Chapter 7

General discussion: risk assessment and management of exotic gene flow from plantations in Tasmania

7.1 Introduction

The present work has provided valuable information on the patterns of pollen-mediated gene flow from *E. nitens* plantations in Tasmania, and the factors that influence the degree to which it may occur. This information can now be used to assess the risk of gene flow and introgression, and determine which species and populations are likely to be most affected. Potts *et al.* (2003) provided a framework for such risk assessment that outlines each step in the process of gene flow, and the points at which barriers may occur to prevent or reduce levels of introgression. This framework will be used as the basis for the present chapter, and represents the process that should be adopted to identify the species at risk that will need further population-by-population risk analysis.
7.2 Framework of risk assessment

7.2.1 Identification of conservation values

Prior to determining the potential for gene flow into native populations, the conservation value of each species should be considered. Species of high conservation value i.e. those that are rare or endangered, within areas of reservation or part of an evolutionary significant unit, may need more thorough assessment of the risks, in the same way that other potential threats are assessed (Potts et al. 2003). Included in this, the proportion of the range of each native species that is at risk will also need to be estimated and monitored. This may result in more abundant species being of concern if they are frequently in the proximity of plantations. This will be best conducted with spatial information and analysis systems (Geographical Information Systems), which will integrate conservation details for individual populations across Tasmania, with the distribution of plantations. In addition to this, information dictating the potential for gene flow, outlined in the present work, will need to be integrated into this system, as well as new information that is gathered in the future. The development of this system will therefore represent a practical conclusion to the research on exotic gene flow in Tasmania.

7.2.2 Pollen quantity

7.2.2.1 Age to first flowering and flower abundance

Gene flow from plantations will not occur if they do not flower. Half of the *E. nitens* in the flowering survey conducted in Chapter 5 were growing as routine plantations, indicating the ability of *E. nitens* to flower under such conditions. In a study of the flowering characteristics of *E. nitens* in Tasmania (Moncur et al. 1994), most of the *E.*
nitens populations that were assessed, were plantations. These plantations ranged in age from four to eleven years of age, and again indicated the capacity of E. nitens to flower prior to harvesting. At least for pulp wood regimes, harvesting usually occurs at 10-14 yrs of age (K. Joyce from Gunns Ltd pers. com.). Similar to the present study, Moncur et al. (1994) used trees that were either in edge rows of plantations, or in seed orchards or fence rows, both of which have similar growing conditions to edge row trees (i.e. high light availability). These conditions promote flowering (Graca 1987; Williams 2000), and therefore levels of flowering documented for edge row trees are greater than trees within plantations. Planting of genotypes or species that flower later than harvest age, as edge trees around the rest of the plantation, may prove an effective strategy for at least reducing exotic pollen output. However, further information on the levels and pattern of flowering within E. nitens plantations are required. An additional influence on flowering will be the change in the management of plantations for pulp wood, to management for saw log production. Interest in this alternative management regime is increasing in Tasmania (Kube et al. 2001). This will result in greater spacing between trees within plantations and a considerably later age of harvesting. Both of these factors will result in greater amounts of flowering and pollen release by the E. nitens and a greater potential for exotic gene flow.

7.2.2.2 “Source vs sink”

The size of the plantation relative to the population of the native species needs to be considered, as this will influence the quantity of pollen that reaches native flowers (Potts and Reid 1988; Potts et al. 2003). Some information on the influence of source to sink ratios came from the assessment of pollen dispersal patterns from E. nitens plantations.
Trees assessed at the most fragmented native site, tended to display higher levels of hybridisation with the local *E. nitens* plantation than trees assessed at the least fragmented site. The more highly fragmented population had much fewer trees in a given area relative to the size of the plantation, resulting in the source to sink ratio being greater. This same pattern was found for hybridisation between *E. risdonii* and *E. amygdalina* (Potts and Reid 1988), where pollen dispersal into small populations resulted in higher levels of F1 hybridisation ($\bar{X} = 42\%$) compared with the boundary of larger populations ($\bar{X} = 23.5\%$). It is certainly clear, therefore, that higher source to sink ratios will increase levels of gene flow (see also Hamrick and Nason 2000; Dick et al. 2003), but in terms of specific guidelines on the impacts of various source to sink ratios, limited information can be provided.

