

THE GENETICS OF HYBRIDISATION IN THE TEMPERATE *EUCALYPTUS*

Brad M. Potts¹, Peter W. Volker^{1,2}, Paul A. Tilyard¹ and Kelsey Joyce³

¹Cooperative Research Centre for Sustainable Production Forestry and School of Plant Science, University of Tasmania, GPO Box 252-55, Hobart, 7001, Tas., Australia.

²Serve-Ag Pty Ltd, PO Box 149, Glenorchy, Tasmania, Australia 7010.

³North Eucalypt Technologies, North Forest Products, PO Box 63 Ridgley, Tasmania, Australia 7005.

SUMMARY

The use of hybrid eucalypts in commercial forestry has generally resulted from opportunistic crossing events with superior individuals being vegetatively propagated in large numbers. To develop strategies to breed hybrids, it is important to understand the barriers to hybridisation in the genus and as well as the genetic behavior of hybrid populations. Using F₁ hybrid populations of *E. gunnii* × *globulus*, *E. nitens* × *globulus* and outcrossed parental controls we demonstrate, firstly, the importance of environment on hybrid performance and secondly, that high levels of F₁ and advanced generation hybrid inviability can occur at an early age, even in crosses between closely related species. Inviabile F₁ hybrids are a sensitive indicator of genomic incompatibility and add a cost to hybrid selection and production. However, surviving F₁'s may be vigorous and of interest to breeders. F₁ hybrid populations do not appear to conform to classical quantitative genetic models for growth with inflated estimates of additive genetic variance and poor predictability of hybrid performance. Nevertheless, this does not appear to be so for other more highly heritable traits. Advanced generation hybridisation is one means of overcoming the constraints and costs of poor clonal propagation and F₁ hybrid seed production, but hybrid breakdown may substantially reduce genetic gains.

INTRODUCTION

With interest in *Eucalyptus* hybrids for plantation forestry, and more than 800 species currently recognised (Hopper 1997), it is important to develop general principles to guide the selection of suitable combinations for testing. While crossing of species with complementary traits has been suggested (Nikles and Griffin 1992), this approach must be mediated by considerations of crossability and genetic compatibility. Such indications can initially be obtained from knowledge of natural hybrid combinations (e.g. Griffin *et al.* 1988). However, ultimately the success of artificial hybridisation and vigour of hybrids of known pedigree requires quantification. Further, with increasing interest in specifically breeding superior hybrids (Vigneron 1991; Bouvet and Vigneron 1995; Martin 1989; Nikles and Griffin 1992), particularly F₁'s, the rationale and the genetics of hybrid populations must be better understood. This paper summarizes experiments we have undertaken to provide a genetic framework for hybrid breeding, focusing on the main temperate plantation eucalypts *E. globulus* ssp. *globulus* and *E. nitens*.

CROSSABILITY

Hybridization between species from the major eucalypt subgenera does not occur either naturally or artificially (Pryor and Johnson 1971; Griffin *et al.* 1988) as most pollen tube growth is arrested in the upper style (Ellis *et al.* 1991). Controlled pollination studies have revealed few post-mating barriers to seed set and the production of F₁ hybrids amongst closely related species in the genus (Cauvin 1983; Potts *et al.* 1987; Tibbits 1989; Potts *et al.* 1992). However, two major pre-zygotic barriers to hybridization have been identified. The

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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). The second is a physiological barrier which results in pollen tube abnormalities and pollen tube arrest in the pistil, the frequency of which has been shown to increase with increasing taxonomic distance between the parents (Ellis *et al.* 1991).

