New Forests **27:** 115–138, 2004.

Interspecific hybridization of *Eucalyptus*: key issues for breeders and geneticists

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Received 15 May 2002; accepted in revised form 7 February 2003

Key words: Breeding strategy, Genetics, Heterosis, Hybrid inviability, Hybrids, Incompatibility, Seed production

Abstract. Eucalypt hybrids are significant in forestry, particularly in sub-tropic and tropical regions, where cost efficient, clonal propagation is the key to their exploitation. However, the outstanding success of selected hybrid clones has given a biased impression of the vigor of eucalypt hybrids and the strength of reproductive barriers in the genus. When full account is made of losses through the life cycle, a picture of high incompatibility and inviability often emerges. Hybrid inviability tends to increase with increasing taxonomic distance between parents, but there are exceptions. Hybrids also seem more susceptible to pests than their pure species. Intense selection may still result in elite hybrid clones, but such inviability and susceptibility adds a significant cost to their development. Breeders must carefully evaluate the costs of hybrid development and deployment compared with pure species options. A key to hybrid selection is the rapid development and testing of large populations and application of high selection intensities. However, eventually this approach must be linked with more formal breeding strategies. As most traits are intermediate in F_1 hybrids there is increasing interest in advanced generation hybrids to provide desirable trait combinations. In such cases, there is a clear role for marker assisted selection to speed introgression.

Introduction

Interspecific hybrids of *Eucalyptus* have been used in forestry for decades (Griffin et al. 1988; Martín 1989; Nikles and Griffin 1992; Khurana and Khosla 1998). They achieved notoriety in tropical and sub-tropical forestry with the widespread use of *E. urophylla* Blake × *grandis* Maiden clones in Brazil (Ikemori 1984; Bertolucci et al. 1995) and Congo (Vigneron and Bouvet 2000). Initially plantations were established from spontaneous hybrids that arose in exotic plantings in botanical gardens, species trials, plantations and early seed orchards (Eldridge et al. 1993; Ferreira and Santos 1997). Such selection of phenotypically outstanding hybrid individuals, often from a limited genetic base, was the basis of the initial plantations in Congo (Souvannavong 1992; Verhaegen 1996), Brazil (Campinhos and Ikemori 1977; Ferreira and Santos 1997; Wright 1997) and India

(Bowden 1964; Varghese et al. 2000). However, manipulated hybridization programs were rapidly commenced (e.g. 1978 in Congo - Vigneron and Bouvet 2000). While less utilised in more temperate zones, manipulated eucalypt hybridization was also undertaken early in countries such as Russia (Pilipenka 1969) and France (Cauvin 1983; Potts and Potts 1986), but hybrid development was curtailed by extreme frost events.

Most eucalypt hybrids tested or deployed are either first generation (F_1) or composites derived from spontaneous hybridization (e.g. Río Claro hybrid in Brazil - Campinhos and Ikemor 1977; Mysore hybrid in India - Varghese et al. 2000) or more recently manipulated F_1 hybrids (Campinhos and Ikemori 1989; Mesbah 1995; Vigneron and Bouvet 2000). These hybrids are mainly from the sections *Maidenaria* (e.g. *E. globulus* Labill., *E. nitens* (Deane & Maiden) Maiden), *Exsertaria* (e.g. *E. camaldulensis* Dehnh., *E. tereticornis* Sm.) and *Transversaria* (e.g. *E. pellita* F.Muell., *E. grandis*, *E. urophylla*) of the subgenus *Symphyomyrtus* (Griffin et al. 1988; Eldridge et al. 1993). The main hybrids (including reciprocals) used commercially appear to be *E. grandis* × *urophylla*, *E. grandis* × *camaldulensis*, and hybrids including at least one of *E. saligna* Sm., *E. pellita*, *E. exserta* Muell. and *E. tereticornis* (Dungey and Nikles 2000). Such hybrids are planted on a large scale in Brazil and the Congo, although sizeable plantations also occur in China, Indonesia and South Africa. There are also small areas of these or other eucalypt hybrids in other countries in Asia (e.g. Philippines, Vietnam, Thailand, and Malaysia) and South America (e.g. Chile, Uruguay, Argentina, Paraguay) (Dungey and Nikles 2000).

While eucalypt hybrids are widely used in plantation forestry outside Australia, there appear to be only about 200 hectares of eucalypt hybrids currently planted within Australia, although many combinations are currently being field tested (Dungey and Nikles 2000). The oldest program, from North Forest Products (now Gunns Ltd.), aimed at developing *E. nitens* × *globulus* F_1 hybrids and commenced in 1986 (Tibbits 1986, 1988). 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. Seedlings or clones of other combinations derived from crossing programs in either South Africa or South America are also currently being tested or are in quarantine (Barbour et al. 2000; Robson and Kelley 2000; Lee et al. 2000). There is also interest in hybridization amongst species in the genus *Corymbia* (Lee et al. 2000).

The present article reviews some of the key issues in the genetics and breeding of eucalypt hybrids, focusing on papers presented at a recent symposium on this topic (Dungey et al. 2000a). We have used the taxonomy of Pryor and Johnson (1971) for historical reasons. However, in the future, Brooker's (2000) taxonomic treatment will be adopted, with the exception that the tropical bloodwoods (*Corymbia*) will be retained as a separate genus (Hill and Johnson 1995) based on molecular evidence (Ladiges and Udovicic 2000; Steane et al. 2002).

