

Inbreeding and Interspecific Hybridization in *Eucalyptus gunnii*

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Summary

The success and vigour of plants arising from self and close matings of *Eucalyptus gunnii* are compared with wide intraspecific crosses and a range of interspecific crosses. The barriers to inbreeding in *E. gunnii* are strong, in many cases stronger than the barriers to interspecific hybridization. The success (number of plants obtained/flower pollinated) of self-pollination and close intraspecific crosses was less than wide intraspecific crosses and most interspecific crosses investigated, as was the height and survival after 1 year's plantation growth. *E. gunnii* females demonstrate wide crossability, with the success of most interspecific hybrid combinations tried with species from the section *Maidenaria*, not significantly different from that of wide intraspecific crosses. The only major barrier to interspecific hybridization found was with *E. globulus*. There was not a strong association between crossability and the taxonomic/genetic distance between parents, although after 1 year's plantation growth, F_1 hybrids from the only interseries cross examined (*E. gunnii* \times *ovata*) showed reduced vigour. The implications of these results for the development of breeding strategies as well as for gene flow and hybridization in natural populations are discussed. Strong barriers to inbreeding in *Eucalyptus* may result in a disparity between pollen dispersal and gene flow in natural stands, with more distant matings favoured.

Key words: *Eucalyptus*, breeding system, inbreeding depression, self-incompatibility, hybridization, crossability, gene flow.

Zusammenfassung

Erfolg und Wüchsigkeit von Pflanzen aus Selbstbestäubung und Kreuzung naher Verwandten von *Eucalyptus gunnii* werden mit intraspezifischen Kreuzungen weiter entfernter Verwandter und mit Artkreuzungen verglichen. Die Kreuzungsbarrieren gegen Inzucht sind bei *Eucalyptus gunnii* groß, in vielen Fällen größer als Barrieren gegen Artbastardierung. Der Erfolg (Anzahl entstandener Pflanzen pro bestäubter Blüte) war bei Selbstungen und bei Kreuzungen naher Verwandter innerhalb der Art geringer als bei Kreuzung weiter entfernter Verwandter und als bei den meisten Artkreuzungen. Dies gilt auch für Höhe und Überlebensrate nach einjährigem Wachstum in einer Plantage. *E. gunnii*-Mütter weisen eine große Kreuzbarkeit auf. Der Erfolg der meisten Bastarde aus versuchten Artkreuzungskombinationen mit Arten der Sektion *Maidenaria* war nicht signifikant anders als der bei Kreuzungen weiter entfernter Verwandter innerhalb der Art. Die einzige Hauptbarriere gegen Artbastardierung wurde bei *E. globulus* gefunden. Dort bestand keine enge Beziehung zwischen Kreuzbarkeit und dem taxonomisch-genetischen Abstand zwischen den Eltern, obwohl die F_1 -Bastarde der einzigen untersuchten Interserienkreuzung (*E. gunnii* \times *ovata*) nach einjährigem Wachstum auf der Plantage eine reduzierte Wüchsigkeit zeigten. Die Folgerungen dieser Ergebnisse für die Entwicklung von Züchtungsstrategien wie auch für die Genverteilung und Hybridisierung natürlicher Populationen werden diskutiert. Große Inzuchtbarrieren bei *Eucalyptus* können eine Ungleichheit zwischen Pollen- und Genverteilung in einheimischen Beständen zur Folge haben, mit einer Bevorzugung der Paarung entfernter Verwandter.

Résumé

La réussite et la vigueur des plants issus d'autofécondation et de croisements de parents génétiquement proches