The structural barrier is a major problem for producing F₁ hybrids with *E. globulus* ssp. *globulus* which has a much larger flower than most species that breeders wish to cross with it (e.g. *E. gunnii*, *E. camaldulensis*, *E. nitens*, *E. grandis*, *E. dunnii*). In these cases, F₁ hybrid seed can only be produced using *E. globulus* ssp. *globulus* as the pollen donor, but even then, seed set may be significantly reduced compared to intraspecific outcrosses (Gore *et al.* 1990; Potts *et al.* 1992; Espejo *et al.* 1995). This reduction in seed set may be partly due to the longer pollen tubes 'overshooting' the ovules of the small-flowered species. Exactly how different in size flowers/styles must be before this structural barrier causes a significant reduction in seed set is unclear at present. Our studies have shown that no seed is obtained when *E. nitens* pollen is directly applied to *E. globulus* ssp. *globulus* females but the cross is successful using F₁ hybrid pollen. However, seedset per flower was slightly reduced when *E. nitens* pollen was applied to the *E. nitens* × *globulus* F₁ hybrid females (which have intermediate style lengths) compared to pollinations with either *E. globulus* or unrelated F₁s. For pure species females, there was a trend for greater seed set to occur when the female is crossed with pollen of the same cross type, but no significant reduction in seed per capsule was detected within females. There was a trend for greater seed set to occur when the female is crossed with pollen of the same cross type, but no significant reduction in seed per capsule was detected within females. We have also successfully produced inter-subspecies F₁ hybrids using the large-flowered *E. globulus* ssp. *globulus* as a female and pollen of *E. globulus* ssp. *maidenii*, which has the smallest flower of the four *E. globulus* subspecies. Shortening the style by cutting (e.g. Harbard *et al.* 1999; Williams *et al.* 1999) may be one means of allowing the pollen tubes of the small-flowered species to reach the *E. globulus* ssp. *globulus* ovules. This treatment has not been successful with *E. nitens* (Potts *et al.* 1992) to date, but has been with *E. dunnii* (Barbour and Spencer, present volume).

F₁ HYBRID PERFORMANCE

There is mounting evidence to suggest that F₁ hybrid performance decreases with increasing taxonomic distance between species (Pilipenka 1969; Potts *et al.* 1987; Griffin *et al.* 1988). Inter-series and inter-sectional F₁ hybrids have been produced in the subgenus *Symphyomyrtus* (e.g. *E. grandis* × *tereticornis*, *E. camaldulensis* × *E. globulus* Mesbah 1995; Oddie 1996; see also Tibbits this volume). While relatively vigorous selections can be obtained, the frequency of F₁ inviability is higher than that encountered in taxonomically closer species (Pilipenka 1969; Griffin *et al.* 1988). A high level of seedling abnormalities and dwarfs are common in such wide crosses. For example, extremely high rates of F₁ hybrid disfunction has been reported in the intersectional *E. camaldulensis* × *globulus* hybrid over 22 months of nursery growth (72% c.f. <1% in pure species controls; Oddie 1996), with the level differing between *E. globulus* pollen provenances. However, high levels of abnormal individuals of poor vigour may also occur in F₁ hybrids between relatively closely related species. This is certainly the case for F₁ hybrids between *E. nitens* and *E. globulus* (Potts *et al.* 1992; Volker 1995), where 13% of seedlings in the nursery were reported as abnormal compared with <3.3% for pure species controls (Potts *et al.* 1992; see also Espejo *et al.* 1995). The F₁ hybrid families were quite variable with some families producing a high proportion of plants of extremely poor vigour and, as is often the case, the surviving full-sibs of normal phenotypes are relatively

vigorous. Operationally, such inviable seedlings would be culled in the nursery or would die in the early years of field growth and are rarely reported in the tree breeding literature. Nevertheless, their levels provide a sensitive indicator of genome incompatibility and their occurrence adds a cost to hybrid selection and production.