Production of F_1 hybrid seed

Barriers to seed set

Hybridization between species from the major eucalypt subgenera does not occur (Griffin et al. 1988), but controlled pollination studies have revealed F_1 hybrids can often be readily produced amongst closely related species within subgenera. In many cases, seed set from such interspecific crossing is not significantly different from that obtained from intraspecific crossing (Potts et al. 1987; Tibbits 1989, 2000; Lopez et al. 2000b). Nevertheless, two major pre-zygotic barriers to hybridization within subgenera have been identified. The first is a structural barrier that is unilateral, and due to the pollen tubes of small flowered species not being able to grow the full length of the style of large flowered species (Gore et al. 1990). This structural barrier is a major problem for producing F_1 hybrids with *E. globulus*, a species that has a much larger flower than most other plantation eucalypts (e.g. *E. gunnii* Hook.f., *E. camaldulensis*, *E. nitens*, *E. grandis*, *E. dunnii* Maiden). In these cases, F_1 hybrid seed can only be produced using *E. globulus* as the pollen parent, but even then, seed set may be significantly reduced compared with intraspecific outcrosses (Gore et al. 1990; Potts et al. 1992; Espejo et al. 1995). This structural barrier appears to be overcome to some extent when backcrossing (Potts et al. 2000). The second pre-zygotic barrier to hybrid seed production is a physiological barrier that results in pollen tube abnormalities and pollen tube arrest in the pistil. The amount of pollen tube inhibition has been shown to increase with increasing taxonomic distance between the parents (Ellis et al. 1991). However, this does not appear to always be the case, as poor seed set in the intersectional cross *E. camaldulensis* × *globulus* does not seem to be due to abnormal pollen tube growth in the style (McComb et al. 2000).

Physiological barriers to hybrid seed set may also act after fertilization with the hybrid embryo failing to divide, the embryo developing slowly, or reduced cellularization of the endosperm (Sedgley and Granger 1996). From a practical viewpoint, slower embryo development could mean that some hybrid crosses might require longer to mature than intraspecific crosses. There are reports of reciprocal effects at the embryological level that may result in unilateral success of hybridization. Such reciprocal effects have been reported for embryo development, cellularization of the endosperm and reduced germination in *E. spathulata* Hook. × *platypus* Hook. (Sedgley and Granger 1996). Furthermore, in *E. dunnii* × *grandis* reciprocal crosses, Harbard et al. (2000a) showed that while the over-all success of the reciprocal crosses may be similarly low, this may be due to reciprocal effects operating at different stages of development in the different crosses.

Advances in hybrid seed production

The recent development of single visit pollination procedures for eucalypts

(one-stop-pollination OSP Harbard et al. 1999; single-visit-pollination SVP Williams et al. 1999) has now substantially reduced the cost of producing control-pollinated seed and revolutionized hybrid seed production (Harbard et al. 2000b, 2000a). The stigma is not necessary for successful pollination and pollen will germinate just as readily on the cut surface of the style (Cauvin 1988). This technique was first operationally implemented with *E. globulus* spp. *globulus* where the large style can be either cut transversely (Williams et al. 1999) or longitudinally (Harbard et al. 1999) at anthesis or even pre-anthesis (Trindade et al. 2001). However, in the case of many small-flowered species maximum pollen adhesion is obtained by a transverse slice across the stigma and into the top of the style rather than straight style decapitation (e.g. *E. camaldulensis*, *E. grandis*, *E. urophylla, E. dunnii* - Harbard et al. 2000b). Using *E. globulus* as a female in hybrid crosses would be highly advantageous as it has large robust flowers, seed set is relatively high and clones are often already established in arboreta or seed orchards. Style decapitation is seen as one means of allowing the pollen tubes of small-flowered species to reach the *E. globulus* ovules (Vergara-Rojas et al. 2001). This approach has already been successfully used to produce *E. globulus* × *dunnii* F_1 hybrids (Barbour and Spencer 2000).

Single visit pollination may lead to cost-efficient systems to mass produce F_1 or, more likely, backcross hybrid families for deployment. The other approach is the development of bi- or multi-clonal seed orchards where self-incompatible clones are used as females. Such multi-clonal seed orchards are used for the production *E. urophylla* × *grandis* F_1 hybrid seed in Brazil, where average hybridization rates range from 70% (Campinhos et al. 1998) to 96% (Junghans et al. 1998). However, Rezende and de Resende (2000) argue that while specific combining effects are low relative to additive effects, they are sufficiently large to warrant a clonal deployment strategy.

F_1 hybrid inviability

There is little doubt that specific eucalypt hybrid combinations are extremely successful (e.g. *E. urophylla* × *grandis* and *E. urophylla* × *pellita* - de assis 2000; Dungey and Nikles 2000; Vigneron and Bouvet 2000) and have impacted on forestry world-wide, particularly in tropical and sub-tropical areas. However, such vigorous eucalypt hybrid combinations have historically dominated the tree breeding literature, often giving a biased impression of the general viability of eucalypt hybrids. Many of the vigorous F_1 hybrid combinations reported have been heavily selected from a highly variable pool of F_1's that contain a high proportion of poor performing individuals (e.g. Tables 1, 2). Indeed, careful account of losses throughout the lifecycle often reveals a picture of strong reproductive barriers and hybrid inviability in many desirable species combinations (Potts et al. 1992; Oddie 1996; Shelbourne et al. 1999; Shelbourne 2000; de Assis 2000; Griffin et al. 2000; Lopez et al. 2000b; McComb et al. 2000). For example, Griffin et al. (2000) estimate that only 0.15% of *E. grandis* × *globulus*

F_1 seed produces 'normal' plants after 2 yr field growth. They calculate that even a moderate selection intensity (1 in 5) on three traits (growth rate, specific consumption and rooting ability) in the population of 'normal' plants would require 83,300 seed to produce one good selection (i.e. crossing 13,400 *E. grandis* flowers). While such seed numbers are achievable with OSP, the crossing program to achieve this is still extremely large by any standard. Such high levels of inviability have been reported in other desirable hybrid combinations such as *E. urophylla* × *dunnii*, *E. dunnii* × *grandis* (and reciprocal) (Griffin et al. 2000; Harbard et al. 2000a) and *E. camaldulensis* × *globulus* (McComb et al. 2000).

Inviability of F_1 hybrids may be expressed at germination, in the nursery and even after planting in the field. Slower germination of hybrid seed may occur (e.g. *E. ovata* Labill. × *globulus* - Lopez et al. 2000b). However, there are cases where germination of hybrid seed is as successful as intraspecific crosses (Tibbits 1988; Ellis 1991; Lopez et al. 2000b). Nevertheless, hybrid inviability can be rapidly manifested thereafter as reduced survival of germinants in the nursery (e.g. *E. nitens* × *globulus*, *E. nitens* × *gunnii*, *E. nitens* × *morrisbyi* Brett - (Tibbits 1988); *E. dunnii* × *grandis* - Harbard et al. 2000a) and a high proportion of seedlings with abnormal phenotypes (e.g. *E. camaldulensis* × *globulus* - Oddie 1996; *E. nitens* × *grandis* - Shelbourne et al. 1999; Shelbourne 2000; *E. grandis* × *globulus* - Griffin et al. 2000; *E. dunnii* × *grandis* - Harbard et al. 2000a) (see also Robson and Kelly 2000).

