

Advances in reproductive biology and seed production systems of *Eucalyptus*: The case of *Eucalyptus globulus*

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Abstract

Eucalyptus globulus is the main eucalypt species grown in Australian plantations. The focus on seedling deployment systems, coupled with exploitation of large, open-pollinated base populations for breeding purposes over the last two decades, has required a detailed understanding of the reproductive biology of this species. We review our research on the reproductive biology of *E. globulus*, with a focus on its breeding system and advances made in seed production systems. While most improved seed is still obtained from open-pollinated seedling or grafted seed orchards, the development of the one-stop/single-visit pollination procedure has revolutionised the breeding and deployment of this species. The reduced costs of controlled pollination has meant full pedigree-control can now be maintained in large advanced generation breeding populations and *E. globulus* is one of the few eucalypt species where large-scale production of manually pollinated seed for family forestry is being undertaken.

Introduction

Eucalyptus globulus Labill. (Tasmanian Blue Gum) occurs naturally in southeastern Australia and is one of four taxa in the *E. globulus* complex that intergrade extensively and are variously given specific (Brooker 2000) or subspecific (Euclid 2006) status. These taxa are differentiated on reproductive traits, including the size and number of flower buds per umbel. Core *E. globulus* has the largest and normally solitary flower buds and capsules, although intergrade populations included in breeding programs have smaller flowers and may have up to three buds per umbel (Jordan *et al.* 1993; Jones *et al.* 2002). *Eucalyptus globulus* is genetically variable across its geographic range and the broad-scale, quantitative genetic variation in numerous traits has been summarised by classifying the native gene pool into a hierarchy of 13 races and 20 subraces (Dutkowski and Potts 1999; Cañas and Toval 2004). Subsequent molecular genetic studies have shown that these genetically differentiated races form three major lineages comprising the main populations from (i) Victoria, (ii) King Island and Western Tasmania, and (iii) eastern Tasmania and the Furneaux Islands (Steane *et al.*

2006). There is also increasing evidence that the *E. globulus* gene pool has been affected by interspecific hybridisation through its evolutionary history. This is certainly the case for the chloroplast genome (McKinnon *et al.* 2004), and may also be the case for the nuclear genome (McKinnon *et al.* 2005; Poke *et al.* 2006).

Eucalyptus globulus is the main eucalypt grown in industrial plantations in temperate regions of the world (Eldridge *et al.* 1993; Cotterill *et al.* 1999; Potts *et al.* 2004). There are breeding programs in at least eight countries - Argentina, Australia, Chile, China, Ethiopia, Portugal, Spain and Uruguay (Potts *et al.* 2004; Hunde *et al.* 2007), many of which are two or more generations removed from the native or landrace populations. While plantations are mainly grown for pulpwood production, there is increasing interest in their use for veneer and solid wood products (Raymond 2000; Greaves *et al.* 2004). *Eucalyptus globulus* is the main hardwood species grown in Australian plantations. In 2005 the *E. globulus* plantation estate in Australia was 454,095 ha, most of which was established over the last decade (Parsons *et al.* 2006). This estate is comparable to that in Portugal (c. 700,000 Potts *et al.* 2004), Spain (c. 500,000 ha Potts *et al.* 2004), Chile (c. 320,000 ha Potts *et al.* 2004) and Uruguay (c. 268,000 ha, Dirección General Forestal 2005).