There are many reports of superiority of inter-specific F₁ hybrids of *Eucalyptus* mostly from overseas and involving tropical or sub-tropical taxa (e.g. Paramathma *et al.* 1997; Venkatesh and Sharma 1977; Vigneron 1991; Darrow 1995; Wright and Osorio 1996). In many cases these successful hybrids have developed through opportunistic crossing between species in gardens, trials or plantations and have been propagated vegetatively. Many of the successful hybrids used in commercial forestry in tropical and sub-tropical environments may actually result from very few crossing events. Intra-specific controls are often absent, or of poor accuracy (i.e. open-pollinated or unrelated to the F₁'s). This lack of adequate controls makes it difficult to assess whether differences between the hybrid and pure species is simply a result of removing inbreeding effects or the complimentary effects of fitness traits from parental species. The question remains whether comparable genetic gains could have been achieved simply through removing inbreeding effects through wide intra-specific outcrossing (Eldridge *et al.* 1993). Hybrid superiority may arise through either heterosis, epistasis or trait complementarity. Complementarity is obtained through additive effects and results from synergy amongst independent traits in specific environments where both parent species are less well adapted than their hybrid (Nicholas 1987; Sedgley and Griffin 1989; Martin 1989). Key points in assessing the performance and genetic behaviour of interspecific hybrids therefore include firstly, the use of non-inbred, common parental controls (see Potts *et al.* 1992; Volker 1995) and secondly, the importance of defining the test environment (Martin 1989; Nikles and Griffin 1992).

We have undertaken several studies to compare the success and performance of interspecific F₁ hybridisation with non-inbred, pure species outcrosses as parental controls.

E. gunnii × *globulus*

Hybridisation between *E. gunnii* and *E. globulus* is of interest as this would allow the combination of genes of one of the most cold resistant eucalypts with genes of the premier temperate pulpwood species. These two species are classified into the same *Symphomyrtus* series (Series *Viminales*: Section *Maidenaria*) by Pryor and Johnson (1971). Frost resistance is inherited in an intermediate manner in the F₁ hybrids but with a slight partial dominance towards *E. globulus* (Tibbits *et al.* 1991; Manson and Potts 1995) and, if the hybrids were of sufficient vigour, this would allow the extension of *E. globulus*-like plantings into colder environments. However, any hybrids developed must out perform *E. nitens*, which is the species often used to replace *E. globulus* in plantations on colder, wetter sites (Tibbits *et al.* 1997).

In 1990, 14 unselected *E. gunnii* females in native stands on the Central Plateau of Tasmania were crossed in a factorial design with 8 *E. globulus* ssp. *globulus* pollen parents selected by North Forest Products (NFP) on the basis of growth rate and pulp yield. One intra- and two inter-provenance outcrosses of *E. gunnii* were undertaken on each *E. gunnii* female as controls. Single-pair, inter-provenance crosses involving the 8 *E. globulus* ssp. *globulus* parents were provided by NFP as outcross controls for *E. globulus*. Details of the cross success are given in Potts *et al.* (1992). In 1992, the most complete subset of the hybrid factorial (7 *E. gunnii* × 4 *E. globulus*) as well as corresponding pure species controls were

replicated using hardwood cuttings. Genotypes were cloned by NFP and in 1993, successful cuttings were established into 4 field trials along an altitudinal gradient in NW Tasmania (650m, 530m, 400m, 200m). The trials were established as 5 replicates, with each cross type included as a sub-block within each replicate to minimise competitive effects. Generally one clonal replicate of each genotype was allocated to a random position within each sub-block. However, as cutting success was variable, the representation within and across sites was not even. Seedlings of routine plantation, seedling stock of *E. nitens* were also included as a cross-type in the design and at the highest altitude site where *E. globulus* was unlikely to survive, the hardwood cuttings were supplemented with seedling stock.

These trials are significant in clearly demonstrating the importance of environment on the expression of hybrid superiority (Fig. 1). Significant ($P < 0.001$) cross type by site interactions were detected for both survival and average basal area per planted