Even sorting plants in the nursery and discarding abnormal seedlings prior to planting may not eliminate abnormal phenotypes from the population (Griffin et al. 2000; Lopez et al. 2000b). de Assis (2000) notes that plants with apparently normal phenotypes at planting may become abnormal up to two years after planting, but the phenotype stabilises thereafter. Such abnormal phenotypes usually die early. However, there is some evidence of continued expression of inviability with differential mortality of F_1 hybrids continuing at later ages (e.g. *E. ovata* × *globulus* - Lopez et al. (2000b), *E. nitens* × *globulus* - Potts et al. 2000). The expression of abnormal phenotypes or other forms of inviability in inter-specific hybridization can also depend upon the direction of the cross and vary widely between parents of the same species (Volker 1995; Oddie 1996; de Assis 2000; Harbard et al. 2000a; Griffin et al. 2000; Meddings et al. 2001).

Abnormal phenotypes are rarely planted (e.g. Barbour et al. 2000) or, if they are, then they are rarely reported when tree breeders screen hybrid combinations for elite individuals. Nevertheless, they provide an early and sensitive indicator of genetic incompatibility between species. Many intersectional F_1 hybrids within *Symphyomyrtus* are unsuccessful or exhibit high levels of inviability (Table 1,2), although elite selections can be obtained from such crosses with sufficiently intense selection (Griffin et al. 2000). There is a broad trend for the expression of F_1 hybrid inviability to increase with increasing taxonomic distance between parents (Pilipenka 1969; Martín 1989; Potts et al. 1987; Griffin et al. 1988, 2000; Delaporte et al. 2001; see Tables 1, 2). However, there are exceptions and more detailed studies with appropriate parental controls are required. de Assis (2000) considers that abnormal phenotypes are more often encountered when species from

Table 1. Germination and seedling viability of some eucalypt F_1 hybrids. Summary of the percentage seed germination, the number of normal phenotype in the nursery as a percentage of the number of seed germinated and seed sown as reported in the literature. The data from Griffin et al. (2000) 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 80%

Cross	% germination	Normal seedlings as % number germinated	Normal seedlings in nursery as % of seed sown
Potts et al. (1992)			
E. gunnii	81	75[3]	61[3]
E. gunnii × *globulus*	77	58[3]	45[3]
E. globulus	95	68[3]	65[3]
Potts et al. (1992)			
E. nitens		92	
E. nitens × *globulus*		87	
E. globulus		98	
E. globulus × *bicostata*		82	
E. bicostata		100	
Espejo et al. (1995)			
E. nitens	71	98	70
E. nitens × *globulus*	60	92	55
E. globulus	81	100	81
Lopez et al. (2000b)			
E. ovata	100	80	80
E. ovata × *globulus*	92	44	41
E. globulus	98	86	84
Oddie (1996)			
E. camaldulesis	64	100	64
E. camaldulensis × *globulus*	73	28	20
E. globulus (op)	52	100	52
Griffin et al. (2000)			
Inter-series			
E. nitens × *globulus*	48	91	44
E. dunnii × *globulus*	31	63	20
Inter-sectional			
E. urophylla × *globulus*	42	47	20
E. urophylla × *dunnii*	17	54	9
E. grandis × *globulus*	9	80	7
E. dunnii × *grandis*	50	18	6
E. grandis × *dunnii*	17	39	6
Backcrosses			
E. grandis × (*grandis* × *globulus*)[1]	61	77	47
E. globulus × (*grandis* × *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). [2] As above but only a single family. [3] % transferred from agar medium to the nursery. Only a very low % of abnormal seedlings occurred in the nursery.

the section *Maidenaria* are involved in intra- or inter-sectional crosses. It also appears that crossing between species from the sections *Exsertaria* and *Transversaria* is atypically successful (Table 2). Indeed, Vigneron and Bouvet (2000) note that the most promising hybrid combinations developed in Congo were within

Table 2. The proportion of viable F_1 hybrid combinations between *Symphyomyrtus* species from the three main sections used in forestry. The table shows the percentage (n) of species combinations for which no viability problems have been reported in manipulated crosses

Section	Maidenaria	Exsertaria	Transversaria
Maidenaria (SP)	80% (27)	0% (3)	9% (11)
Exsertaria (SN)		100% (5)	91% (11)
Transversaria (SE)			100% (7)

or between sections *Transversaria* and *Exsertaria* (e.g. *E. urophylla* × *grandis*, *E. urophylla* × *pellita*, *E. tereticornis* × *grandis*). This success is note-worthy, as a recent molecular study has questioned the separation of these two sections (Steane et al. 2002).

The main genetic causes of inviability of the F_1 hybrid include: (i) genome disharmony (e.g. irregularities during mitosis from major chromosomal differences) and incompatible development cues; (ii) the deleterious, complementary action of one or a few genes; or (iii) cytoplasmic effects (Levin 1978; Tiffin et al. 2001). The deleterious interactions of genes from the same (Papopoli and Wu 1994; Orr 1995) or different loci (Rieseberg et al. 1996) have been implicated in many cases of inviability of F_1 hybrids (Levin 1978; Tiffin et al. 2001). Such genes have no deleterious effects within a species, probably accumulate as a bi-product of divergence, but may cause inviability or sterility in combination with genes from another species. A feature of many eucalypt F_1 hybrid families which exhibit abnormal, inviable plants is that many full-sibs are of normal phenotype and often relatively vigorous (Volker 1995; de Assis 2000; Perrow (MacRae) and Cotterill 2000; Tibbits 2000). One explanation for this pattern could be heterozygosity at (i) one or more loci harbouring deleterious complementary dominant genes or (ii) the same loci where deleterious recessive genes are involved.

