *Symphyomyrtus* (data from Griffin *et al.* 1988). Only 40 natural intersectional hybrids had been reported in *Symphyomyrtus*. The figure shows the frequency of natural inter-sectional hybrids as a percentage of the number of intersectional combinations possible amongst proximal species (with a 10’ x10’ area). The area of the circle indicates the number of species in each section. Sections follow Pryor and Johnson (1971).

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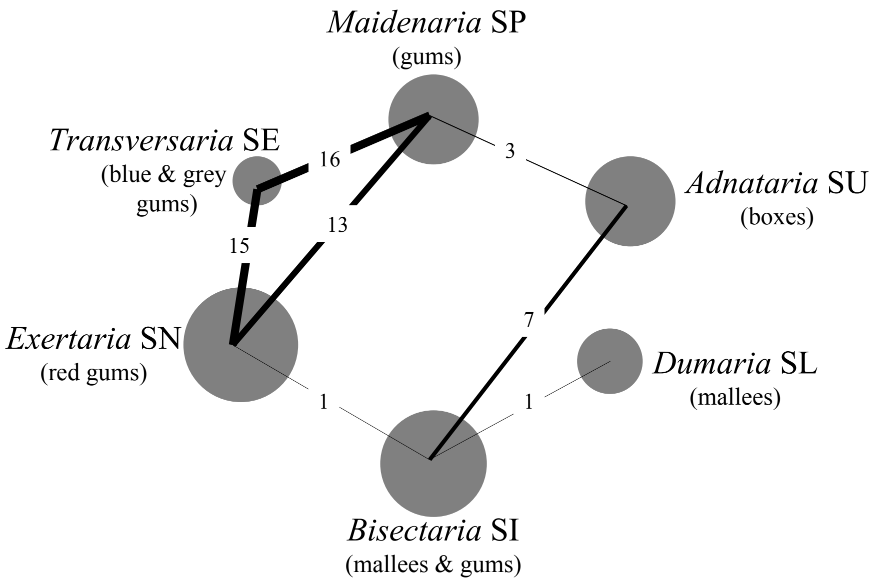

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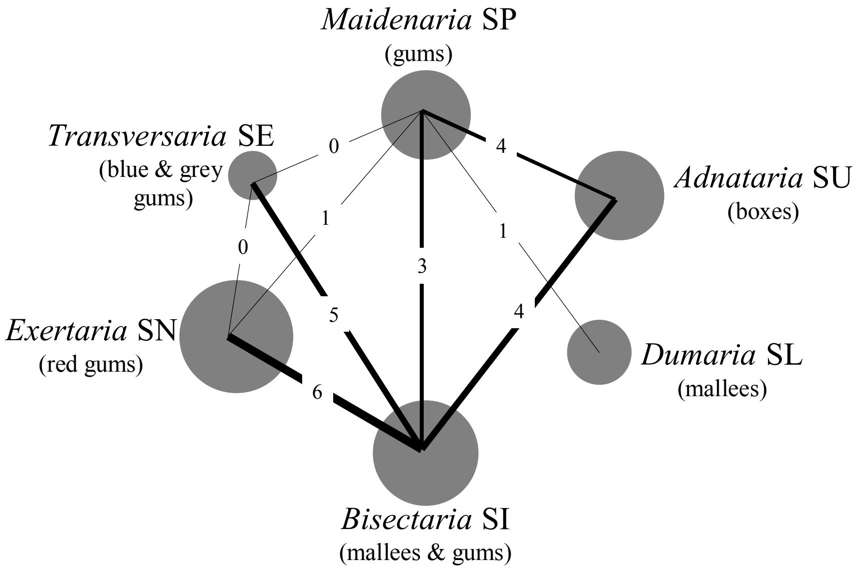

Figure 5.9 Manipulated inter-sectional hybridisation in *Symphyomyrtus*.
The number of manipulated inter-sectional cross combinations within *Symphyomyrtus* reported as successful or failed. Sections follow Pryor and Johnson (1971). Data is compiled from Griffin *et al*. (1988), Ellis (1991) and Appendix 1.