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pour *Eucalyptus gunnii*, sont comparés avec ceux issus de croisements intra-spécifiques de parents génétiquement éloignés et toute une série de croisements inter-spécifiques. Dans *E. gunnii* les barrières à l'autofécondation sont puissantes, et dans beaucoup de cas plus fortes que celles des croisements inter-spécifiques. La réussite (estimée par un rapport entre le nombre de plants obtenus par rapport au nombre de fleurs pollinisées) des croisements autoféconds et intra-spécifiques de géniteurs génétiquement proches a été inférieure aux croisements intra-spécifiques faisant appel à des géniteurs génétiquement éloignés et à la plupart des croisements inter-spécifiques étudiés. Il en est de même pour les hauteurs et la survie de plants après une année de végétation en plantation. Les mères *E. gunnii* ont montré une grande aptitude hybridogène, au travers de la plupart des croisements inter-spécifiques essayés; avec les espèces de la section *Maidenaria* aucune différence significative est apparue entre ces croisements inter-spécifiques et les croisements intra-spécifiques de parents génétiquement éloignés. La seule barrière importante dans les croisements inter-spécifique a été trouvée avec *E. globulus* (le croisement réciproque *E. globulus* × *E. gunnii* n'a pas été essayé). Il n'y a pas de puissants liens entre l'aptitude hybridogène et la distance génétique taxonomique des parents; cependant, après une année de croissance en plantation, l'examen de la seule famille hybride F₁ issue de croisement inter-série (*E. gunnii* × *E. ovata*) a montré une réduction de vigueur. L'implication de ces résultats dans le cadre du développement d'une stratégie d'amélioration tel que la dispersion des gènes et l'hybridation dans les populations naturelles, est discutée. Dans le genre *Eucalyptus*, les puissantes barrières à l'autofécondation peuvent provoquer une disparité entre la dispersion du pollen et les gènes dans les aires naturelles, avec un appariement en faveur des plus éloignés.

Introduction

The genetic system of *Eucalyptus* is a classic open recombination system (sensu GRANT 1958), typical of temperate forest-tree genera such as *Pinus*, *Populus*, *Cupressus* and *Quercus* (e.g. STEBBINS 1950; BARBER 1965; STERNE and ROCHE 1974). Eucalypts have a mixed mating system (e.g. PRYOR 1976; ELDRIDGE 1976, 1978; MORAN and BROWN 1980), with relatively high outbreeding rates (0.69–0.84, MORAN and BELL 1983) maintained by proterandry (e.g. PRYOR 1951, 1976; HODGSON 1976a; GRIFFIN and HAND 1979) and varying degrees of self-incompatibility (e.g. PRYOR 1957b, 1961, 1976; HODGSON 1976c; ELDRIDGE and GRIFFIN 1983) and reinforced by selection against products of self-fertilization in later stages of the life cycle (e.g. PHILLIPS and BROWN 1977; MORAN and BROWN 1980; FRIPP 1982; ELDRIDGE and GRIFFIN 1983; MORAN and BELL 1983; GRIFFIN *et al.* 1987). Barriers to interspecific hybridization are generally weak as evidenced by the prolific reports of natural and artificial hybridization (see PRYOR and JOHNSON 1971, 1981; PRYOR 1976; POTTS and REID 1983; GRIFFIN *et al.* in press). However, hybridization does not occur between subgenera (e.g. PRYOR and JOHNSON 1971, 1981; PRYOR 1976; GRIFFIN *et al.* in press) and, while there are general trends (e.g. PRYOR 1957a, 1976; PILIPENKO 1969; PRYOR and JOHNSON 1971, 1981; PRYOR and WILLING 1974; GRIFFIN *et al.* in press), crossability patterns within subgenera are not well explored.

Inbreeding effects have been detailed in several *Eucalyptus* species (e.g. ELDRIDGE 1970; VAN WYK 1976, 1977, 1980; HODGSON 1976b, 1976c; VENKATESH and VAKSHASYA 1977; PHILLIPS and BROWN 1977; ELDRIDGE and GRIFFIN 1983) but studies quantifying the success of natural (e.g. DRAKE 1981a, 1981b; POTTS 1986) or artificial (e.g. PRYOR 1951, 1957a, 1957c; PILIPENKO 1969; CAUVIN 1984) interspecific hybridization are few.

There are no studies reported which compare the relative importance of barriers to inbreeding and interspecific hybridization, although such studies are important for a full understanding of gene flow and the evolutionary consequences of hybridization in the genus (e.g. PRYOR 1976; PRYOR and JOHNSON 1981; POTTS and JACKSON 1986) and the development of breeding strategies.

Eucalyptus gunnii (section *Maidenaria*; subgenus *Symphyomyrtus* - sensu PRYOR and JOHNSON 1971) is one of the most cold resistant eucalypts (PRYOR 1957b; POTTS and REID 1985; DAVIDSON and REID 1985) and is thus one of the main species being investigated for pulpwood production in France. However, its relatively slow growth rates and poor pulping qualities when compared to more frost sensitive species from the same section, such as *E. globulus*, *E. nitens*, *E. dalrympleana* and *E. viminalis*, prompted the investigation of artificial hybridization as a means of breeding fast growing cold resistant genotypes for clonal selection (CAUVIN 1984). This crossing program enabled the crossability of *E. gunnii* to be examined by comparing the success and vigour of a wide range of intraspecific and interspecific crosses.