Some clonal plantations of *E. globulus* have been established in countries such as Chile (Vergara and Griffin 1997; Griffin 2001), Portugal (Araújo *et al.* 1997), Spain (Toval 2004) and Uruguay (de Aguiar 2004), and there is increasing interest in clonal deployment in Australia (Anon 2004). Nevertheless, with its relatively low average rooting success and the general higher costs of clonal propagules compared to seedlings (Borralho 1997; Cañas *et al.* 2004; deLittle 2004; Dutkowski and Whittock 2004), most plantations in Australia have, and continue to be, established using seedlings. While early plantations were established from open-pollinated seed sourced directly from the best native provenances (Eldridge *et al.* 1993; Potts *et al.* 2004), improved germplasm is now mainly derived from open-pollinated seedling (Griffin 2001; Tibbits *et al.* 1997; McGowen *et al.* 2004a) or grafted (Patterson *et al.* 2004b) seed orchards, or through large-scale manual pollination systems (Patterson *et al.* 2004a; Callister 2007). Most of the older *E. globulus* seed orchards in Australia have been derived from thinning open-pollinated family trials (e.g. Volker *et al.* 1990) (Photo 1), although open-pollinated seed is increasingly being derived from grafted clonal seed orchards (e.g. Barbour and Butcher 1995; Barbour 1997).

The focus on seed deployment systems in Australia, coupled with exploitation of large, open pollinated base populations of *E. globulus* and its intergrades for breeding purposes over the last two decades (Dutkowski and Potts 1999; McRae *et al.* 2001), has required a detailed understanding of the reproductive biology of this species. This paper reviews our research on the reproductive biology of *E. globulus*, with a focus on its breeding system and advances made in seed production systems.

Pollination ecology and breeding system

Eucalyptus globulus is heteroblastic, with different juvenile and adult leaf forms (Jordan *et al.* 1999; Jordan *et al.* 2000; Lawrence *et al.* 2003). The onset of sexual reproduction is normally associated with adult leaves and first occurs in plantations at 3-4 years of age, although flowering levels are usually reduced in closed plantations (Barbour *et al.* 2007). However, the age of first flowering (Chambers *et al.* 1997; Jordan *et al.* 2000), reproductive output (McGowen *et al.* 2004a) and season of flowering (Gore and Potts 1995; Apiolaza *et al.* 2001; McGowen 2007) are genetically variable both between and within races/subraces. No significant genetic correlation between these reproductive traits and selection traits such as tree diameter and wood density have been detected (Chambers *et al.* 1997; McGowen 2007).

Eucalyptus globulus flower buds take approximately 1 year to develop from initiation to flowering (Espejo *et al.* 1996). The flowers of *E. globulus* are bi-sexual, protandrous and relatively large (Gore *et al.* 1990). The flowers produce copious nectar (Hingston *et al.* 2004b) compared to small flowered species such as *E. nitens* (Hingston 2002) and are mainly pollinated by birds and insects (Hingston and Potts 1998; Hingston *et al.* 2004b). The endangered swift parrot (*Lathamus discolor*) is one of the key native bird pollinators (Hingston and Potts 1998; Brereton *et al.* 2004). This native parrot feeds on both pollen and nectar and is a very effective pollinator of *E. globulus*, with chin, beak and tongue contact contributing to pollination (Hingston *et al.* 2004a). Just one visit of a swift parrot to a flower results in an average of 76% of the maximum possible seed set for open-pollinated flowers, whereas single flower visits by native insects do not result in detectable seed production (Hingston *et al.* 2004c). In contrast, flowers visited once by introduced social bees, the honeybee (*Apis mellifera*) or the bumblebee (*Bombus terrestris*), produced less than 7% of the maximum possible seed set for open-pollinated flowers (Hingston *et al.* 2004c). The honey bee is a major consumer of nectar but is an inefficient pollinator, and potentially deposits a high proportion of self pollen (Hingston *et al.* 2004b; Hingston *et al.* 2004c). Hence, despite suggestion for their introduction into *E. globulus* seed orchards (Moncur *et al.* 1995), easily managed social bees appear to be poor substitutes for bird pollinators in commercial seed orchards of *E. globulus*, at least in Australia.