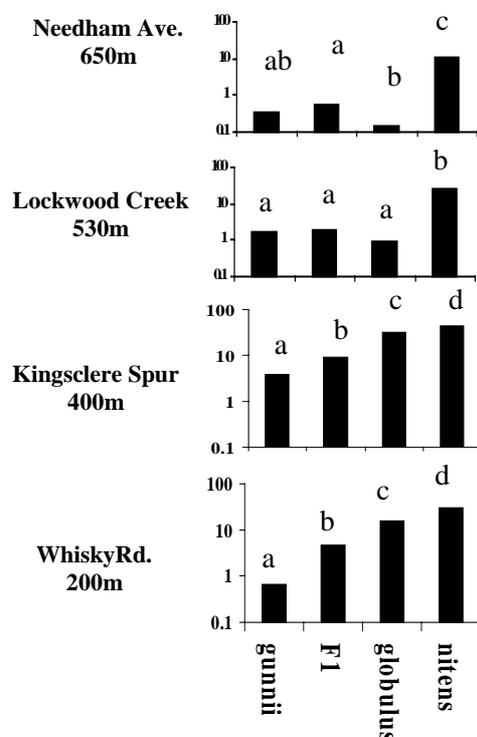


Figure 1: The mean basal area (cm²) per planted individual at age 3 years of *E. gunnii*, *E. globulus* ssp. *globulus*, *E. gunnii* × *globulus* F₁ hybrids and routine plantation stock of *E. nitens* at four sites along an altitudinal gradient in NW Tasmania. Each site was analysed separately using the square root transformed sub-block means. Cross type means were back-transformed and common letters indicate groups which are not significantly different at $P < 0.05$ level using the Tukey test. F₁ hybrid families were represented by an average of 4.9 (1 to 6) individuals. Each parent was represented in pure species combination by 5 to 6 individuals, with all crosses involving the parent approximately equally represented.

individual at age 3 years. Later performance will be influenced by defoliation of the *E. gunnii* and F₁ hybrids by brush-tail possums (Scott *et al.* this volume), but this would have had little impact on the 3-year diameter measurements. The basal area of the F₁ hybrids was intermediate between *E. gunnii* and *E. globulus* spp. *globulus* at the two low altitude sites, but below the mid-parent value (200m site -10% $P > 0.05$; 400m site -21% $P < 0.01$). Significantly higher mortality and persistent frost damage to the *E. globulus* at the two high altitude sites resulted in the basal area of the F₁ hybrid sub-blocks being greater than the mid-parent value (530m 20% $P > 0.05$; 600m 57% $P < 0.01$) and both parents. However, at no site did the F₁ hybrid or either parent out-perform the routine plantation stock of *E. nitens* (Fig. 1).

E. nitens × *globulus*

There has been considerable interest in developing F₁ hybrids between the closely related *E. nitens* and *E. globulus* (Series *Viminales*: Section *Maidenaria*) (Tibbits 1989; Volker 1995; Tibbits this volume). This interest has been tempered in Australia by the difficulty and cost of clonal propagation (Rasmussen *et al.* 1995; Borralho 1997) or of mass-producing hybrid seed using *E. nitens* females, but there is still strong interest elsewhere (e.g. Chile, Espejo *et al.* 1995). Following the initial success of small-scale plantings in the 80's (Tibbits 1988), a large program of crossing between and within these species was undertaken by the CSIRO. The crossing design involved an 8 × 26 factorial within *E. globulus*, a 10 × 10 half-diallel amongst *E. nitens* parents from the Toorong provenance, and a 6 × 14 *E. nitens* × *globulus* factorial. Open-pollinated seed was obtained from all parents and included in the design. The major *E. globulus* factorial was partitioned into smaller inter- and intra-provenance factorials involving trees from the Bass Strait Islands (King Island and Flinders Island) and the southern Tasmanian provenance at Taranna. This resulted in four different levels of inbreeding within *E. globulus* (selfs, o.p.'s, intra- and inter-provenance crosses; see Dutkowski and Potts 1999 for details of provenances). Progenies of these crosses along with a few crosses of *E. bicostata* and its F₁ hybrid with *E. globulus* were planted on 8 sites across Australia in 1990 using a modified α -lattice design (4 reps of 5 tree plots per family per site). Within each incomplete block, the *E. globulus*, *E. nitens* and F₁ hybrids were arranged in 3 separate sub-blocks. Due to limited seed availability, most hybrid families were planted only at a single site at West Ridgley, Tasmania, but some were planted at two other sites. Full crossing and trial details and various early results are given in Volker (1995) and Dungey *et al.* (1997).