Methods

Crosses (self, open and controlled pollinations) were from the 1983 hybridization program undertaken by Association Forêt-Cellulose (AFOCEL) near Toulouse in the south of France. Results are presented for self, open, close and wide intraspecific crosses and interspecific crosses using *E. gunnii* females and pollen from the faster growing, but more frost sensitive species — *E. cordata*, *E. dalrympleana*, *E. viminalis*, *E. macarthurii*, *E. nitens*, *E. globulus* and *E. ovata*.

The close intraspecific crosses were amongst 5 descendants from 1 to 3 surviving trees in an old French plantation (Claraic-Hérault). While their exact pedigree cannot be determined, they have a high probability of being related (some being at least half-sibs) and represent a narrow genetic base. Wide intraspecific crosses involved unrelated parents from different provenances. Details of the hybridization orchard containing the 7 *E. gunnii* females and the methods used for artificial hybridization are given by CAUVIN (1984). The crossing pattern was not orthogonal due to limitations on the availability of flowers, although cross types were generally well distributed across females. For each cross type, details are given in Tab. 1 of the number of crosses and total number of plants surviving and measured after 1 season's growth in a plantation (with one third of the progeny from each cross arranged in linear rows randomized in each of 3 blocks) established at Lamasquère, in the south of France.

The overall success of crosses was measured using the number of plants obtained per flower crossed. This integrates effects due to flower abortion (number of capsules obtained per flower crossed), the number of germinants obtained per capsule, the survival of germinants in the nursery and the proportion of stunted weak plants (runts) in a multiplicative manner. Analyses of initial measures of the success of cross types were based on individual cross values, whereas families of each cross type were pooled for comparisons of growth and mortality. Cross types were compared using a model-1, oneway analysis of variance (ANOVA) or in the case of mortality, a contingency Chi-squared test. Proportions were angular transformed prior to analysis of variance. Where the ANOVA was significant, general comparisons between means were made using the

Table 1. — The total number of crosses, different females and males used, the total number of flowers crossed and the number of plants alive after 1 season's plantation growth.

Type of cross	Number of				
	crosses	females	males	flowers crossed	plants alive
Intraspecific (<i>E. gunnii</i> x <i>E. gunnii</i>)					
self-pollinated	8	8	8	251	64
open-pollinated	7	7	-	274	75
close	9	5	4	243	94
wide	14	5	8	229	214
Interspecific (<i>E. gunnii</i> - female x species)					
<i>cordata</i>	7	7	1	239	79
<i>dalrympleana</i>	23	6	6	496	224
<i>viminialis</i>	14	7	5	466	124
<i>macarthurii</i>	15	5	5	195	200
<i>nitens</i>	5	4	2	106	42
<i>globulus</i>	4	4	2	95	0
<i>ovata</i>	4	4	2	94	70
TOTAL	110			2688	1186

Student-Newman-Kuells multiple range test. Specific *a priori* comparisons between means were made using the Students t-test.

Results

There appear to be strong barriers to inbreeding in *E. gunnii* as the success (plants obtained/flower crossed) of both self-fertilization and close intraspecific crosses were significantly ($P < 0.05$) less than that of wide intraspecific and most interspecific crosses (Fig. 1). This mainly reflects the low number of plants obtained per capsule in these cross types, which no doubt reflects poor seed set. The results from self-pollination were combined from assisted (flowers emasculated and pollinated manually) and non-assisted (flowers bagged only) crosses. While not strictly comparable with the controlled crosses, the data available indicated no significant difference in the abortion rate or the number of plants/capsule between assisted and non-assisted selfs. Open-pollination resulted in significantly ($P < 0.01$) less flower abortion than the controlled crosses. However, the number of plants obtained/flower crossed was comparable to self and close intraspecific crosses (Fig. 1) due to the low seed set in open-pollination suggesting that pollen availability may be a limiting factor in natural pollination. There was no significant difference between the cross types in the proportion of plants scored as runts, although survival in the nursery of seedlings from close intraspecific crosses was significantly ($P < 0.01$) less than other intraspecific crosses.