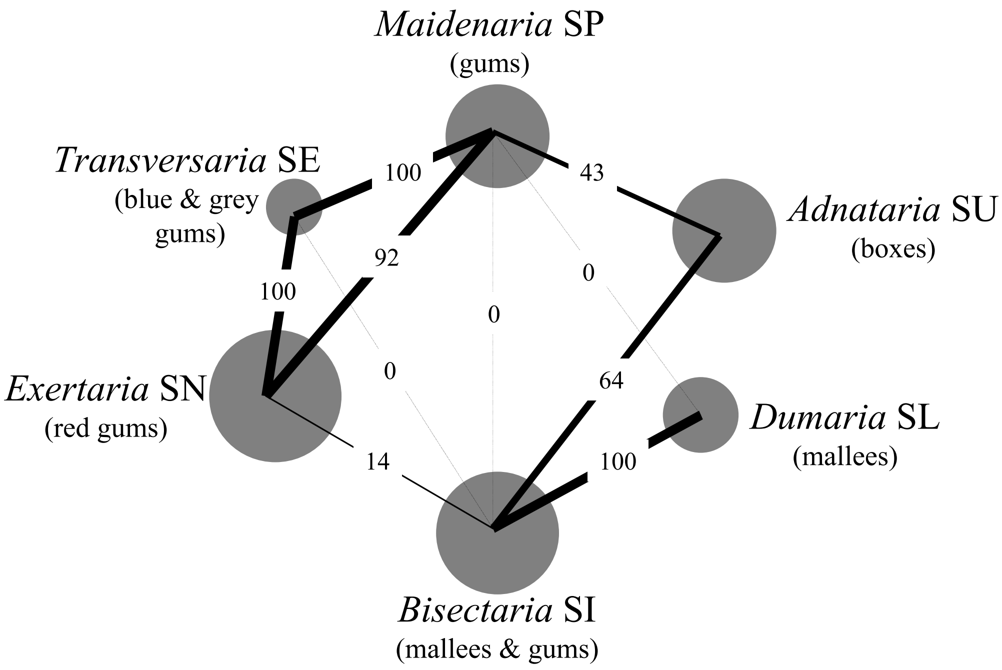

Figure 5.10 Manipulated inter-sectional hybridisation in *Symphyomyrtus*.
The percentage of successful species combinations produced from manipulated inter-sectional cross combinations within *Symphyomyrtus*. Compiled from the data shown in Figure 5.9. Sections follow Pryor and Johnson (1971).

* 25 *Plantation species from the* Exertaria (SN i.e. E. camaldulensis) could potentially hyridise *with all other major sections, except possibly the mallees,* Dumaria *(SL).*

The reported natural hybrid combinations would suggest that the *Exertaria* (SN e.g. *E. camaldulensis*) could potentially hyridise with all other major sections, except the mallees, *Dumaria* (SL). However, while many manipulated crosses have been undertaken with this section (most involving *E. camaldulensis* Appendix 1), and vigorous plants have been selected, the strength of the barriers to inter-subgeneric hybridisation and gene flow are often masked in the presentation of the data. For example, even though considerable effort is going toward the development of *E. camaldulensis* x *globulus* hybrids, hybridisation is not successful when *E. globulus* is used as the female due to its large flower size. When the cross is undertaken using *E. camaldulensis* as the female, seed set is reduced to 25% that of intraspecific outcrosses and due to high levels of abnormal seedlings which die within 12 months in the nursery, there is a 92% reduction in the number of healthy plants obtained per flower pollinated in the F_1 crosses compared to the intraspecific controls (McComb *et al.* 2000). A similar conclusion is reached from Table 3.2.

* 26 *Plantation species from the section Transversaria (SE e.g.* E. grandis, E. pellita*) are more likely to hybridise with species from either the* Exertaria *(SN) or* Maidenaria *(SP) than the other sections of* Symphyomytus.

According to Ladiges (1997), the section *Transversaria* is suggested to be the oldest lineage and sister to the remaining sections. It is mainly an eastern section. The only previous western representative, *E. diversicolor*, has been now classified into a monotypic section by Brooker (2000). The *Transversaria* has the highest overall level of intersectional hybrids and all are with either the *Exertaria* (SN) or *Maidenaria* (SP), consistent with their higher frequency of natural intersectional crosses. All crosses attempted with the *Bisectaria* have failed, and although none have been reported having been attempted with *Dumaria* or *Adnataria* species. The absence of reported natural hybrids when the sections Maidenaria**,** Exertaria and Transversaria co-occur with species from the sections *Bisectaria*, *Adnataria* and *Dumaria (*Figure 5.8*)* would suggest that the likelihood of successful hybridisation with these three sections is very low.

* 27 *Plantation species from the section* Maidenaria (e.g. E. globulus, E. nitens, E. dunnii) *are unlikely to hybridise and introgress with species from* Bisectaria *(SI) or* Dumaria *(SL) and potentially even* Adnataria *(SU).*

Crosses of *Maidenaria* with *Transversaria* and *Exertaria* species have been reasonably successful. However, as noted by Assis (2000) F_1 hybrid inviability problems were most frequent when species from the *Maidenaria* were involved, both in intra-sectional crosses as well as crosses with other sections, such as *Transversaria* (see also comments above regarding *E. camaldulensis* x *globulus*). No natural hybrids were reported with *Bisectaria* and *Dumaria* species and all manipulated crosses attempted have failed, suggesting a strong barrier to hybridisation. While there are few natural or successful manipulated crosses with the *Adnataria* species, the barrier to crossing appears to be less than with the two mallee sections.