Assessment of F_1 hybrid performance

Comparison with parental controls

There are many reports of superiority of interspecific F_1 hybrids of *Eucalyptus* (de Assis 2000; Potts et al. 2000; Vigneron and Bouvet 2000; Verryn 2000). However, intra-specific controls are often absent, or of poor accuracy (i.e. open-pollinated or unrelated to the F_1's) making it difficult to assess whether differences between the hybrid and pure species is simply a result of removing inbreeding. Indeed, one of the key issues is whether comparable genetic gains could be achieved simply through removing inbreeding effects through wide intra-specific outcrossing (Eldridge et al. 1993).

In the late 1980's various research organizations in Tasmania (University of Tasmania, CSIRO Division of Forestry and Forest Products and North Forest Products) commenced experiments to understand the genetics and gain from

hybridization. The crossing programs focused on the two temperate species, *E. nitens* and *E. globulus*. These species are the major plantation species in this zone, where the elite pulpwood species, *E. globulus*, was restricted to lower altitudes (Tibbits et al. 1997). Many of the early F_1 hybrid tests only included open-pollinated controls of one or both parental taxa for convenience as the main concern was assessing crossability patterns (e.g. *E. globulus* - Potts and Savva 1989; *E. nitens* - Tibbits 2000). For example, in the large number of earlier *E. nitens* crosses reported by Tibbits 2000, stem diameters of surviving F_1 hybrids were compared after 13 yr growth to outcrosses of the female parent, *E. nitens*, and open-pollinated progenies collected from the pollen parents (*E. cordata* Labill., *E. dalrympleana* Maiden, *E. globulus*, *E. gunnii*, *E. johnstonii* Maiden, *E. morrisbyi*, *E. viminalis* Labill., *E. ovata* and *E. rodwayi* R.T.Baker & R.T.Sm.). Such open-pollinated eucalypt progenies will contain varying proportions of selfs and are therefore likely to exhibit some degree of inbreeding depression and cause over-estimation of the growth performance of the F_1 hybrid compared to non-inbred parental controls. The level of inbreeding depression for stem volume in these open-pollinated progenies may be as much as 23% and 13% for diameter and height growth (Potts and Wiltshire 1997; Hardner and Tibbits 1998). Later hybrid experiments were undertaken on a larger scale and established with non-inbred outcrosses as parental controls, allowing a more accurate estimate of F_1 hybrid performance (*E. ovata* × *globulus* - Lopez et al. 2000b; *E. nitens* × *globulus* - Potts et al. 1992; volker 1995; Dungey et al. 1997; Potts et al. 2000; *E. gunnii* × *globulus* - Potts et al. 2000).

All the Tasmanian experiments involved species from the section *Maidenaria* and in no case was there evidence of the mean F_1 hybrid growth being better than the mean of the better parent. In most cases the F_1 hybrid mean was intermediate, or more commonly, below the mid-parent value (see also Cauvin et al. (1987)). In the case of *E. nitens* × *globulus*, although one hybrid family did exhibit exceptional growth, there were more families of both pure species with good combinations of high wood density and high growth than there were for the F_1 hybrid families (Volker 1995, 2002). This result suggests combined gains on both these traits could just as easily be achieved by selection within either species. The relatively poor average F_1 performance occurred despite the fact that in virtually all experiments, hybrids were planted in family plots and/or hybrid sub-blocks where high mortality often meant surviving trees were in a less competitive environment than the *E. nitens* or *E. globulus* controls. This spacing effect would result in surviving hybrid trees achieving greater size than under greater competition, potentially inflating later-age hybrid performance.

At the cross type level, similar conclusions are reached by de Assis (2000) from a study of factorials of *E. grandis* × *camaldulensis*, *E. urophylla* × *camaldulensis*, *E. urophylla* × *pellita* F_1 hybrids grown with various types of open-pollinated and outcrossed seed orchard parental controls in Minas Gerais, Brazil. The F_1 hybrid showed neither better nor mid-parent heterosis for average growth. However, all F_1 factorials had high performing families and the phenotypically best individual in each comparison was an F_1 hybrid. de Assis (2000) also found

outstanding individuals for growth in the *E. urophylla* seed orchard population. From a pragmatic viewpoint he notes that in terms of pulp production per unit area, which combines wood density and growth, *E. urophylla* × *grandis* hybrids are hardly ever surpassed by pure species in Brazil. He considers that despite little evidence for hybrid superiority at the cross-type level, production of outstanding families or individuals through hybridization is a 'functional heterosis' which explains the advances made in forestry where hybrid programs have been implemented. Therefore, for commercial forestry purposes it is not the mean hybrid performance, but the performance of the best clones and the best families that is of interest.

In another experiment planted in Rio Grande do Sul State, Brazil, de Assis (2000) does report better parent hybrid superiority for growth at the cross type level for *E. urophylla* × *grandis*, *E. urophylla* × *maidenii* (F.Muell.) Kirkp. and *E. dunnii* × *maidenii*, but not for *E. grandis* × *maidenii* nor *E. grandis* × *dunnii*. However, the exact nature of the parental controls is unclear. Kha and Cuong (2000) give a good example of the superiority of F_1 hybrids for growth. In this case, *E. urophylla* × *camaldulensis* and *E. urophylla* × *exserta* F_1 hybrid families significantly outperformed *E. urophylla* inter-provenance and *E. exserta* × *camaldulensis* F_1's with common parentage. This superior hybrid performance occurred on two quite different sites in Vietnam. *E. urophylla* × *tereticornis* and *E. urophylla* × *camaldulensis* F_1 hybrids created in China are also reported as out-performing unspecified parental controls (Shen 2000). Clonally replicated *E. camaldulensis* × *grandis* F_1 hybrids being tested for growth on saline affected areas showed slightly better average 1 yr height growth compared to the *E. camaldulensis* parental clone and open-pollinated seedlings from the *E. grandis* parents (Dale et al. 2000; Sasse et al. 2000). The differences between the hybrid families and the potentially inbred *E. grandis* controls were not statistically significant at this early stage, but the difference had increased 6 mo later (G. Dale unpubl. data).