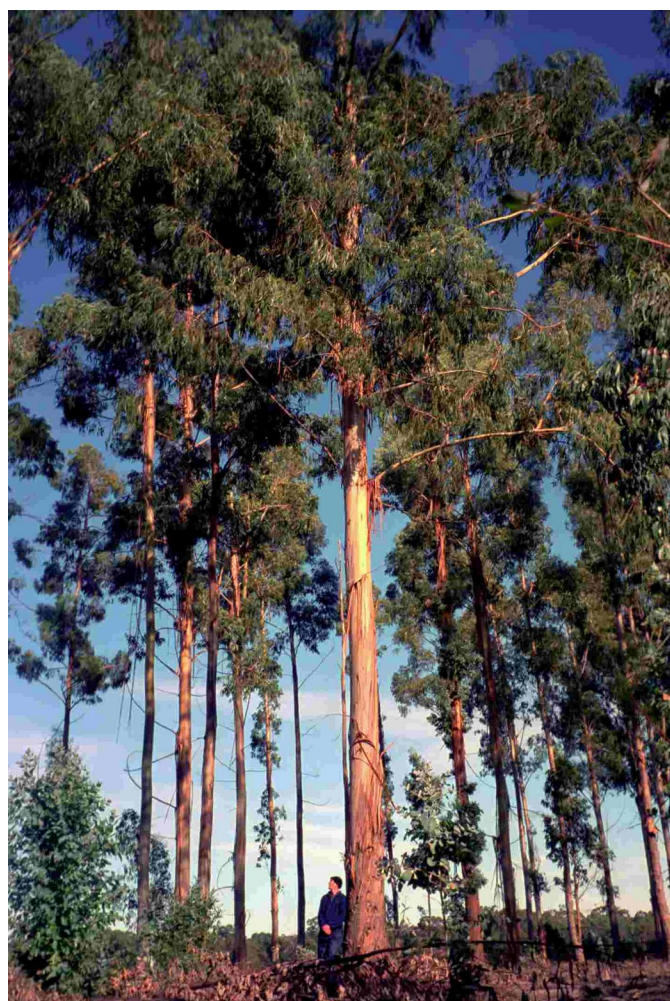


Photo 1. An open-pollinated seedling seed orchard of *E. globulus* in South Australia derived from thinning an open-pollinated family trial.

The seed orchard was established in 1988 and contained 297 families from open-pollinated native stand seed collections. It was established as a randomised complete block design, with four replicates, and each family represented in each replicate as a 5-tree line plot. The trial was measured for diameter at age six years and pilodyn penetration, an indirect measure of wood density, at age five. The data was included in the evaluation of the Southern Tree Breeding Association (STBA) National *E. globulus* breeding population undertaken in 1995. Based on estimates of the genetic worth of each tree in the orchard, it was thinned in 1997 with approximately 60% of the trees removed. Some lowly ranked families were completely removed, along with 3-4 of the lowest ranking trees in each 5-tree plot. The orchard is managed by seedEnergy Pty Ltd and seed harvested using a mechanical hoist.

Like most eucalypts, *E. globulus* has a mixed mating system. Outcrossing rates in native stands range from 38 to 100% (Hardner *et al.* 1996; Patterson *et al.* 2001; McGowen *et al.* 2004c; Jones 2005a; Foster *et al.* 2007), increasing with stand density (Borralho and Potts

1996; Hardner *et al.* 1996) and degree of self-incompatibility (Patterson *et al.* 2001; Patterson *et al.* 2004b). Outcrossing rates appear to be relatively stable across seasons (McGowen *et al.* 2004c), but can vary within the tree canopy. Increased outcrossing rates in the upper canopy of self-compatible *E. globulus* trees have been observed in native trees (Patterson *et al.* 2001) and in an open-pollinated grafted seed orchard (Patterson *et al.* 2004b). This trend is consistent with the behaviour of bird pollinators, which not only tend to commence foraging in the upper canopy of *E. globulus*, but also spend significantly more time foraging there (Hingston and Potts 2005), and rarely visit flowers within 5m of the ground (Hingston *et al.* 2004b). Flowers in the upper canopy would therefore be expected to receive a higher proportion of outcross pollen than those in the lower canopy. Foraging in the upper canopy was particularly marked in small bird species where it is suggested they are less exposed to attack from other birds feeding above (Hingston and Potts 2005). While pollinator movement and pollen dispersal is poorly understood, the only paternity study to date showed that in a dense native forest, c. 60% of successful pollination occurred between trees separated by less than 63m (Jones 2005b).