Mortality in the plantation after 1 season's growth was significantly (X^2 , $P < 0.001$) higher in seedlings from intraspecific crosses than for the interspecific hybrids (Fig. 1). This was due to significantly higher mortality in seedlings from self as compared to the wide intraspecific crosses (X^2 , $P < 0.01$) and there was a trend within the intraspecific cross types for increasing mortality with an increasing

degree of relatedness. Furthermore, there is strong evidence for inbreeding depression in the vigour of surviving seedlings. The difference in vigour of the intraspecific cross types was not significant in the nursery, but was highly significant ($P < 0.001$) after 1 season's plantation growth (Fig. 1). This was due to the marked depression in the height of seedlings from self and close intraspecific crosses when compared to the height of seedlings from the wide intraspecific crosses. The growth of the open-pollinated progenies was on the average intermediate between that of self and wide intraspecific crosses.

The success of most interspecific crosses was not significantly different from that of wide intraspecific crosses (Fig. 1). The only major barrier to interspecific hybridization observed was with *E. globulus*. Of the species used, this was the most morphologically different from *E. gunnii*. Out of 95 *E. gunnii* flowers crossed in 1983 with *E. globulus* pollen only 1 capsule was obtained but no seedlings (1 plant was obtained from 68 flowers pollinated in the 1982 crosses but was subsequently killed by frost). This was not due to inviability of the *E. globulus* pollen as other types of

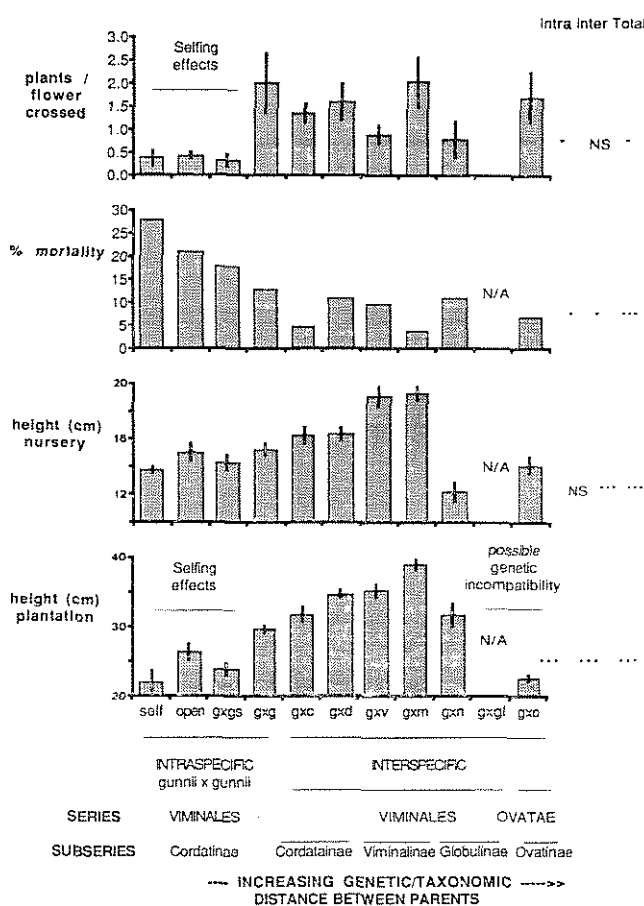


Figure 1. — The success of self (self) and open (open) pollinations and artificial intraspecific (gxgs = close; gwg = wide) and interspecific crosses using *E. gunnii* as the female parent. Interspecific crosses were made with pollen of *E. cordata* (gxc), *E. viminialis* (gxv), *E. dalrympleana* (gxd), *E. macarthurii* (gxm), *E. nitens* (gxn), *E. globulus* (gxgl) and *E. ovata* (gxog). The taxonomic ranking of species follows Payson and Johnson (1971). The diagram indicates the mean (\pm S.E.) number of plants obtained per flower crossed, mortality in the plantation, and mean (\pm S.E.) seedling height (cm) in the nursery and after 1 season's plantation growth. The significance of the ANOVA and Chi-squared (% mortality) tests for the difference between intraspecific (Intra), interspecific (Inter) and all (Total) crosses is indicated (NS = not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

crosses using the same pollen were successful (unpublished data). The only interseries cross type examined (*Viminales* × *Ovatae*, *E. gunnii* × *ovata*) was one of the most successful in terms of plants obtained/per flower crossed (Fig. 1). This limited study provides no evidence for an association within the section *Maidenaria* between taxonomic/genetic distance and genetic barriers to the artificial formation of F_1 hybrids. Most of the artificial interspecific hybrids examined were significantly more vigorous than the wide intraspecific crosses of *E. gunnii* (Fig. 1). However, the average height of F_1 hybrid seedlings from the wider interspecific crosses (*E. gunnii* × *nitens* — in the nursery and particularly *E. gunnii* × *ovata* — after 1 season's plantation growth) was less than those of the other interspecific cross types. The height of seedlings from the interseries cross (*E. gunnii* × *ovata*) was also significantly less in the plantation than seedlings from wide intraspecific crosses of *E. gunnii* despite *E. ovata* generally being of greater vigour than *E. gunnii*.