Environment dependent 'hybrid superiority'

Hybrid superiority may arise through either heterosis, epistasis or trait complementarity (Nikles and Griffin 1992). Complementarity is obtained through additive effects and results from synergy amongst independent traits in specific environments where both parent species are not as adapted as their hybrid (Nicholas 1987). If complementarily is the key to hybrid superiority then defining the target environment is critical (Martín 1989; Nikles and Griffin 1992). Indeed, the most common reason to breed hybrids would appear to be to provide suitable genotypes for planting in areas which are marginal for the parental species in terms of frost, drought and disease.

The classic example of complementarity is the use of *E. urophylla* × *grandis* hybrids in Congo (Vigneron and Bouvet 2000) and Brazil (Campinhos and Ikemori 1989). High humidity in Congo allows development of canker and leaf fungi to which *E. grandis* is highly susceptible despite being the more favoured

species due to its normally fast growth, coppicing potential and suitability for pulping. The canker also caused severe losses in early plantations of *E. grandis* and *E. saligna* in Brazil. *E. urophylla* confers disease resistance in the hybrid. Thus hybrid superiority seems to be the result of multiplicative effects of additively inherited traits (i.e. resistance × growth) (Vigneron and Bouvet 2000). Improved disease resistance is no doubt an important complementary trait in explaining hybrid superiority. Shelbourne (2000) also describes a similar case for *E. grandis* × *nitens* hybrids grown in northern New Zealand along with open-pollinated controls of either parent. Although high levels of inviability were observed, 'normal' hybrids outperformed *E. grandis* as it was mal-adapted to the site and many hybrids also outperformed the *E. nitens* due to its susceptibility to defoliation by two leaf fungi to which *E. grandis* is resistant. However, with difficulties in propagation and testing of elite, disease resistant hybrids, Shelbourne considered the introduction of an alternative species (e.g. *E. maidenii*) a more cost-effective and ecologically safer approach.

Hybrid superiority may also arise simply through the additive inheritance of a single adaptive trait, such as drought or frost resistance. The hybrid simply outperforms the parental species at an intermediate position along an environmental gradient. In South Africa pure species such as *E. nitens*, *E. grandis*, *E. tereticornis* and *E. camaldulensis* are preferred on 'non-intermediate' sites, and hybrids are only deployed onto specific intermediate sites where they show better growth and survival than the parental species (Verryn et al. 1996; Verryn 2000). In fact, predictive modelling for KwaZulu-Natal province in South Africa suggests that the *E. grandis* × *nitens* F_1 is only preferred over *E. nitens* on a relatively small proportion of the forest estate (Verryn et al. 1996). In Western Australia, Barbour et al. (2000) found that in areas with more than 700 m rainfall, seed orchard *E. globulus* (which is normally deployed) outperformed any *E. grandis* × *globulus* F_1 family clones. It was only on a single low rainfall site (534 mm) that was marginal for *E. globulus* that this species was outperformed by the hybrid clones.

The importance of the environment on the expression of hybrid superiority is demonstrated in an experiment described by Potts et al. (2000) using *E. gunnii* × *globulus* F_1's and parental outcross controls planted along an altitudinal gradient in Tasmania. *E. gunnii* is one of the most frost-resistant eucalypt species and the F_1 hybrids have intermediate frost resistance. It was thought that by hybridising *E. gunnii* with the fast growing, but more frost-sensitive *E. globulus* a genotype may be found which could replace *E. nitens* as the species of choice on colder, wetter sites but retain the pulp properties of *E. globulus*. At the two lower altitude sites, the *E. globulus* was far superior to the slower growing *E. gunnii* with the F_1 hybrid intermediate but below the mid-parent value for mean basal area at three yr of age. Significantly higher mortality and persistent frost damage of the *E. globulus* at the two highest altitude sites resulted in the basal area of the F_1 sub-blocks being greater than both parents. However, at no site did the F_1 or either parent outperform the routine *E. nitens* plantation stock. In addition, *E. gunnii* and the F_1 hybrid were highly susceptible to browsing by a native marsupial possum

(*Trichosurus vulpecula* Kerr - Scott et al. 2002; Dungey and Potts 2002) and this damage resulted in extremely poor tree form.

Inheritance of other characters in F_1's

Apart from growth, key traits which have been identified for improvement by hybridization include clonal propagation, coppicing, frost, drought and salt resistance, resistance to pests, wood density and pulp yield (Griffin et al. 2000; Verryn 2000; Dungey and Nikles 2000; Dale et al. 2000). At the cross type level, most morphological, physiological and wood property traits are inherited in a more-or-less intermediate manner in F_1 hybrids, although there are exceptions, and the exact degree of dominance may vary between traits and species combinations (Pilipenka 1969; Cauvin et al. 1987; Tibbits et al. 1991). Maternal effects have been reported in a few cases (e.g. de Assis 2000), but detailed experimentation is required to verify the importance of such effects. In fact, Griffin et al. (2000) consider that in practice, there is little evidence that reciprocal effects are important in determining the set of genotypes available for evaluation.

High rooting ability is important for the deployment of hybrid selections and most indications to date suggest it will be inherited in a predominantly additive manner in the F_1 (e.g. *E. nitens* 0% F_1 30% *E. grandis* 60% - Verryn 2000). However, partial dominance towards the higher rooting parent was noted in *E. torelliana* (F.Muell.) Hill & Johnson × *citriodora* (Hook.) Hill & Johnson F_1's and maternal effects have been reported in the *E. urophylla* × *maidenii* F_1, with the rooting ability of the F_1 closer to the maternal parent (de Assis 2000).

Flowering time has revealed some unexpected patterns of inheritance (Lopez et al. 2000a). In most species combinations, the flowering time of the F_1 hybrids is intermediate or synchronous with either parent. However, an exception occurred in *E. ovata* × *E. globulus* F_1's. While the pure species overlap extensively in their flowering time, the flowering of the F_1 hybrids was delayed and there was virtually no overlap with the parental species. This appears to be a consequence of the additive inheritance of the timing of flower bud development. *E. globulus* flower buds take approximately one year between initiation and flowering whereas *E. ovata* buds require two years. The intermediate inheritance of development time would then result in flowering in the F_1 being offset. Such differences in the timing of bud development are not confined to these species and similar displacement of the F_1 flowering time may occur in other instances.