### 7.2.3 Pollen dispersal

The inability of *E. nitens* pollen to reach receptive stigma of native species will prevent exotic gene flow. Patterns of pollen flow are typically variable and can be influenced by a range of factors. These include the behaviour of pollen vectors (i.e. insect, bird, mammal or wind), inter and intraspecific flowering patterns, pollen longevity and the structure of donor and recipient populations (Adams 1992; Ellstrand 1992b; Hamrick and Nason 2000). Consequently, determining effective guidelines based on patterns of pollen movement can be difficult. Chapter 2 describes the pattern of pollen flow from three plantations in Tasmania. Pollen flow across all the sites resulted in a steep drop in the levels of hybridisation from the boundary (14%) through to 2-300 m (1%), which then continued at this level to the limits of the studied area. However, a trend was evident at the more fragmented sites, for higher levels of hybridisation occurring at
greater distances from plantation boundaries. This result suggests that 300 m would be an effective buffer distance for substantially reducing levels of gene flow into continuous synchronously flowering forests. However, for fragmented forest populations or where source to sink ratios are higher, isolation distances will have to be much greater.

7.2.4 Divergence in season of flowering

The potential exists for flowering time differences between *E. nitens* and native populations to prevent gene flow (Chapter 5). The present work demonstrated that, despite high levels of variability in the time of flowering across sites for each species, the level of flowering overlap they displayed with *E. nitens* was relatively similar and predictable, allowing for species wide generalisations to be made. Combined with the spatial proximity of plantations to native species, these data reduced the number of species at substantial risk of pollination by *E. nitens* in Tasmania down to eight; these were *E. brookeriana*, *E. gunnii*, *E. johnstonii*, *E. ovata*, *E. perriniana*, *E. rodwayi*, *E. rubida* and *E. subcrenulata*. The rare species *E. perriniana*, was particularly at risk of pollination due to its small population size, high flowering overlap and close spatial proximity to *E. nitens*.

The analysis of the flowering time data further indicated that the protandrous nature of eucalypt flowering appeared to be biasing the direction of pollen flow and hybridisation. If a native species flowered later than *E. nitens* in a season, but still overlapped in flowering, it appeared to result in lower levels of hybridisation than in the reciprocal cross onto *E. nitens*. The species for which protandry is likely to reduce levels of gene
flow from plantations are *E. cordata* (highland populations), *E. dalrympleana*, *E. rodwayi*, *E. subcrenulata*, *E. urnigera* and *E. viminalis*. Four of these species, *E. cordata*, *E. dalrympleana*, *E. urnigera* and *E. viminalis*, were already identified as having low potential for pollination by *E. nitens* based on flowering time and spatial proximity, and therefore the influence of protandry may further reduce this likelihood.

### 7.2.5 Crossability

For the species that are not reproductively isolated from *E. nitens* by pre-pollination barriers, post-pollination mechanisms appear to further reduce the likelihood of gene flow. Firstly, a strong barrier exists to crossing between species from subgenus *Eucalyptus* and *Symphyomyrtus* (Griffin *et al.* 1988; Ellis *et al.* 1991). This results in almost half of Tasmania’s native eucalypt species being incompatible with *E. nitens* (which belongs to *Symphyomyrtus*). Of the native *Symphyomyrtus* species, *E. globulus* is also unable to be pollinated by *E. nitens* due to style length incompatibility (Gore *et al.* 1990). Combined with this, work conducted in Chapter 6 provided the first suggestion that further post-mating barriers exist between *E. nitens* and many native *Symphyomyrtus* species. Supplementary pollination of *E. nitens* pollen onto open-pollinated flowers of native *Symphyomyrtus* species produced hybrids with only six of the 13 species tested. Controlled pollination with *E. nitens* pollen compared to intraspecific pollen, also showed a significant decrease in seed per flower. Of the eight species identified as at risk of *E. nitens* pollination, based on their flowering time and spatial proximity, four did not produce hybrids after supplementary pollination (*E. johnstonii*, *E. rodwayi*, *E. rubida* and *E. subcrenulata*). This therefore could further reduce the number of species at substantial risk. However, these results from
supplementary pollination have to be verified, as low numbers of seed were tested for all four of these species. Nevertheless, the potential does appear to exist for effective post-mating barriers to exotic gene flow.