A significant reduction in seed set is usually obtained following self compared to outcross pollinations (Hardner and Potts 1995; Hardner *et al.* 1998; Pound *et al.* 2002b). Self-incompatibility levels (%SI), calculated as the percentage reduction in seed set per flower pollinated following artificial selfing compared to unrelated outcrossing, vary from 0 to 100% (McGowen *et al.* 2004a; Pound *et al.* 2002b). More than half of the genotypes, however, exhibit levels greater than 90% and a third appear to be 100% self-incompatible (McGowen 2007). Self-incompatibility is mainly driven by late-acting post-zygotic mechanisms (Pound *et al.* 2002a; Pound *et al.* 2003) and is under some degree of genetic control (McGowen 2007). There is some evidence to suggest that the self-incompatibility level of genotypes may vary slightly, potentially decreasing where reproductive loads are lower as competition for maternal resources is less (McGowen 2007).

Inbreeding depression

When self-pollination of *E. globulus* is successful, severe reductions in growth and survival of offspring occur in comparison with those derived from unrelated outcrosses (Hardner and Potts 1995; Hardner *et al.* 1998). As related trees tend to grow in close proximity in the native forest (Skabo *et al.* 1998; Jones *et al.* 2007b), their mating can also result in some inbreeding depression (Hardner *et al.* 1998). Related matings would also be favoured by the strong genetic control of flowering time (Gore and Potts 1995), which means related individuals in native stands and seed orchards will tend to flower more synchronously. Both selfing and bi-parental inbreeding can significantly reduce the growth of open-pollinated progenies (Hardner *et al.* 1998; Jones 2005b). For example, decreased outcrossing in low-density native stands of *E. globulus* is paralleled by poorer performance of open-pollinated progenies (Borralho and Potts 1996; Hardner *et al.* 1996). Variation in inbreeding depression is believed to be a major factor affecting the variation in growth of open-pollinated progeny and associated estimates of genetic parameters and breeding values (Potts *et al.* 1995; Hodge *et al.* 1996; Dutkowski *et al.* 2001; Volker 2002). However, other traits including wood density are not affected (Volker 2002; Potts *et al.* 2004). The higher outcrossing rates in the upper canopy argue for the collection of open-pollinated seed from the upper canopy to minimise inbreeding and homogenise variation in outcrossing rates (Patterson *et al.* 2004b).

While significant depression has been reported in the growth of native stand open-pollinated progenies compared to progenies derived from crosses between unrelated parents (Hardner and Potts 1995; Hodge *et al.* 1996), at least one study has shown this depression to be less for open-pollinated seed lots derived from a seedling seed orchard (Hodge *et al.* 1996; Volker 2002). Nevertheless, published outcrossing rates vary from 77% (Moncur 1995) to 92% (Russell *et al.* 2001) for two seedling seed orchards of *E. globulus* studied and are as low 60% for a grafted seed orchard (Patterson *et al.* 2004b). As in most eucalypts (Griffin

1990), the minimisation of self-pollination and associated inbreeding depression has therefore been a major consideration in the design of seed production systems for *E. globulus*. In the case of open pollinated seed orchards, this has involved strategies such as the spatial grouping of selections based on their predicted flowering time through specialised thinning regimes or planting designs, targeting self-incompatible trees for seed collection and direct progeny testing of seed orchard seed lots. However, in addition to inbreeding (Dutkowski 2004a), genetic gains from open-pollinated orchards may be reduced by high contamination from external pollen sources, particularly when they are established from thinned open-pollinated progeny trials planted near plantations or native forests. For example, contamination of open-pollinated orchards of *E. grandis* have been reported to be as high as 39% (Chaix *et al.* 2003) and 46% (Jones *et al.* 2007a).