5.8.3 Between species within sections

Natural and manipulated interspecific hybridisation between species from different series is relatively commonly reported, and details of natural hybrid combinations are given in Griffin *et al.* (1988; Table 7) on the frequency of interseries hybrids in each of the major sections. In the case of hybridisation between species from the same taxonomic series or different series from the same genus, the probability of successful hybridisation will be high and must then be examined on a case by case basis and other criteria utilised to minimise the risk. Specific natural and manipulated hybrid combinations reported for the main plantation species are given in Appendix 1.

6. Summary of research priorities

Key research required for the refinement of risk management is detailed below.

6.1 Distance and levels of pollen dispersal and gene flow

The definition of pollen dispersal patterns for the major plantation species is a high priority to better define buffer distances. This research should encompass determination of the major pollinators and factors affecting their movements as well as direct studies of pollen dispersal using morphological or molecular markers. It is important to determine the levels of long-distance dispersal, how extensive is the tail of the dispersal curve, and how population structure, resource patchiness and changing pollinator communities affect dispersal patterns.

This research should include studies directly monitoring current levels and patterns of hybridisation and gene flow across plantation/native forest interfaces using older plantations that have reached reproductive maturity. Measuring these rates of hybridisation is critical for risk assessment (Ellstrand *et al.* 1999), and studies should be aimed at determining factors which will allow better prediction of the risk of gene flow.

6.2 Crossability of the main plantation species

A detailed update of natural and manipulated hybrids in the genus should be undertaken to provide land managers with a first alert on the potential for hybridisation with local species. This research should be aimed at updating the last review of hybridisation in the genus to better predict trends in hybridisation in the genus. The hybrid information is required to be aligned with the new taxonomy and the last 12 years of literature reviewed for new natural and artificial hybrid combinations. However, the potential of the main plantation species to cross as pollen donors and produce fit hybrids should be directly assessed for the native species considered at risk in planting zones. In cases, this will require manipulated crossing as well as knowledge of flowering times. The flowering time of plantation species may vary markedly across the planting estate and differ from that recorded in their native populations. Research is required to understanding factors affecting flower abundance and flowering time in plantations and native species at risk in the estate.

6.3 Selection of sustainability traits

The possibility of integrating sustainability as a secondary breeding or deployment objective should be investigated. Traits that allow the risk of genetic pollution to be minimised should be identified and the potential for traditional means of selection investigated to allow targeted deployment in high-risk areas. Such traits could include flowering precocity, flowering abundance, flowering season and male sterility.

6.4 Modelling of reproductive loads

This research should be aimed at minimisation of reproductive output in high-risk situations to be linked to plantation management in terms of silvicultural and thinning regimes and optimal harvest time.

6.5 Spatial patterns of genetic diversity

Research and/or integration of the literature on spatial patterns of genetic variation in the native gene pools of the main plantation species should be undertaken in order to develop gene pool management strategies for the main plantation species. This research should also encompass monitoring of the degree of genetic differentiation between planted and native forest gene pools, for both adaptive traits and neutral markers.

6.6 Long-term monitoring of introgression

Base-line molecular data should be established for key sites to allow for long-term monitoring of introgression.

6.7 Impacts on local biodiversity

Due the dearth of knowledge regarding how biodiversity in eucalypt plantations compares to that in native forest and other vegetation types being replaced by tree farms, basic survey work is needed as a starting point. By comparing biodiversity in plantations with even-aged regrowth native forest and old-growth native forest, the effects of reduced structural diversity and reduced species diversity in tree farms could be separated. The importance of understorey vegetation to biodiversity could be investigated by comparing plantations where the understorey has been suppressed with those with well-developed understoreys. Such studies would need to be carried out in numerous different situations because of the highly varied composition of native forests and the range of eucalypt species used in plantations.

The effects tree farms have on biodiversity in nearby native vegetation could be investigated by surveying fauna in native vegetation at varying distances from plantations. In particular, the effects on insect herbivores and their predators and parasites, as well as pollinators, may be affected. Understanding these impacts requires greater knowledge of food webs in Australian native ecosystems. Of greatest interest are the relationships between vegetation, incorporating species compositions and structural elements, and the predators and parasites of herbivorous insects that experience population explosions in plantations.