Discussion

There are strong barriers to inbreeding in *Eucalyptus gunnii* with self and close intraspecific crosses less successful than wide intraspecific crosses and most interspecific crosses examined. This clearly supports PRYOR's (1961) observations that selfing occurs in the genus, but less readily than outcrossing and frequently less readily than interspecific hybridization. Barriers to self-fertilization have been noted in other *Eucalyptus* species (e.g. PRYOR 1957b, 1961, 1976; ELDRIDGE 1970, 1976, 1978; VAN WYK 1976, 1977, 1980; HODGSON 1976b, 1976c; VENKATESH and VAKSHASYA 1977; ELDRIDGE and GRIFFIN 1983) and PRYOR (1961, 1976) indicates there is some evidence for a gene controlled self-incompatibility system in some species. While barriers to self-fertilization are occasionally complete (PRYOR 1961, 1976), they are generally manifest as a reduction in seed set (e.g. present study; HODGSON 1976a, 1976c; PRYOR 1961; ELDRIDGE 1970, 1978; ELDRIDGE and GRIFFIN 1983) and subsequent reduced vigour (e.g. present study; HODGSON 1976b; PRYOR 1976; VAN WYK 1976, 1977, 1980; ELDRIDGE and GRIFFIN 1983) and survival (e.g. present study; ELDRIDGE and GRIFFIN 1983). Reduced seed set following self-fertilization may result from incompatibility (pollen-pistil or zygote-mother) or seed inviability. Increases in estimated outcrossing rates between seed and germinants (PHILLIPS and BROWN 1977; FRIPP 1982) and with increasing age of the seed crop (MORAN and BROWN 1980) would favour the latter alternative. Furthermore GRIFFIN *et al.* (1986) note successful growth of pollen tubes in self crosses but a predominance of outcrossed seed following pollination of *E. regnans* with a 1:1 (self : outcross) pollen mix.

Seedlings from open-pollination of *E. gunnii* were, on the average, intermediate in vigour and survival between self and wide intraspecific crosses (Fig. 1). A similar reduction in the vigour of open-pollinated progenies compared to those arising from controlled outcrosses has been noted previously in *Eucalyptus* (e.g. HODGSON 1976b; VAN WYK 1976; ELDRIDGE and GRIFFIN 1983). There is little doubt this effect is a result of inbreeding depression in the 10–30% (MORAN and BELL 1983) of open-pollinated seed arising from self-fertilization and clearly, the use of open-pollinated as opposed to controlled outcrossed seed in plantations may result in a significant loss of productivity (e.g. HODGSON 1976b; ELDRIDGE 1978).

An understanding of the extent to which inbreeding depression extends to other degrees of relatedness is important, although virtually unstudied in *Eucalyptus*. VAN WYK (1976) noted generally better performance of families from 'close' than from 'wide' crosses of *E. grandis*, and in a small scale study (VAN WYK 1980) found inbreeding effects to extend to full-sib matings, although half-sib matings were no different from other outcrosses. Inbreeding depression appears to be evident in seedlings from close crosses in the present study. However, while the exact pedigree of individuals involved in these close crosses is unknown, they are probably more distantly related than full-sibs. This effect requires careful investigation using individuals of known pedigree as the implications are important to the development of breeding strategies and the understanding of the dynamics of natural populations.