7.2.6 Post-dispersal fitness

7.2.6.1 F1 hybrid establishment and vegetative fitness

If F1 hybrid seed is produced, it appears likely that post-dispersal selection will reduce the proportion of exotic hybrids that establish in the wild, compared to the native species (Chapter 4). This selection is also likely to be sustained through the older ages of the hybrids. However, whether it will prevent them from reaching reproductive maturity is uncertain. Nevertheless, combined with other partial barriers to gene flow, post-dispersal barriers may be effective at reducing gene flow and introgression to very low levels. The environment in which the exotic E. nitens F1 hybrids establish in, may influence the degree to which post-dispersal selection will restrict gene flow (Anderson 1948; Arnold 1997). Due to the limited seed dispersal capacity of eucalypts (Chapter 3, Cremer 1966; Potts and Wiltshire 1997), exotic E. nitens hybrids are unlikely to establish out of the maternal parent’s habitat. This therefore provides a greater focus for future assessments of the fitness of exotic hybrids in the wild, which will need to be conducted for the species at high risk of exotic gene flow. If particular exotic F1 hybrid combinations do prove to have poor fitness, this will impact on the reproductive output of the native maternal parent, as fewer offspring will be capable of surviving. This is likely to be an insignificant impact when levels of hybridisation are low. However, in cases when levels of hybridisation are high, particularly in small populations such as that for E. perriniana, this impact may be significant.
Chapter 7: General discussion

The work described in Chapter 4 also verified the importance of disturbance for the establishment of exotic *E. ovata x nitens* F₁ hybrids and pure *E. ovata*, which is the case for the establishment of most species of eucalypts (Ashton and Williams 1973; Ashton 1975a; Bowman and Kirkpatrick 1986; Gill 1997). This information could potentially be used for the management of exotic gene flow. If, for example, a plantation had been established next to a population at risk of gene flow, preventing disturbance of that native population until after the plantation was harvested, and then avoiding future planting in that area, would prevent the establishment of most hybrid seed. In addition to this, the distinct characteristics of the *E. nitens* F₁ hybrids, documented in Chapter 6, would allow the confident identification of exotic hybrids in the wild. Consequently, if exotic hybrids did establish in a native population of concern, a program of manual weeding could be developed for their removal.

7.2.6.2 *F₁* hybrid reproductive fitness

If the hybrids were to reach an older age, evidence indicates that they will be able to produce flowers and therefore reproduce (Drake 1981b; Potts 1986; Potts and Reid 1988; Potts and Wiltshire 1997). No evidence of inviability of *F₁* hybrid pollen appears to exist in the literature for eucalypts. Flower or capsule abundance of hybrids in the wild appears to vary from intermediate to below that of parental species (Drake 1981a; Drake 1981b; Potts 1986; Potts and Wiltshire 1997), but does not appear to represent a strong barrier to subsequent gene flow. Nevertheless, literature on the reproductive output of *F₁* hybrids of *Eucalyptus* in the wild is limited.
7.2.6.3 Potential for later generation hybridisation

The flowering characteristics, and in particularly the inheritance of characters that influence flowering time, appear to greatly influence the potential for later generation hybridisation. In many cases, the F1 hybrid will flower at an intermediate time relative to their parents and therefore have a high potential for backcrossing with the parental species. In other cases, such as expected for *E. ovata* × *E. nitens*, the F1 hybrids may be asynchronous in flowering with parental species and therefore have limited potential for backcrossing (Chapter 5, Lopez *et al.* 2000b; Barbour *et al.* 2002a). In these situations, the potential for three-way hybridisation then arises (Barbour *et al.* 2002a). However, while successful three-way hybridisation was reported in the present work (Chapter 6), their performance appeared poor relative to that of intraspecific outcrosses and many F1s, which would reduce the probability of introgression with a third species. In comparison, the backcross hybrids that were produced appeared to be as successful as intraspecific crosses, and their level of performance appeared unlikely to represent a barrier to introgression (a trend also seen for *E. globulus* and *E. nitens*) (Tilyard *et al.* 2000).

7.2.7 Guidelines based on taxonomic relatedness

While it is recognised that hybridisation is less likely to be successful between species that are more distantly related (Griffin *et al.* 1988; Ellis *et al.* 1991; Tibbits 2000; Delaporte *et al.* 2001b), this trend was not found to be the case in the present work under supplementary pollination (Chapter 6). Highest levels of hybridisation were recorded between species that were more distantly related to *E. nitens*. However, there was trend across the four series of native species in their ability to hybridise with *E. nitens*. 
irrespective of how closely related they were to *E. nitens*. Hybridisation was recorded for species from the series *Foveolatae* and *Orbiculare* (*E. nitens* belongs to *Globulares*) while it was limited with species from *Semiunicolores*, and no hybridisation was recorded with *Viminalae* under supplementary pollination.