Advances in seed production

Three major advances have occurred in the production of improved eucalypt seed in the last two decades, with initial experimental work being undertaken using *E. globulus*. The first was the discovery that the gibberellin inhibitor, paclobutrazol, could be used not only to reduce tree growth and allow easier canopy management (Hetherington and Jones 1990), but also to enhance flowering (Hetherington *et al.* 1991; Griffin *et al.* 1993) and reduce generation times (Hasan and Reid 1995) (Photo 2). Paclobutrazol is applied either through stem injection as an ethanol suspension, or in aqueous suspension as a soil drench or sprayed on the foliage (Hasan and Reid 1995). However, the response is dependent upon the type and timing of application. Paclobutrazol has low solubility and relies on being “flushed” by water movement from the site of application to the site of effect. This transport is dependant on water availability and plant transpiration to move the chemical to the site of effect (meristematic tissue) which must occur at the time of flower stimulation (Leaver 1986). These conditions may only occur for a few months of the year (Moncur *et al.* 1994). As with *E. nitens* (Williams *et al.* 2003b), the effectiveness and reliability may be enhanced with nitrogen fertilisation on specific sites (Williams *et al.* 2003a; Williams *et al.* 2003b). No deleterious effects of paclobutrazol application has as yet been detected on seed quality (Hasan and Reid 1995) or subsequent seedling growth (D Williams and BM Potts unpubl. data). However, higher capsule abortion rates have been recorded in paclobutrazol treated *E. globulus* trees (Callister 2007), and on ramets of treated trees with heavier crops (Suitor *et al.* 2007). For most eucalypt species, paclobutrazol application is now a routine part of the management of seed orchards and breeding arboreta; with the main research issues associated with reducing the economic and environmental costs of its use.



Photo 2. The enhanced flower bud production and reduced vegetative growth evident following paclobutrazol application to grafted trees of *E. globulus*.

The tree shown has an atypically high flower bud load for the vegetative canopy size. While flower bud abundance is enhanced, there is evidence that capsule abortion rates increase with paclobutrazol application, no doubt due to the larger reproductive crops. (photo: R. Wiltshire)

The second major advance in seed production was the discovery that the stigma is not necessary for successful pollination in some eucalypts and that the pollen will germinate on the cut surface of the style at (Harbard *et al.* 1999; Williams *et al.* 1999), or even prior to (Trindade *et al.* 2001), operculum shed, which often occurs 5-7 days before stigma receptivity in *E. globulus* (Patterson *et al.* 2004a). While initially reported for *E. gunnii* in 1988 (Cauvin 1988), it was not until a decade later that this discovery was operationalised. This development has enabled pollination to be undertaken at the same time as emasculation and, coupled with style-isolation using tubes or isolating single or multiple flowers with perishable balloons or paper bags, has allowed controlled pollination to be undertaken in a single visit to the flower (termed 'One-stop pollination' – OSP Harbard *et al.* 1999 or 'Single-visit pollination' - SVP Williams *et al.* 1999) (Photo 3).

This advance in pollination technique has revolutionised breeding and deployment strategies for *E. globulus*. With its large flower and the OSP/SVP pollination technique, most major *E. globulus* breeding programs are now generating large, advanced generation breeding populations of full-sib families (Potts *et al.* 2004). Full pedigree control enhances the accuracy of breeding and deployment value prediction (Dutkowski *et al.* 2006). Such large-scale controlled crossing would be considerably more expensive in small-flowered species, such as *E. nitens*, for which the OSP/SVP techniques have not been successfully developed (Williams *et al.* 1999; Venter and Silval 2007). Traditional controlled pollination, involves

(a)



(b)



Photo 3. The OSP/SVP cut-style pollination technique used by seedEnergy Pty Ltd for the production of mass supplementary pollinated (MSP) seed of elite full-sib *E. globulus* families for family forestry.