Drought (Verryn 2000) and freezing (Tibbits et al. 1991; Almeida et al. 1994; Manson and Potts 1995) resistance are generally inherited in an additive manner in F_1 hybrids. However, in the case of freezing resistance there is a tendency for partial dominance towards the more sensitive species in some combinations. Meddings et al. (2001) showed that tolerance to saline waterlogging in nursery trials was also inherited in a more-or-less additive manner in *E. camaldulensis* × *globulus* F_1 hybrid seedlings, although there appeared to be a partial bias towards the more susceptible *E. globulus* in terms of both survival response with increasing salinity and growth rate under mild salinity. Abnormal F_1 seedlings were not

included in the experiment. The *E. camaldulensis* females were previously selected for their salt tolerance and were represented as clones and controlled outcrosses in the experiment. The *E. globulus* pollen parents in the trial were represented by their open pollinated progeny.

Verryn (2000) reports stem straightness exhibits partial dominance toward the straight parent when *E. grandis* or *E. urophylla* are crossed with species of poor form such as *E. camaldulensis*, *E. tereticornis* and *E. saligna*. Wood density is inherited in an additive manner in virtually all species combinations examined (*E. grandis* × *camaldulensis*, *E. grandis* × *tereticornis* - Verryn 2000; *E. nitens* × *globulus* - Tibbits et al. 1995; Volker 1995; *E. saligna* × *maidenii*, *E. urophylla* × *maidenii, E. saligna* × *tereticornis* - de Assis 2000). Other wood property traits reported to be inherited in an additive manner in F_1's include radial shrinkage (Verryn 2000), lignin and ash content, viscosity and pulp hemicellulose content (de Assis 2000). Pulp yield appears to show dominance or partial dominance towards the low yielding parent in the three cross types studied by de de Assis (2000).

Hybrid susceptibility

Increased resistance to disease was noted above as a cause of hybrid superiority in several cases. However, this would appear to simply be a consequence of additive inheritance of the disease resistance *per se*. If anything, eucalypt hybrids in Australia tend to be more susceptible to pests than parental types. In the wild, eucalypt hybrids support a greater number of 'pest' taxa than pure species types (e.g. Whitham et al. 1994; Morrow et al. 1994). A genetic basis to this pattern has now been shown in two field trials established in Tasmania with artificial hybrids and parental types (*E. amygdalina* Labill. × *risdonii* Hook.f. - Williams et al. 1999; Dungey et al. 2000b; *E. nitens* × *globulus* - Lawrence et al. 2000). In both experiments, hybrid trees support significantly greater numbers of dependent taxa than trees of either pure species. At the level of individual marsupial, insect and fungal taxa, a general pattern is now emerging (Dungey et al. 1997, 2000b; Dungey and Potts 2002; Scott et al. 2002). When susceptible and resistant eucalypt hosts are crossed, the pest susceptibility of the F_1 tends to be intermediate to varying degrees or similar to the more susceptible parent. In contrast, crossing eucalypt hosts that are equally resistant results in F_1 hybrids that are as resistant as the parents or more susceptible. No cases have been published to date where the average resistance of eucalypt hybrids exceeds that of both parents. Such reports are also rare in other genera (Fritz 1999). However, this does not exclude the possibility that specific hybrid individuals may exhibit resistance, particularly in later generations (e.g. Hardiyanto and Tridasa 2000).

In the case of *E. nitens* × *globulus* hybrids, our studies have shown that on average, the interspecific F_1 hybrid was as, or more, susceptible to *Mycosphaerella* leaf disease than the more susceptible parental taxa (Dungey et al. 1997). In addition, three separate field trials showed that the F_1 hybrids are more susceptible to browsing by brush-tail possums than the relatively resistant parental species

(Dungey and Potts 2002). This susceptibility partly extends to advanced generation hybrids. These hybrids have also been shown to support greater numbers of insect and fungal taxa (Lawrence et al. 2000).

The above observations of hybrid susceptibility occurred within Australia, where the natural pests and diseases of both parent species could readily colonise the hybrid host trees. The success of inter-specific hybrids in exotic environments such as Congo and Brazil may be related to the absence of the majority of such pests and diseases. While the additive inheritance of resistance to one or two diseases has given the *E. grandis* × *E. urophylla* hybrid an advantage in these exotic environments compared with the susceptible *E. grandis* (see *Environment dependent 'hybrid superiority'*), it is possible that if exposed to the greater pest numbers and the different communities present within Australia, results may be different. This hypothesis is consistent with a recent test of bulk seedlots of *E. grandis* × *E. tereticornis* and *E. grandis* × *E. camaldulensis* F_1 hybrids imported from South Africa and tested in Queensland, Australia (Lee et al. 2000). These hybrids were outperformed by unselected open-pollinated seed lots of *E. dunnii* and *E. maidenii* in the trials (see also Robson and Kelly 2000) and were badly damaged by fungal and insect pests. However, other factors, including other forms of genotype by environment interactions, cannot be completely excluded as causes of the poor performance of these hybrids.