Barriers to crossing of related individuals may have important consequences on gene flow in natural stands. Limited seed dispersal in *Eucalyptus* (e.g. GILBERT 1958; KIRKPATRICK 1977; CREMER 1977) probably results in stands comprising a mosaic of individuals having full-sib or more likely half-sib relationships (GRIFFIN 1980). Pollen dispersal is probably greater than seed dispersal due to active bird and insect vectors (e.g. BARBER 1965; HOPPER and MORAN 1981; GRIFFIN 1983), especially long distance dispersal. The only data on pollen dispersal curves in the genus, based on pollinator foraging observations (BARBER 1965; HOPPER and MORAN 1981), suggest dispersal curves favouring near neighbour matings. Matings between neighbours would also be favoured by greater coincidence in flowering times (e.g. GRIFFIN 1980). However, the present results clearly support LEVINS' (1981) thesis for a disparity between pollen dispersal and actual gene flow. Reduced seed set and vigour and greater mortality in selfs and related matings, likely to arise with nearest-neighbour matings in natural stands, would clearly favour matings arising from distant, even long distant, pollen dispersal. However, the genetic difference between parents is probably larger in such matings (e.g. MORAN and HOPPER 1983), which may lead to the disruption of local coadapted gene combinations and thus outbreeding depression (WADDINGTON 1983). An optimum degree of divergence for seed set and heterosis has been noted in intraspecific crosses of several plant species (PRICE and WASER 1979; LEVIN 1981) and WADDINGTON (1983) argues the optimum outcrossing distance is a balance between inbreeding and outbreeding depression. However, the amplitude of interspecific cross-compatibility demonstrated in *Eucalyptus* (present study; PRYOR 1951, 1957a; PILIPENKO 1969; PRYOR and WILLING 1974; CAUVIN 1984) suggests a degree of genetic homeostasis and that outbreeding depression, arising from genetic as opposed to ecological causes, is unlikely to be a significant factor restricting gene flow within species or between closely related species, at least up to early stages in the life cycle. In fact, the success of many interspecific cross types when compared to the wide intraspecific crosses suggests that the use of interspecific F_1 hybrids as a means of monitoring gene flow patterns (e.g. PRYOR 1976) may be just as effective as the use of intraspecific gene markers. However, in this study, cross success has been assessed in the absence of competition between pollen types, and this effect requires investigation using pollen mixes (e.g. GRIFFIN *et al.* 1987).

While examination of intraspecific cross types on a finer scale is warranted, this study suggests that the optimum crossability for *E. gunnii*, and probably most *Eucalyptus*

species, encompasses a broad range of genetic differentiation. At one extreme, marked inbreeding depression is evident, yet at the other extreme, outbreeding depression does not seem to be manifest until fairly wide interspecific crosses are performed where incompatibility or seed abortion (e.g. *E. gunnii* × *globulus*) and reduced F_1 vigour (e.g. *E. gunnii* × *ovata*) appear to become evident (Fig. 1). The latter result accords with the observations of PRYOR (1957a, 1976) and PILIPENKO (1969) for the vigour of interspecific F_1 hybrids to decrease with increasing taxonomic distance between the parents. However, the reduction in height of the interseries cross (*E. gunnii* × *ovata*, Fig. 1) may not be a true indication of vigour as these F_1 s tended to exhibit plageotropic growth, a tendency also noted by PILIPENKO (1969) for *E. maidenii* × *ovata* F_1 s. Furthermore, the height of other families of this cross type produced in 1982, were not significantly less than that of intraspecific outcrosses and several of AFOCEL's clones are putative natural *E. gunnii* × *ovata* hybrids.

Most of the artificial interspecific hybrids examined from the series *Viminalis* were significantly more vigorous than the wide intraspecific crosses of *E. gunnii* (Fig. 1). However, rather than reflecting hybrid vigour, the few comparisons where open-pollinated progeny from the male parents were available suggested that the early growth rate of hybrid progenies was intermediate between that of *E. gunnii* and the faster growing, lowland species used as male parents (unpublished data). The hybridization of *E. gunnii* females with *E. globulus* is of particular interest as this cross would allow the combination of genes of one of the most vigorous, but frost sensitive, species with one of the most frost resistant species in the genus. The reciprocal cross has not been attempted as yet. However, the success of crosses using natural hybrids (unpublished data) suggests there is the possibility that genes of these two species can be combined using another species (e.g. hybrids with *E. viminalis* or *E. ovata*) as a 'genetic bridge' to overcome any direct barrier to the formation of F_1 hybrids.

Cross-incompatibility may become more evident in later stages of the life cycle or in advanced generations (e.g. PRYOR 1956; PILIPENKO 1969). Nevertheless, the broad crossability demonstrated by *E. gunnii* indicates the importance of pre-mating (e.g. spatial and temporal isolation) and ecological barriers (e.g. PRYOR 1976) in the maintenance of species integrity in the genus. The importance of ecological barriers is demonstrated by the fact that the introduction of genes from these faster growing lowland species into *E. gunnii*, significantly reduced the probability of surviving an extreme frost (1982 crossing program — unpublished data). Furthermore, this broad crossability emphasises the evolutionary flexibility in the genus, allowing the potential exploitation of a wide range of genetic variability through interspecific hybridization in the adaptive response to a changing environment (e.g. PRYOR and JOHNSON 1981; POTTS and JACKSON 1986).

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