To date, studies of the performance of the hybrid at West Ridgley have indicated:

- (i) The F₁ hybrid crosses have reduced success compared to pure *E. nitens* crosses (Potts *et al.* 1992).
- (ii) The F₁ hybrids exhibit high levels of abnormal phenotypes (e.g. dwarfs) and mortality in the nursery and subsequent field trial (Potts *et al.* 1992; Volker 1995). There appears to be provenance specific differences in hybrid compatibility within *E. globulus*, with parents from the Taranna provenance showing high levels of poorer performing individuals.
- (iii) The frost resistance of hybrid seedlings was closer to the more frost sensitive species, *E. globulus* (Volker 1991; see also Tibbits *et al.* 1991).
- (iv) The surviving F₁ hybrids are on average intermediate in growth between the two parental species (e.g. age 4 years Volker 1995). There are hybrid families and individuals that show good performance, but at later ages individual and family performance in this experiment will be biased upward by the higher mortality within hybrid plots and sub-blocks.
- (v) On average, the surviving hybrids are intermediate in wood density, but slightly biased towards the less dense parent (measured using a pilodyn; Volker unpubl. data) (see also Tibbits *et al.* 1995).
- (vi) The interspecific F₁ hybrids were as, or more, susceptible to *Mycosphaerella* leaf disease than the most susceptible pure species whereas inter-provenance F₁'s of *E. globulus* exhibited intermediate levels of susceptibility (Dungey *et al.* 1997).

- (vii) The interspecific F_1 hybrids appear to be more susceptible to browsing by brush-tail possums than pure species (Dungey 1996). This trend has now been confirmed on two other sites.

ADVANCED GENERATION HYBRIDISATION

While most hybrids deployed in forestry are first generation hybrids (F_1), advanced generation (F_2 or BC's) hybrids have been considered due to greater ease of seed production in several cases (reviewed in Dungey 1999). Further, F_1 hybrids are often only intermediate in the array of desirable traits and recombination and introgression through backcrossing may allow better combinations of traits to be selected. As deployment of advanced generation hybrids was one option to overcome the constraints of F_1 propagation, we tested the cross success and relative performance of advanced generation *E. nitens* \times *globulus* hybrids. This was important as recombination and segregation in the F_2 may result in advanced generation hybrid breakdown (e.g. genomic incompatibility or disruption of gene complexes). However, it is important to differentiate advanced generation hybrid breakdown from the effects of inbreeding that are often confounded in advanced generation hybrids. For example, we detected a high level of a semi-lethal abnormal phenotype in an F_2 family obtained from selfing an *E. gunnii* \times *globulus* F_1 hybrid, but not in an outcross of the same female to an unrelated F_1 (Vaillancourt *et al.* 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.

The families generated from the *E. nitens* \times *globulus* crossing program were planted in two field trials in 1995. These crosses were undertaken using parents selected only for flower abundance and accessibility in the West Ridgley F_1 hybrid trial detailed above. Each female was crossed with several random samples of *E. nitens*, *E. globulus* or F_1 pollen unrelated to the female in order to generate populations of single pair-crosses. Pedigree links were maintained both within and between cross types. The F_1 and *E. globulus* cross types were supplemented with addition families provided by NFP and derived from crossing parents selected on growth and wood properties. One trial was located near Tyenna in southern Tasmania on a relatively poor mudstone derived soil type, the other near Ridgley in NW Tasmania on high quality basalt-derived soil. The families were arranged in a completely randomised design in single tree plots to avoid confounding mortality effects with estimates of later age growth at the family and cross type levels.

Key elements to emerge from these trials to date are:

- (i) There was no evidence of major pre-zygotic barriers to advanced generation hybridisation between these two species and F_1 hybrid pollen viability was similar to the more viable *E. globulus* pollen (Tilyard and Potts, unpubl. data).
- (ii) The F_1 exhibited higher mortality in the first four years than the outcrossed F_2 's, backcrosses or pure species crosses (Fig. 3a).
- (iii) While the surviving F_1 's at 4 years were not significantly different in vigour from the parental controls on average, the surviving outcrossed F_2 's were of poor vigour (Fig. 3b).