Advanced generation hybrids

Eucalypt hybridization has focused on the exploitation of F_1 hybrids. However, with many of the traits of interest inherited in an intermediate manner in the F_1, gains in one trait may compromise other traits of interest. To provide suitable character combinations it may be necessary to breed beyond the F_1 hybrid generation. There is thus increasing exploration of backcross and other advanced generation eucalypt hybrids (Vaillancourt et al. 1994, 1995; de Assis 2000; Griffin et al. 2000; Potts et al. 2000; Verryn 2000). Backcrosses, F_2's as well as three-way crosses amongst selected *E. grandis*, *E. urophylla* and *E. tereticornis* have been established in China (Gunagxi Dongmen Forest Farm - Zheng Bai, pers. com.), some of which have been clonally replicated (Hardiyanto and Tridasa 2000). Multiple species (double) hybrids are also being investigated in Brazil (de Assis 2000) and South Africa (Verryn 2000). Varying degrees of inviability may be encountered in advanced generation hybrids (Vaillancourt et al. 1994; de Assis 2000; Griffin et al. 2000; Potts et al. 2000). Griffin et al. (2000) notes that even selection of superior F_1's does not eliminate inviability problems in later generations (Table 1) and three-way hybrid combinations (de Assis 2000). Compared to F_1's, such crosses have the additional complexity that recombination and segregation may result in advanced generation hybrid breakdown due to disruption of co-adapted gene complexes, or loss or duplication of chromosomal segments. Advanced generation hybridization of *E. nitens* and *E. globulus* has clearly demonstrated that on average, F_1 and F_2 (outcrossed) generations exhibit

poorer performance than the backcross and parental crosses (Potts et al. 2003). However, it is important to differentiate advanced generation hybrid breakdown from the effects of inbreeding that are often confounded. For example, a high level of a semi-lethal abnormal phenotype was detected in an F_2 family obtained from selfing an *E. gunnii* × *globulus* F_1 hybrid, but not when the same tree was crossed to an unrelated F_1(Vaillancourt et al. 1994, 1995). Molecular mapping and analysis of other cross types suggested that the abnormality was an effect of inbreeding, resulting from the expression of a deleterious recessive allele derived from the *E. gunnii* female.

Molecular genetics is set to play a major role in understanding and implementing advanced generation hybridization. It has a role in understanding hybrid inviability and identifying compatible individuals (Griffin et al. 2000). For example, DNA markers showed that high levels of segregation distortion occur in both a selfed *E. gunnii* × *globulus* F_2 (Vaillancourt et al. 1994, 1995) and an *E. grandis* × (*E. grandis* × *globulus*) backcross (Myburg et al. 2000). In both crosses, the contribution of genetic material from the various parents was not even, with a deficit of *E. globulus* markers. Such distortion may arise from the markers being linked to genes (or chromosomal segments) causing gamete or zygote death prior to sampling, or even linkage to genes controlling reproductive processes such as pollen tube growth. A QTL for later age death was detected in the *E. gunnii* × *globulus* F_2 which was independent of QTL associated with the semi-lethal abnormality previous discussed (R. Vaillancourt, unpubl. data).

There is also a clear role for marker-assisted selection (MAS) in advanced generation hybridization strategies (Griffin et al. 2000; Verryn 2000). Marker assisted backcrossing has great potential to speed the introgression of favourable genes into the recurrent species (Vaillancourt et al. 1994; Myburg et al. 2000). It is being proposed to aid with the introgression of salt tolerant genes into *E. grandis* and *E. globulus* through hybridization with salt-tolerant selections of *E. camaldulensis* in Australia (Dale et al. 2000; Sasse et al. 2000). Quantitative trait loci (QTL) for growth have been identified in two clonally replicated, outcrossed *E. urophylla* × *grandis* F_2 hybrid families developed in Dongmen, China (Hardiyanto and Tridasa 2000). These clones were planted on three sites in Indonesia for testing the expression of the QTL (Hardiyanto and Tridasa 2000). The broad-sense heritabilities for growth traits measured at 1.5 yr of age ranged from 0.05 to 0.47, dependent upon site, however no growth advantage was detected for clones with QTL for increased growth. These QTL were detected using 5.5 yr growth data in China where clones with the marker had a 105–128% growth advantage over clones without the marker. Hardiyanto and Tridasa (2000) suggest failure to express the QTL may be due to the young age of the trial or genotype × environment interactions. The later could be due to the severe impact of foliar leaf disease on growth in Indonesia as all sites were heavily infested by leaf rust and leaf spot disease. Genetic variation in foliar disease susceptibility did exist (broad-sense heritabilities ranged from 0.31–0.41) and a number of resistant clones were identified. However, genes affecting disease resistance, and hence growth in Indonesia, may well be independent of genes affecting growth in China.

Hybrid breeding

The primary objective of hybrid breeding is to extend the gene pool available. This is particularly the case when attempting to confer resistance traits into a fast-growing species already accepted by the forest industry. For example, *E. nitens* × *E. globulus* was always intended as a frost resistant alternative to *E. globulus* (Tibbits et al. 1991). However, gains can also be made through the capture of heterosis (Griffin et al. 2000; Verryn 2000; Rezende and de Resende 2000).

A key to hybrid selection is the rapid development and testing of large populations and application of high selection intensities (Perrow (MacRae) and Cotterill 2000; Griffin et al. 2000). Female choice is also important (Perrow (MacRae) and Cotterill 2000; Griffin et al. 2000), with well-adapted and tested clones favoured that are usually easily accessible. There are advantages of selecting females for both sexual and vegetative propagation traits. Pre-screening of females for hybrid compatibility has also been proposed before large-scale crossing is undertaken (Griffin et al. 2000). Initially, gains may be achieved through a relatively unstructured crossing approach; however, eventually this approach will need to be linked with more formal breeding strategies. Hybrid breeding has been historically dominated by two strategies for breeding F_1's - reciprocal recurrent selection (RRS; as proposed by Comstock et al. 1949, Hyun 1976) and recurrent selection (RS). These strategies were probably first critically evaluated in forestry by Pâques (1989). Shelbourne et al. (1993), Shelbourne (2000), Verryn (2000) have reviewed proposed and commercially used strategies for breeding eucalypt hybrids.