### 7.3 Management of the species at risk

The broad-scale study identified four species appear to be of particular concern of exotic gene flow in Tasmania. These are *E. brookeriana*, *E. gunnii*, *E. ovata* and *E. perriniana*. This was based on their high proximity to plantations, flowering synchrony, and confirmed crossability with *E. nitens*, with the rare species *E. perriniana* being of particular concern. Several of the species that were found at risk of pollination did not produce *E. nitens* hybrids after supplementary pollination (i.e. *E. johnstonii*, *E. rodwayi*, *E. rubida* and *E. subcrenulata*). However, these findings will need to be verified before a post-mating barrier can be declared as effective at preventing the production of hybrids.

Of the species found at low risk of exotic pollination, i.e. *E. barberi*, *E. cordata*, *E. dalrympleana*, *E. urnigera* and *E. viminalis*, some displayed additional barriers that would act further to reduce the potential for gene flow. These were bias in the direction of gene flow due to protandry, apparent poor crossability of *E. nitens* pollen, and likely post-zygotic selection against the exotic hybrids in the wild. This would result in the risk of gene flow into populations of these species being even lower than that based on the potential for pollination alone. The same applies to the remaining species with low potential for exotic pollination, *E. archeri* and *E. vernicosa*. While they did not display all of these additional barriers, the high degree of spatial and/or ecological isolation
between the habitats where plantations are established and that of the populations of these species, would suggest that the potential for gene flow is low. The remaining species, *E. morrisbyi*, again would have virtually no opportunity for pollination by plantations. However, its close proximity to residential areas and small population size may place it at risk of gene flow from ornamental species.

Because of the difficulties in predicting gene flow, the broad-scale risk assessment presented here will need to be combined with strategies for monitoring levels of gene flow, to ensure that predicted levels are comparable to actual levels. The techniques developed in Barbour *et al.* (2002b), proved an effective way of easily assessing levels of hybridisation. Open-pollinated seed collections from trees in closest proximity to plantations, followed by its germination and growth under glasshouse conditions, allows for simple morphological screening for exotic *F₁* hybrids. The morphological characteristics of the *E. nitens* *F₁* hybrids with eleven of the 16 potential native seed parents have been outlined in Chapter 6. The allozyme marker developed in Barbour *et al.* (2002b) and in Chapter 3 could also be developed further, as well as new molecular markers, for verification of *E. nitens* *F₁* hybrids with other native species. In addition, monitoring the potential for pollination through flowering surveys of specific sites may be necessary, to verify the trends described in Chapter 5.

### 7.4 Concluding comments

Prior to this study and based on the limited data available, there appeared to be a high potential for pollen-mediated gene flow from exotic *E. nitens* plantations into large areas of native eucalypt forest throughout Tasmania. This prediction was based on a number
of factors. The large area, broad distribution and recent expansion of *E. nitens* plantations in Tasmania, which is likely to result in large quantities of exotic pollen being released into native forests, as the plantation estate matures (Wood *et al.* 2001, Fig. 5.1). Combined with this, patterns of recorded interspecific hybridisation, suggested that *E. nitens* could hybridise with over half the native species (Griffin *et al.* 1988; Williams and Potts 1996), and artificial pollination studies had also shown that *E. nitens* could also act as a mother tree in hybridising with many of these species (Tibbits 1989; Tibbits 2000). In addition, hybridisation between plantation grown *E. nitens* and *E. ovata* had already been detected (Barbour *et al.* 2002b). Consequently, a high potential for exotic gene flow was evident. Nevertheless, the results from the present work have shown that this potential is considerably restricted compared to initial predictions. This was due to the existence of a number of natural barriers to gene flow. A stronger understanding of these barriers and the factors influencing gene flow has allowed the broad-scale detection of species and populations at risk.


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General appendix: publications and other output from PhD candidature
Hybridisation between plantation and native Eucalyptus

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1 There is a risk of hybridisation

Eucalypt species are renowned for their propensity to hybridise. With the massive expansion of the eucalypt plantation estate in Australia, it is important to assess the risk of introgression of genes from plantations into native forest gene pools. Exotic E. nitens plantations cover c. 68 000 ha of the island of Tasmania. 17 of the 29 native eucalypt species belong to the subgenus Symphyomyrtus and may hybridise with E. nitens, hence the potential for hybridisation and gene flow exists. As a test-case, we have quantified the extent of hybridisation between a E. nitens trial and adjacent native eucalypts.

2 Mass screening detected hybrids in OP progeny of E. nitens and E. ovata

Open-pollinated (OP) seed was collected from 36 E. viminalis and 11 E. ovata adjacent to the trial, and 46 E. nitens from within the trial. Capsules were separated by age. The seed was germinated and grown in the same box, with different families and capsule ages in separate boxes. F₁ hybrids were only found between E. nitens and the native E. ovata and were identified from their distinct, intermediate morphology. They occurred in 1.4% and 4.2% of OP progenies from E. nitens and E. ovata females, respectively.