7. Conclusions

The introduction of non-native species, hybrids and provenances into the range of a potentially interbreeding species may have a direct effect on the gene pool through genetic pollution as well as have indirect effects through impacts on other components of biodiversity. Hybridisation appears to have been an integral part of the evolution of eucalypts. However, while eucalypts have a reputation for hybridisation, there are in fact strong reproductive barriers that prevent hybridisation amongst a large component of the flora. In many cases the risk of genetic pollution will be small due to strong barriers to hybridisation between distantly related species, differences in flowering time or differences in other floral traits. For example, there is no risk of hybridisation between species from the different major eucalypt genera/subgenera and even within the *Symphyomyrtus* there are strong barriers to hybridisation amongst many of the taxonomic sections. Within sections, the inherent barriers to hybridisation are generally much weaker, although even hybrids between relatively closely related species often exhibit reduced vegetative vigour and reduced reproductive output compared to parental types which would limit the possibility of gene flow between planted and native forest gene pools. Nevertheless, there will be many species or provenance combinations where the conservation status of adjacent forest and risk of hybridisation and introgression are assessed to be high. Naturally small or remnant populations are going to be at particular risk. Under such circumstances, the challenge is to define acceptable isolation distances, planting stock or silvicultural regimes that will decrease this risk.

No major additional genetic risk is seen from the deployment of exotic hybrids as opposed to an exotic species in the landscape. The planting of non-local provenances or improved material within the range of the native gene pool has the potential to genetically impact on local gene pools to varying degrees and gene pool management strategies should be developed for the major plantation species. Such strategies will require a detailed knowledge of the spatial patterns of genetic differentiation in the native forest gene pool of these commercial species and the degree of differentiation between the local and exotic genotypes.

While genetically modified eucalypts have been developed, there are no reports of genetically modified eucalypts being field tested in Australia. Most authors consider reproductive sterility would be a prerequisite for the release of such eucalypts in Australia and, at least for the major plantation species in temperate regions, the constraints of vegetative propogation must first be overcome.

Pollen flow between plantation and native forest eucalypt species has already been reported and implementation of strategies to minimise the risk and consequences of genetic pollution is important if Australian forestry is to be certified as sustainable. There are many stages at which barriers may act to prevent gene flow between plantation and native species, and numerous opportunities to minimise the risk of genetic pollution. Such risk assessment should be an integral part of environmental impact assessments of eucalypt plantations and farm forestry.

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9. Appendix 1 Hybrids of the major plantation eucalypts

The major commercial eucalypt species likely to be used in farm forestry in Australia and reported natural and manipulated hybrids. Data is updated from Griffin *et al.* (1988).

<u>Vigour rating (**V**)</u>

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

<u>Female/male (**FM**)</u>

Whether the species listed was used as the female or male in the cross.

Code corresponds to that used by Pryor and Johnson (1971) for *Corymbia* species the codes used by Hill and Johnson (1995) are given. For alignment with Brookers' (2000) sections see Table 5.5.

Subgenus (first letter of P&J code)
I *Idiogenes* M *Monocalyptus* S *Symphyomyrtus* C *Corymbia*

Section (second letter of P&J code)
Monocalyptus

MA	Renantheria

Symphyomyrtus

SB	*Equatoria* *(Telocalyptus)*
SD	*Tingleria*
SE	*Transversaria*
SI	*Bisectaria*
SL	*Dumaria*
SN	*Exertaria*
SP	*Maidenaria*
SQ	*Umbra-warrenses*
SS	*Howittiannae*
SU	*Adnataria*
SW	*Sebaria*

Temperate regions

Eucalyptus globulus

P&J Subgenus *Symphyomyrtus* Section *Maidenaria* Series *Viminales* (SPIFL)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SPEA?	*E. barberi*		Williams and Potts 1996
SPEA?	*E. brookeriana*		Williams and Potts 1996
SPEAB	*E. ovata*		Williams and Potts 1996 Jordan *et al.* 1993
SPIAC	*E. kitsoniana*		Griffin *et al.* 1988
SPIFB	*E. goniocalyx*		Griffin *et al.* 1988
SPIFC	*E. nortonii*		Griffin *et al.* 1988
SPIFE	*E. cypellocarpa*		Kirkpatrick *et al.* 1973
SPIFJ	*E. pseudoglobulus*		Griffin *et al.* 1988
SPIFK	*E. bicostata*		Griffin *et al.* 1988
SPIJAC	*E. johnstonii*		Griffin *et al.* 1988
SPIKKA	*E. viminalis*		Griffin *et al.* 1988
SPIND	*E. cordata*		Williams and Potts 1996
SPINF	*E. rubida*		Griffin *et al.* 1988
SPINL	*E. urnigera*		Griffin *et al.* 1988
SPINN	*E. perriniana*		Williams and Potts 1996