Both RS and RRS have different limitations and advantages. If the performance of the hybrids can be predicted easily from the performance of parents in the pure-breds, then RS is the best alternative. However, RRS has obvious advantages where tests of both pure species are not possible (e.g. Congo - Vigneron and Bouvet 2000) or if there is a poor correlation between performance of parents in hybrid and pure species combinations. A poor correlation could arise if (i) different genes are the determinants of a trait, such as growth, in the hybrid population compared to those in one or other parental population (e.g. genes determining disease resistance - Vigneron and Bouvet 2000), (ii) hybrid combinations are influenced more by non-additive than additive genetic effects (Dieters and Dungey 2000) or (iii) other genetic factors such as chromosomal structural differences impact on hybrid performance. Specifically, what is important is the correlation of the general combining ability (GCA) of parents in pure species to the GCA of parents in hybrid crosses, termed general hybridising ability (GHA) by Nikles and Newton (1991). This correlation varies between species and traits. Poor GCA/GHA correlations occur for growth traits in *Eucalyptus nitens* × *globulus* hybrids tested in Tasmania (Volker 2002), but the correlation is better with other traits such as disease resistance (Dungey et al. 1997) and wood density (Volker 2002). However, previously derived pure *E. urophylla* breeding values for growth were well correlated with GHA values derived from *E. urophylla* × *grandis* (0.63) and *E. urophylla* × *pellita* (0.83) F_1 factorials grown in Congo (Vigneron and

Bouvet 2000). As expected, a strong correlation between the *E. urophylla* GHA values estimated from the two different hybrid combinations (0.64) was also reported. In South Africa, Verryn (2000) also reports a positive, but insignificant correlation (0.65) between previously estimated GCA of *E. grandis* parents and their GHA in a *E. grandis* × *saligna* F_1 hybrid trial.

Practical questions such as costs, generation interval, selection intensity and inbreeding should also be considered when comparing strategies (Rezende and de Resende 2000). For the majority of cases, the extent of non-additive genetic variance is unknown or minimal, and so RS is often the preferred starting point (Shelbourne et al. 1993). Such crossing has initially been undertaken using pollen mixes (e.g. Griffin et al. 2000; Barbour and Spencer 2000) or single-pair mating (e.g. de Assis 2000; Harbard et al. 2000a; Potts et al. 2000). The relative advantage of polymix or single-pair mating depends upon the levels of non-additive as opposed to additive genetic effects expressed in the hybrid population.

de Souza (1993) showed using a theoretical approach (assuming no epistasis and Hardy-Weinberg equilibrium) that RRS was generally superior to half-sib RS for inbred lines. However, his study suggested that genetic gains may be more efficiently achieved with testcross selection of the higher yielding population combined with half-sib selection of the other population (i.e. RRS for one species and half-sib RS for the other). Experimental validation of this result is required for largely heterogeneous tree 'lines', but there are no known practical comparisons of RRS and RS or a combination of both in forest trees. However, a similar system is used in Queensland, Australia in pines, where parents are selected for the next generation based on intra-specific performance in *Pinus caribaea* var. *hondurensis* and on inter-specific performance in *Pinus elliottii* (Dungey et al. 1999).

Producing a hybrid composite or 'swarm' (Verryn 2000), is an attractive idea used commonly in animal breeding (Kinghorn 2000). However in relatively undomesticated tree species, results are likely to be less predictable for at least the first two generations, due to recombination after admixture (Verryn 2000). Unfortunately this may mean initial limited success (Varghese et al. 2000), something that is unlikely to be pursued where generation intervals are large and population maintenance expensive. Backcrossing to parent species is likely to alleviate this problem to some extent. Even then there may be resistance to introgression of key genes, although the application of molecular genetics may speed this process (see previous section).

No matter what the strategy, genetic information is needed to optimise genetic and operational gains (Balocchi 1997). There is no doubt that the genetics of hybrid trees is less understood than in pure species. Currently, it is assumed that much of the variation is additive and, applying the standard quantitative genetic models has shown that this is the case for a number of crosses (e.g. *E. urophylla* × *grandis* in Congo - Vigneron and Bouvet 2000). Indeed, Best Linear Unbiased Prediction methodology offers great opportunities to improve the precision of breeding and deployment value estimates by integrating data from purebreed and hybrid populations (Newman and Reverter 2000). However, there are clearly instances of segregation distortion and hybrid inviability that can challenge such models (Griffin et al. 2000). In addition, there is increasing evidence that epistatic

genetic effects are important in explaining hybrid vigor (Copper and Merrill 2000). Models may therefore need to be developed that better explain the genetic behaviour of hybrid populations *per se*.

Conclusions

Hybrids between eucalypt species can be outstanding, and there is therefore undoubtedly a solid future for them in plantation forestry. However, the success of the hybrids is dependent on site, species used and within-species selection, without even taking the viability issues into account. There will always be two very important aspects to the development of these hybrids for commercial deployment. Firstly, hybrid variation and therefore selection within hybrids of 'winners' is dependent on the diversity of the parent species involved. Secondly, successful hybrid development is intimately linked to an efficient breeding and propagation system, as with any breeding strategy (e.g. Balocchi 1997). Indeed, successful hybrid utilization is largely dependent on the vegetative propagation ability of the species (de Assis 2000).

Shelbourne (pers. comm.) advocates that hybrid breeding should not be the starting point to a new forestry project, rather between-species selection. This is probably a fair appraisal of many situations and breeders should carefully evaluate the costs of hybrid development and deployment compared to the option of larger scale pure species testing and breeding. Nevertheless, with increased international exchange of germplasm between breeding programs, tested hybrid clones or families can be exchanged or purchased 'off the shelf' for testing without having to carry the expertise and infrastructure overheads for their development (Perrow (MacRae) and Cotterill 2000). This is certainly a cost efficient way to enter the hybrid arena, although its effectiveness depends upon the importance of genotype $\times$ environment interactions. Shelbourne (2000) suggests that hybrids are genetic dead-ends, that cannot lead to cumulatively improved populations. This is also undoubtedly the case, at least for F_1 hybrids, however it seems that hybrids still have their place - and some species combinations are superior on specific sites for specific products. Furthermore, even though hybrid inviability is high in a number of combinations (Griffin et al. 2000; Potts et al. 2000), it is not always so extreme and will not always be limiting. In sub-tropical pines, for example, inviability has not been an issue in creating highly successful inter-specific hybrids in a commercial context (Nikles 2000). This also appears to be the case for many of the sub-tropical and tropical eucalypt hybrids. de Assis (2000) summed it up well when he stated that, after all, it is not the average hybrid performance that is of interest to the breeder, but the performance of the best families and the best clones.

Acknowledgements

This review was present as an invited paper at the IUFRO International

Symposium 'Developing the Eucalypt of the Future' held on the 10–15th September 2001 in Valdivia, Chile.

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