- (iv) The combination of high mortality and poor growth resulted in major reduction in basal area per planted seedling in both the F₁ and F₂ cross types compared to pure species crosses, with the back-crosses showing intermediate levels (Fig. 3c).
- (v) The top 20% of families for 4 year basal area were dominated by *E. nitens* outcrosses, whereas the 20% worst families were all hybrids, particularly F₁'s and F₂'s.

In addition to F₁ hybrids exhibiting specific susceptibility (e.g. *Mycosphaerella* leaf disease, brush -tail possums), studies of insect herbivore and fungal pathogen communities on foliage of subsets of each cross type in the field trial Tyenna showed that all the *E. nitens* × *globulus* hybrid classes support greater numbers of dependent taxa than pure parental host species (Lawrence 1998). The trend for hybrids to have greater numbers of dependent taxa (including pests) is consistent with observations on natural hybrids (e.g. Morrow *et al.* 1994; Whitham *et al.* 1994) and another study of artificial eucalypt F₁ hybrids (Dungey 1996; Whitham *et al.* 1994).

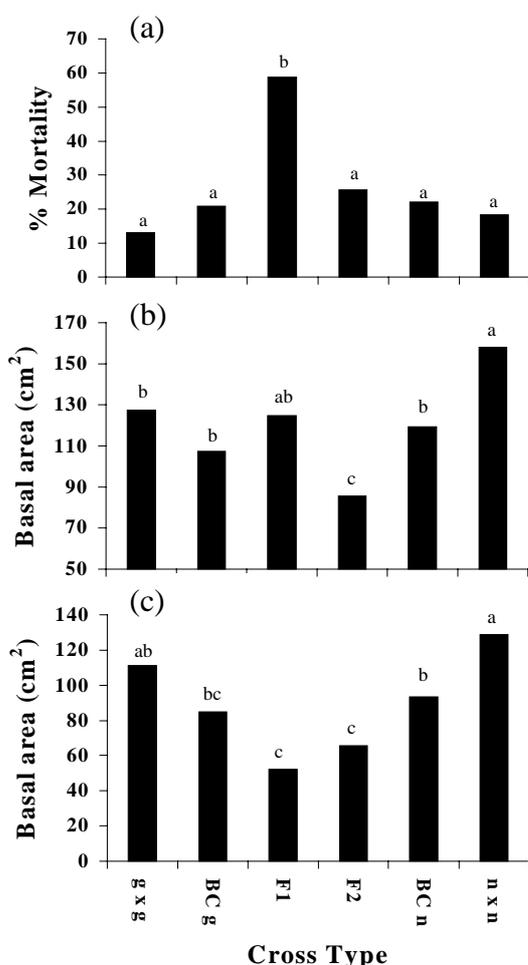


Figure 2: a) Mortality b) mean basal area (cm²) per surviving tree and c) mean basal area (cm²) per planted seedling (treating deaths as zero), for each cross type in the West Ridgley trial at age 4 years. Cross types correspond to *E. globulus* (gxg) or *E. nitens* (nxn) outcrosses, backcrosses of the F₁ hybrids to *E. globulus* (BCg) or *E. nitens* (BCn), F₁ and outcrossed F₂ hybrids. Common letters indicate groups that are not significantly different at P<0.05 level using the Tukey test. The significance test was based on the family within cross type error term. The significance test for basal area was based on square transformed data and means derived following back-transformation.