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SECA-	*E. urophylla*	3	f	Griffin *et al.* 2000
SECAB	*E. grandis*	3	f	Griffin *et al.* 2000
SECAF	*E. robusta*	1		Griffin *et al.* 1988
SECCA	*E. pellita*			D. Boomsma pers. com.
SECGA	*E. longifolia*			Griffin *et al.* 1988
SIN:AA	*E. loxophloeba*			Griffin *et al.* 1988
SNEEPA	*E. camaldulensis*	3	f f	McComb *et al.* 2000 Mesbah 1995 Sasse *et al.* 2000
SPIDA	*E. dunnii*	3	f m	Griffin *et al.* 2000 Barbour and Spencer 2000 cut style
SPIFG	*E. nitens*	3	f	Potts *et al.* 2000 Griffin *et al.* 2000
SPIFI	*E. maidenii*	1	m	Potts unpubl. data
SPIFK	*E. bicostata*	1	f	Potts unpubl. data
SPIKKA	*E. viminalis*	1		Griffin *et al.* 1988
SPINIA	*E. gunnii*	1	f	Potts *et al.* 2000
failed				
SUX:A	*E. sideroxylon*	7	f	Griffin *et al.* 1988

Eucalyptus nitens

Symphyomyrtus Section *Maidenaria* Series *Viminales* (SPIF)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SPIHA	*E. quandrangulata*		Tibbits et al. 1997

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SECAB	*E. grandis*	3 2	f	Shelbourne *et al.* 1999 Verryn 2000 Tibbits 2000
SECAC	*E. saligna*	2	m	Tibbits 2000
SECAD	*E. botryoides*	4	m	Tibbits 2000
SIVEH	*E. oldfieldi*	7	m	Tibbits 2000
SNEEPA	*E. camaldulensis*	3 3	m m	Tibbits 1988; Tibbits 1989 Tibbits 2000
SNEER	*E. rudis*	4	m	Tibbits 2000
SPEAB	*E. ovata*	1	m	Tibbits 2000
SPEAH	*E. rodwayi*	2	m	Tibbits 2000
SPIAA	*E. neglecta*	2	m	Tibbits 2000
SPIBA	*E. parvifolia*	1	m	Tibbits 2000
SPIDA	*E. dunnii*	2	m	Tibbits 2000
SPIFE	*E. cypellocarpa*			Griffin *et al.* 1988
SPIFL	*E. globulus*	3	m m m	Potts *et al.* 2000 Tibbits 1988; Tibbits 1989 Tibbits 2000 Griffin *et al.* 2000
SPIHA	*E. quandrangulata*	6	m	Tibbits 2000
SPIJAC	*E. johnstonii*	1	m	Tibbits 2000
SPIKC	*E. macarthurii*	6	m	Tibbits 2000
SPIKKA	*E. viminalis*	1	 m	Tibbits 1988; Tibbits 1989 Tibbits 2000
SPINCA	*E. dalrympleana*	1	m	Tibbits 2000
SPINF	*E. rubida*	1	m	Tibbits 2000
SPINH	*E. glaucescens*	7	m	Tibbits 2000
SPINIA	*E. gunnii*	1	mf	Tibbits 1988; Tibbits 1989; Tibbits 2000
SPINK	*E. morrisbyi*	2	m	Tibbits 2000
SPINL	*E. urnigera*	S	m	Tibbits 2000
SPINN	*E. perriniana*	2	mf	Tibbits 2000
SPINO	*E. cordata*	1	m	Tibbits 2000
failed				
SIP:G	*E. decipiens*	7	m	Tibbits 2000
SIT:N	*E. gillii*	7	m	Tibbits 2000
SLOAB	*E. incrassata*	7	m	Tibbits 2000
SNEEB	*E. tereticornis*	7	m	Tibbits 2000
SPINQ	*E. pulverulenta*	7	m	Tibbits 2000
SUNEA	*E. lansdowneana*	7	m	Tibbits 2000
SUP:AB	*E. fibrosa*	7	m	Tibbits 2000

Subtropical regions

Eucalyptus grandis

Symphyomyrtus Section *Transversaria* Series *Salignae* (SECAB)

NATURAL HYBRIDS

P&J code	*Species*	Comments	Reference
SECAC	*E. saligna*		Griffin *et al.* 1988
SECAF	*E. robusta*		Griffin *et al.* 1988
SECCA	*E. pellita*		Griffin *et al.* 1988
SNEEB	*E. tereticornis*		Griffin *et al.* 1988