The MSP technique involves (a) transversely cutting the style with small scissors 1-2mm below the stigma to maximise the surface area of the transmission tissue for pollen application and then (b) applying pollen to the freshly cut surface with a small paint brush. Styles are cut on flowers ranging in development from operculum shed to 1 week later, and all suitable flowers on a tree are pollinated on a weekly cycle. Flowers are not emasculated, nor are they isolated or labelled which considerably reduces labour costs.

three visits to the flower – emasculation and isolation at operculum shed, pollination at stigma receptivity and then removal of isolation bags several weeks later (Moncur 1995; termed three visit pollination – TVP, Venter and Silval 2007). This time consuming approach had been previously used for the large-scale production of *E. globulus* full-sib family seed in Portugal (Leal and Cotterill 1997). Now, however, manual pollination of *E. globulus* seed for deployment is being undertaken by many organisations. The OSP/SVP technique with stigma isolation has been used widely in Chile for the production of control pollinated, usually polymix, *E. globulus* seed for deployment (Harbard *et al.* 2000; Espejo J 2001; Ramírez de Arellano *et al.* 2001). While similar pollination techniques have been used by some organisations in Australia, the high labour costs have required the development of further efficiencies. For example, the seed company seedEnergy Pty Ltd, now routinely uses the cut style technique without emasculation, flower isolation or labelling, in an operational system termed “mass supplementary pollination” (MSP - Patterson *et al.* 2004a) (Photos 3 and 4). This system is used for the large-scale production of selected full-sib family seed for deployment in family forestry.

(a)



Photo 4. *Eucalyptus globulus* grafted seed orchard near Hobart, Tasmania.

(a) The orchard was established by seedEnergy Pty Ltd for the large-scale production of elite *E. globulus* full-sib family seed for deployment using mass supplementary pollination (MSP). Genotypes in the orchard are selections from the STBA National *E. globulus* breeding population. (b) Operators pollinate all flowers on the trees on a weekly cycle using the cut style technique (Photo 3) and all capsules on the tree are subsequently harvested. The study of Patterson *et al.* (2004a) suggest that the target pollinations are likely to comprise 87% of the seed obtained, the remainder being selfs (4.6%) and presumably high quality outcrosses from other selected genotypes in the orchard (8.4%). Selfing can be eliminated completely when self-incompatible genotypes are used as females.

(b)



The choice of female genotype can have a significant effect on the costs of seed production with SVP and MSP, due to genetic based differences in reproductive success (Callister 2007; McGowen 2007). A new pollination approach developed by de Assis *et al.* (2005), involving cutting the top of both the operculum and style simultaneously, may offer further efficiencies but has yet to be fully tested with *E. globulus*. The level of contamination with MSP is estimated to be about 13%, most of which is outcross (Patterson *et al.* 2004a). Harbard *et al.* (2000) consider that contamination levels of c. 10% are acceptable for commercial seed production, particularly when contamination is from males of high genetic quality as is most likely with MSP.