GENETIC PARAMETERS

There are reports of genetic parameters for inter-specific hybrid populations estimated for breeding and deployment purposes (e.g. Bouvet and Vigeron 1996; Bouvet and Vigeron

1995; Gwaze *et al.* in press; Dungey *et al.* in press). However, the general lack of pure species controls means that there is little information on whether hybrid populations behave similarly to pure species populations and conform to current quantitative genetic models. Such fundamental information is essential if rigorous strategies are to be developed for breeding improved hybrids. A key issue is whether reciprocal or simple recurrent selection schemes are most appropriate for breeding superior F₁ hybrids (Bouvet *et al.* 1992; Shelbourne 1993; Nikles and Griffin 1992). Reciprocal recurrent selection involves crossing amongst pure species parents following their backward selection after testing in hybrid combination. Alternatively, simpler schemes of recurrent selection based on performance within pure species breeding populations and crossing amongst elite selections are attractive as they offer considerable time and cost saving and flow directly from pure species improvement programs.

Differentiation of these breeding strategies depends on whether the best pure species selections also produce the best hybrid combinations or whether F₁ hybrid performance is unrelated to the General Combining Ability (GCA) of the parent in pure species combination. Nikles and Newton (1991) raise the concept of General Hybridising Ability (GHA) as a measure of the 'additive' performance of a trait in hybrid combination. Which strategy is most suitable will, to a large extent, depend on (i) the correlation between GCA and GHA estimates (tropical *Pinus* hybrids - Nikles and Newton 1991; Powell and Nikles 1996) or, more precisely, the genetic correlation between pure species and hybrid performance (e.g. Volker *et al.* 1994; Dungey *et al.* 1997), and (ii) their relative variability in the pure species and hybrid populations respectively. Similarly, predictability of which parental combination will produce the best F₁ hybrids for deployment, whether by seed (full sib families) or clonal propagation, will depend upon the magnitude of specific combining effects in hybrid crosses, termed Specific Hybridising Ability (SHA; Nikles and Newton 1991). A key point is whether the magnitude of this component of genetic variance can be predicted from the variation in specific combining ability (SCA), or dominance variance, in pure species populations.

Studies of genetic parameters in the CSIRO/NFP *E. nitens* × *globulus* F₁ hybrid trial at West Ridgley have revealed that the genetic behaviour of the interspecific F₁ hybrid population is markedly different from the interprovenance (Taranna × King Island) F₁ hybrid population. This is reflected by:

- (i) Abnormally high levels of poor performing individuals and high mortality in the interspecific F₁ hybrids.
- (ii) Estimates of additive variance and heritabilities for growth are inflated compared to the pure species controls in the interspecific F₁ hybrid population but intermediate between intra-provenance population estimates in the interprovenance hybrids.
- (iii) Hybrid performance is not predictable from parental performance in pure crosses (i.e. GCA and GHA were not correlated) for growth (Volker 1995; Volker unpubl. data) nor susceptibility to *Mycosphaerella* leaf disease (Dungey 1996), but was for wood density (Volker unpubl. data).

DISCUSSION

It appears that both exogenous (site dependent) and endogenous (inherent hybrid inviability) factors are important in determining hybrid performance. Endogenous factors

that determine the vigour of interspecific hybrids are poorly understood at present. There are few studies allowing direct comparison of interspecific and intraspecific hybrid populations. Nevertheless, our studies with *E. nitens* × *globulus* suggest high levels of hybrid inviability in F₁ and outcrossed F₂ populations. This may be due to large epistatic gene effects that inflate estimates of additive genetic variance for growth in interspecific F₁ hybrid populations and result in poor predictability of hybrid performance. Such effects do not appear in inter-provenance F₁'s, where levels of additive genetic variation are intermediate between parental populations.

In generating individuals from more than one breed, population or species we aim to exploit favourable dominance deviations. However, there is a risk that favourable epistatic relationships which have been established within the breeds will be broken down (Kinghorn 1980). In addition, there is evidence that epistatic variance can be converted into additive variance following a founder event (Goodnight 1987) or crosses between distantly related individuals, breeds or species (Lynch 1991). This non-linear response to the degree of outcrossing suggests there is a fundamental change in the predominant gene interactions as mates become more and more distantly related (Lynch 1991). In the case of *E. nitens* × *globulus*, such deleterious interactions appear to be unpredictable and there is no useful correlation between GCA and GHA for growth traits. This unpredictability is problematic for schemes crossing elite selections from pure species breeding programs.

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