MANIPULATED HYBRIDS

P&J code	*Species*	V	FM	Reference
SECA-	*E. urophylla*	1 1		Vigneron and Bouvet 2000 de Assis 2000 Wu *et al.* 1996 D. Boomsma pers. com.
SECAD	*E. botryoides*			D. Boomsma pers. com.
SECCA	*E. pellita*	1 1		Griffin *et al.* 1988 de Assis 2000
SNABAA	*E. alba*	1	f	Griffin *et al.* 1988
SNEEB	*E. tereticornis*	1		Griffin *et al.* 1988 Vigneron and Bouvet 2000 Verryn 2000
SNEEPA	*E. camaldulensis*	1 1 1	f	Griffin *et al.* 1988 de Assis 2000 Verryn 2000 Sasse *et al.* 2000 Dale *et al.* 2000
SPIDA	*E. dunnii*	3 3	fm	Griffin *et al.* 2000 de Assis 2000
SPIFG	*E. nitens*	3 2	m	Shelbourne *et al.* 1999 Verryn 2000 Tibbits 2000
SPIFI	*E. maidenii*	 3	fm	D. Boomsma pers. com. de Assis 2000
SPIFL	*E. globulus*	3	m	Griffin *et al.* 2000
SPINIA	*E. gunnii*	3	f	Potts unpubl. data
SPINQ	*E. pulverulenta*			Paton 1981
SUX:CA	*E. leucoxylon*	7	m	Griffin *et al.* 1988
SECCC	*E. resinifera*			David Lee pers. com.

Eucalyptus pellita

Symphyomyrtus Section *Transversaria* Series *Salignae* (SECCA)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SECAB	*E. grandis*		Griffin *et al.* 1988
SECCC	*E. resinifera*		Griffin *et al.* 1988
SECEDA	*E. punctata*		Griffin *et al.* 1988
SNEE-	*E. brassiana*		Harwood 1998

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SBA:A (T)	*E. deglupta*	7 5 1?	*m*	Griffin *et al.* 1988 Vigneron and Bouvet 2000 Sariot 1991
SECA-	*E. urophylla*	1 3 	fm	Harwood 1998 Vigneron and Bouvet 2000 de Assis 2000 Wu *et al.* 1996
SECAA	*E. deanei*			D. Boomsma pers. com.
SECAB	*E. grandis*	1 1		Griffin *et al.* 1988 de Assis 2000
SNABAA	*E. alba*	6	f	Griffin *et al.* 1988
SNEEB	*E. tereticornis*	1	f	Griffin *et al.* 1988
SNEEPA	*E. camaldulensis*			Harwood 1998
SPIFI	*E. maidenii*			D. Boomsma pers. com.
SPIFL	*E. globulus*			D. Boomsma pers. com.

Eucalyptus pilularis

Monocalyptus Section *Renantheria* Series *Pilularis* (MOIAAA)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
MAHCI	*E. tindaliae*		Griffin *et al.* 1988
MAIBB	*E. planchoniana*		Griffin *et al.* 1988
MOG:C	*E. acmendoides*		Griffin *et al.* 1988
MOHCF	*E. capitellata*		Griffin *et al.* 1988
MOHEF	*E. globoidea*		Griffin *et al.* 1988
MOHELA	*E. oblonga*		Griffin *et al.* 1988
MOTHAA	*E. piperita*		Griffin *et al.* 1988

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
MOIAAA	*E. delegatensis*	1	f	Griffin *et al.* 1988

Eucalyptus cloeziana

Idiogenes Section *Gympiaria* Series *Cloezianae* (IAA:A)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
MAG:C	*E. acmenoides*	cpDNA indicates *E. acemenoides* is the female	Stokoe *et al.* 2000

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
failed				
SNAAA	*E. urophylla*	7	f	Griffin *et al.* 1988
SNEEB	*E. tereticornis*	7	f	Griffin *et al.* 1988

Eucalyptus dunnii

Symphyomyrtus Section *Maidenaria* Series *Viminales* (SPIDA)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SECA-	*E. urophylla*		f	Griffin *et al.* 2000 D. Boomsma pers. com.
SECAB	*E. grandis*	3 3	mf	Griffin *et al.* 2000 de Assis 2000
SPIFI	*E. maidenii*	1		de Assis 2000
SPIFL	*E. globulus*	3	m f	Griffin *et al.* 2000 Barbour and Spencer 2000 cut style

Corymbia henryi/variegata/maculata/citriodora complex[1]

Genus *Corymbia* Section *Politaria* Series *Maculatae* (ACSAAX, ACSAAL, ACSAAS, ACSAAC)
[1] genus *Corymbia* by Hill and Johnson (1995 and codes therein (3rd letter refers to the Section). Also in dry regions.

NATURAL HYBRIDS

***Corymbia citriodora* (ACSAAC)**

P&J code	*Species*	Comments	Reference
ACOYYN	*C. catenaria*		Hill and Johnson 1995
ACSAAL	*C. variegata*		Hill and Johnson 1995
ACSAAS	*C. maculata*		Griffin *et al.* 1988

***Corymbia maculata*(ACSAAS)**

P&J code	*Species*	Comments	Reference
ACIBBA	*C. gummifera*		Hill and Johnson 1995
ACIGGI	*C. intermedia*		Hill and Johnson 1995
ACSAAC	*C. citriodora*		Griffin *et al.* 1988
ACSAAL	*C. variegata*		Hill and Johnson 1995