3 Hybrids were verified using isozymes

Fig. 3 Enzyme gel with differing Pgd-I alleles.

Pgd-I were virtually specific to E. nitens (99%) but rare in both native species (< 0.5%). The majority of seedlings identified as hybrids were heterozygous for Pgd-I and the slower native allele. Such genotypes were rare in the pure species seedlings from the same open-pollinated families, consistent with being F₁ hybrids.

4 Hybridisation decreased with distance

Fig. 4 Hybridisation from E. nitens pollen dispersing into native E. ovata forest (%). A general decrease in the levels of hybridisation can be seen with distance from the trial (pollen source).

5 Flowering overlap enabled hybridisation

Fig. 5 Flowering time of the three Symphyomyrtus species.

Only the local E. ovata overlapped in flowering time with E. nitens at the study site, allowing hybridisation to occur. The flowering of the local E. viminalis did not overlap with the exotic, and hence they did not hybridise. Flowering was recorded as the percentage of the current season’s bud crop remaining to flower.

6 Impact of flower abundance

Table 1 Annual variation in hybridisation in the E. ovata seed lots.

<table>
<thead>
<tr>
<th>Year of fertilisation</th>
<th>Capsule age</th>
<th>n seedlings</th>
<th>n hybrids</th>
<th>% hybrids</th>
</tr>
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<tr>
<td>1996</td>
<td>1</td>
<td>3461</td>
<td>42</td>
<td>1.21</td>
</tr>
<tr>
<td>1997</td>
<td>2</td>
<td>4086</td>
<td>228</td>
<td>4.87</td>
</tr>
<tr>
<td>1996</td>
<td>3</td>
<td>533</td>
<td>4</td>
<td>0.87</td>
</tr>
<tr>
<td>1995</td>
<td>4</td>
<td>92</td>
<td>2</td>
<td>2.17</td>
</tr>
</tbody>
</table>

7 Can the hybrids survive?

This is the first evidence of hybridisation between plantation and native eucalypts. Whether the F₁ hybrids can survive to reproductive maturity in the wild and allow the introgression of E. nitens genes into the native gene pool remains to be determined.
Flowering time as a barrier to introgression in Eucalyptus

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Introduction
Differences in flowering time are a major barrier to inter-specific F₁ hybridisation in the genus Eucalyptus (Potts and Wilshire 1996). The potential for backcrossing and further introgression of genes from one species into another will in part depend upon the manner in which flowering time is inherited in the F₁ hybrids. We have studied the flowering times of eucalypt species and their natural and artificial F₁ hybrids over several seasons on the island of Tasmania (Williams and Potts 1996; Lopez et al. 2000). The flowering of most F₁ hybrids occurs at an intermediate or similar time to the parent species, enhancing the potential of the F₁ hybrids to bridge the reproductive barriers between species. However, we have discovered a case where the crossing of two species, E. ovata and E. globulus, which flower at similar times results in F₁ hybrids which are completely asynchronous with either parent.

The case of E. ovata x globulus
E. ovata and E. globulus are frequently parapatric on the island of Tasmania (Fig. 1) and overlap extensively in their flowering time (Fig. 3). While they are from different taxonomic series, artificial F₁ hybrids have been created (Fig. 2) but exhibit high levels of inviability (Lopez et al. 2000). Nevertheless, some hybrids do survive to reproductive maturity and hybrids have been reported in nature where the two species co-occur (Williams and Potts 1996; Lopez et al. 2000).

Flowering time
While E. ovata and E. globulus overlap extensively in their flowering time, the flowering time of F₁ hybrids is completely asynchronous with either parent species (Fig. 3a-c), but overlaps with a co-occurring species, E. viminalis (Fig. 3a, d). This asynchronous flowering time was evident in both experimental (Fig. 3b) and natural populations (Fig. 3c, d) and appeared to be due to the additive inheritance of the timing of bud development in the F₁. E. globulus takes one year to develop flowers whereas E. ovata takes two years (Fig. 4).

CONCLUSIONS
The flowering of the F₁ hybrids between the synchronously flowering species E. ovata and E. globulus exhibits little overlap with either parent species. The opportunities for backcrossing are minimal and the hybrid is effectively reproductively isolated from both parents. However, the flowering time of the F₁ coincides with another co-occurring species, E. viminalis, enhancing the opportunity for introgression of E. globulus or E. ovata genes into the gene pool of a third species.

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