***Corymbia variegata* ACSAAL)**

P&J code	*Species*	Comments	Reference
ACOYYE	*C. bloxsomei*		Griffin *et al.* 1988 Hill and Johnson 1995
ACOYYO	*C. watsoniana*		Griffin *et al.* 1988 Hill and Johnson 1995
ACSAAC	*C. citriodora*		Hill and Johnson 1995
ACSAAS	*C. maculata*		Hill and Johnson 1995
ACSAAS	*C. maculata*	x *citriodora*	Griffin *et al.* 1988

***Corymbia henryi* (ACSAAX)**

P&J code	*Species*	Comments	Reference
ACQUUT	*C. torelliana*	Cultivated *torelliana*, native *henryi*	Hill and Johnson 1995
ACSAAL	*C. variegata*		Hill and Johnson 1995

MANIPULATED HYBRIDS

P&J code	*Species*	V	FM	Reference
ACQUUT	*C. torelliana x c*	1 1		Griffin *et al.* 1988 Vigneron and Bouvet 2000 de Assis 2000 David Lee (unpubl. data)

Dry zone

Eucalyptus cladocalyx

P&J *Symphyomyrtus* Section *Bisectaria* Series *Cladocalyces* (SIS:A)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SNEEPA	*E. camaldulensis*		Griffin *et al.* 1988

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SIDCB	*E. platypus*	1	m	Wirthensohn *et al.* 1996 Ellis 1991
SIDCD	*E. spathulata*	4	fm	Ellis 1991, M. Wallwork pers. comm. 2000
SNEE?	*E. flindersii*	7	m	Ellis 1991
SUNEH	*E. viridis*	1	m	Ellis 1991

Eucalyptus occidentalis

Symphyomyrtus Section *Bisectaria* Series *Occidentales* (SIDAA)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SIDCD	*E. spathulata*	1	f	Ellis 1991

Eucalyptus camaldulensis

Symphyomyrtus Section *Exertaria* Series *Tereticornis* (SNEEP)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SECAF	*E. robusta*	spontaneous in exotic plantations	Kha and Cuong 2000
SIS:A	*E. cladocalyx*		Griffin *et al.* 1988
SNABAA	*E. alba*		Griffin *et al.* 1988
SNABE	*E. bigalerita*		Griffin *et al.* 1988
SNEEB	*E. tereticornis*		Griffin *et al.* 1988
SNEEFA	*E. blakelyi*		Griffin *et al.* 1988
SNEEL	*E. dwyeri*		Griffin *et al.* 1988
SNEER	*E. rudis*		Griffin *et al.* 1988
SPEAB	*E. ovata*		Griffin *et al.* 1988
SPIDCA	*E. bridgesiana*		Griffin *et al.* 1988
SPIKKA	*E. viminalis*		Griffin *et al.* 1988
SUDEC	*E. largiflorens*		Griffin *et al.* 1988
SUX:A	*E. melliodora*		Griffin *et al.* 1988
SUX:CA	*E. leucoxylon*		Griffin *et al.* 1988

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
SEB:A	*E. diversicolor*		m	Mesbah 1995
SECAB	*E. grandis*	1 1	 m	de Assis 2000 Mesbah 1995 Sasse *et al.* 2000 Dale *et al.* 2000
SECAD	*E. botryoides*	1		Griffin *et al.* 1988
SIS:A	*E. cladocalyx*		m	Mesbah 1995
SNAAA	*E. urophylla*	1 1		de Assis 2000 Kha and Cuong 2000 Wu *et al.* 1996
SNEEB	*E. tereticornis*	1	m	Griffin *et al.* 1988 Mesbah 1995
SNEEFA	*E. blakelyi*	1	f	Griffin *et al.* 1988
SNEEPA	*E. macarthurii*	1	f	Griffin *et al.* 1988
SNEEPA	*E. viminalis*	1	fm	Griffin *et al.* 1988
SNEEX	*E. exerta*	1		Kha and Cuong 2000
SPIFI	*E. maidenii*		m	Mesbah 1995
SPIFL	*E. globulus*	3	m	McComb *et al.* 2000 Sasse *et al.* 2000
SPINIA	*E. gunnii*	5	mf	Griffin *et al.* 1988
failed				
MAHAB	*E. laevopinea*	7	f	Griffin *et al.* 1988
MAKCB	*E. fastigata*	7	f	Griffin *et al.* 1988

Eucalyptus sideroxylon

Symphyomyrtus Section *Adnataria* Series *Melliodoae* (SUX:I)

Includes E. *sideroxylon* ssp. *tricarpa* (subsequently given specific status Hill and Johnson 1991)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SUH:A	*E. intertexta*		Griffin *et al.* 1988
SUL:DA	*E. woollsiana*		Griffin *et al.* 1988
SUL:G	*E. albens*		Griffin *et al.* 1988
SUNCA	*E. bosistoana*		Griffin *et al.* 1988
SUNEBA	*E. odorata*		Griffin *et al.* 1988
SUNEHA	*E. viridis*		Griffin *et al.* 1988
SUP:AA	*E. fibrosa*		Griffin *et al.* 1988
SUP:F	*E. drepanophylla*		Griffin *et al.* 1988
SUT:F	*E. fasciculosa*		Griffin *et al.* 1988
SUX:A	*E. melliodora*		Griffin *et al.* 1988
SUX:CA	*E. leucoxylon*		Griffin *et al.* 1988

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**
failed				
SIVCGA	*E. caesia*	7	f	Griffin *et al.* 1988
SPIFL	*E. globulus*	7	n	Griffin *et al.* 1988
SPIKC	*E. macarthurii*	7	m	Griffin *et al.* 1988

Eucalyptus kochii

Symphyomyrtus Section *Bisectaria* Series *Oleosae* (SIT:E)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**

Eucalyptus horistes

Symphyomyrtus Section *Bisectaria* Series *Oleosae* (SIT:?)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**

Eucalyptus polybractea

Symphyomyrtus Section *Adantaria* Series *Odoratae* (SUNED)

NATURAL HYBRIDS

P&J code	***Species***	**Comments**	**Reference**
SLE:GA	*E. dumosa*		Griffin *et al.* 1988
SUDGA	*E. behriana*		Griffin *et al.* 1988
SUNEHA	*E. viridis*		Griffin *et al.* 1988

MANIPULATED HYBRIDS

P&J code	***Species***	**V**	**FM**	**Reference**

Appendix 2 Eucalypt species listed as endangered or vulnerable

(Environment Australia. Endangered Species Protection Act 1992, Schedule 1 - January 2000.)
(http://www.biodiversity.environment.gov.au/plants/threaten/lists/esp_lists/sched1-ind.htm)

SPECIES THAT ARE ENDANGERED

Eucalyptus absita
Eucalyptus balanites
Eucalyptus beardiana
Eucalyptus bennettiae
Eucalyptus brevipes
Eucalyptus burdettiana
Eucalyptus conglomerata
Eucalyptus copulans
Eucalyptus crenulata
Eucalyptus crucis subsp. *praecipua*
Eucalyptus cuprea
Eucalyptus dolorosa
Eucalyptus graniticola Brooker & Hopper ms
Eucalyptus imlayensis
Eucalyptus impensa
Eucalyptus insularis
Eucalyptus leprophloia
Eucalyptus morrisbyi
Eucalyptus pachycalyx subsp. *banyabba*
Eucalyptus phylacis
Eucalyptus pruiniramis
Eucalyptus recurva
Eucalyptus rhodantha var. *petiolaris*
Eucalyptus sp. Howes Swamp Creek (M.Doherty, 19/7/1985, NSW 207054)

SPECIES THAT ARE VULNERABLE

Eucalyptus aquatica
Eucalyptus argophloia
Eucalyptus argutifolia
Eucalyptus articulata
Eucalyptus beaniana
Eucalyptus benthamii
Eucalyptus blaxellii
Eucalyptus cadens
Eucalyptus caleyi subsp. *ovendenii*
Eucalyptus camfieldii
Eucalyptus cannonii
Eucalyptus ceracea
Eucalyptus cerasiformis
Eucalyptus coronata
Eucalyptus crispata
Eucalyptus crucis subsp. *crucis*
Eucalyptus glaucina
Eucalyptus hallii
Eucalyptus impensa
Eucalyptus infera
Eucalyptus johnsoniana
Eucalyptus kabiana
Eucalyptus kartzoffiana
Eucalyptus langleyi
Eucalyptus lateritica
Eucalyptus leptoloma
Eucalyptus mckieana
Eucalyptus merrickiae
Eucalyptus mooreana
Eucalyptus nicholii
Eucalyptus olivacea Brooker & Hopper ms.
Eucalyptus paedoglauca
Eucalyptus parramattensis subsp. *decadens*
Eucalyptus parvula
Eucalyptus platydisca L.A.S.Johnson & K.Hill ms.
Eucalyptus pulverulenta
Eucalyptus pumila
Eucalyptus raveretiana
Eucalyptus rhodantha var. *rhodantha*
Eucalyptus rhodops
Eucalyptus robertsonii subsp. *hemisphaerica*
Eucalyptus rubida subsp. *barbigororum*
Eucalyptus rubida subsp. *canobolensis*
Eucalyptus scoparia
Eucalyptus steedmanii
Eucalyptus strzeleckii
Eucalyptus suberea
Eucalyptus synandra
Eucalyptus tetrapleura
Eucalyptus virens
Eucalyptus xanthope