The third major advance in seed production systems that should be noted is not biological, but relates to information flow, improved accuracy of prediction of breeding values (although partly achieved through better pedigree control), and the efficient translation of genetic gains in the breeding population to the *E. globulus* plantation estate. For example, the Australian National *E. globulus* breeding program run by the Southern Tree Breeding Association (STBA) aims for close integration of members deployment populations and decisions (e.g. Dutkowski 2004c; Dutkowski 2004b), with a large national breeding population (McRae *et al.* 2001), a rolling front breeding strategy (Borralho and Dutkowski 1998), regular evaluation of breeding values across sites and generation using BLUP (best linear unbiased prediction) mixed model methodology (Kerr *et al.* 2002; Dutkowski *et al.* 2006), and clearly define breeding objectives and economic weights (Greaves *et al.* 1997; Greaves *et al.* 2004). This integration allows the regular delivery of breeding or deployment values based on the economic worth of an individual or family for a variety of breeding objectives using a web-based data management system. The selections in the seedEnergy Pty Ltd orchard (Photo 4) are from this program. Elite full-sib families are generated through MSP based on (i) parental breeding values or, as more data from second-generation full-sib family trials becomes available, (ii) predicted deployment values utilising information available on the specific family performance. In the first case genetic gains are expected through the reduction in levels of selfing and exploitation of additive genetic effects (general combining ability), in the second case through the additional capturing of non-additive (specific combining ability) effects (Dutkowski 2004b). The gain from family forestry as opposed to deploying open-pollinated seed orchard seed is largely dependent on the relative size of the additive and non-additive genetic effects. The evidence for non-additive genetic effects for growth in *E. globulus* includes 1) the existence of severe inbreeding depression, 2) positive mid-parent heterosis in wide cross types, and 3) significant non-additive interactions between parents from the same population (Potts *et al.* 2004). While the evidence for non-additive interactions between parents has been variable (Potts *et al.* 2004), a recent study of early age growth in STBA second-generation progeny trials found that the non-additive genetic variation for stem diameter at breast height was comparable to the additive genetic variation (average $h^2=0.12$ and $d^2=0.12$) (Li *et al.* 2007).

Seed quantity and quality

With greater investment in *E. globulus* seed production through the use of OSP/SVP or MSP systems, there is increasing interest in minimising losses through flower abortion (Callister 2007; Suitor *et al.* 2007) and seed predation (McGowen *et al.* 2004b), and optimising seed quality for mechanised nursery operations in order to provide more uniform germination and seedling quality. Nurseries continually face the problem of variation in seed quality from year to year, even when seed collected from the same seed orchard. In some cases, poor seed quality and consistency can reduce nursery output of specification seedlings by up to 25% through low or asynchronous germination (Photo 5). This amounts to considerable loss in production in large commercial nurseries that may sow about 10 million seeds annually (Photo 6).



Photo 5. Variable germination of *E. globulus* seed can result in large variation in seedling size within the same nursery tray and result in a high percentage of seedlings being discarded as they do not meet planting specifications.



Photo 6. *Eucalyptus globulus* seedlings growing in the Storaenso nursery at Furadouro, Portugal. In 2004, this nursery was producing approximately 7 million plants per year, 3.5 million of which were *E. globulus*.

Eucalyptus globulus seed usually matures within a year of pollination (Sasse *et al.* 2003). However, there is always pressure for early harvest of elite seed to ensure seedlings are ready for planting which risks degrading the seed crop with immature seed. Maternal genetic and environment effects clearly also impact on the quantity and quality of seed produced. Whether under open-pollination or MSP, the quantity of seed obtained is strongly affected by significant, genetic based differences between and within races/subraces for all facets of reproductive success including flower abortion, total capsule crop and seed per capsule (McGowen *et al.* 2004a; McGowen 2007; Callister 2007).

Seed size can similarly be affected by both maternal genetic (McGowen *et al.* 2004a; cf. Watson *et al.* 2001) and environmental factors, including pollination success. For example in the latter case, where seed numbers per capsule are atypically high following SVP/OSP or MSP, seed may be atypically small. A positive association between seed size and early growth has been reported in *E. globulus* (Lopez *et al.* 2003), with early nursery growth affected by carryover of maternally induced variation in seed mass, affecting germinative capacity and seedling growth. However, these maternal effects only lasted one year in the field. The positive effect of seed mass on early growth was independent of the negative effect of germination time (Watson *et al.* 2001; Lopez *et al.* 2003). Replicated sampling from a seed orchard has demonstrated large genetic-based differences between subraces in seed size (McGowen *et al.* 2004a) and one of the most favoured races for pulpwood plantations, the Strzelecki Ranges, (Apiolaza *et al.* 2005) has relatively small seed. Large eucalypt seeds are preferred by nurseries as they germinate faster, produce large seedlings and show higher seedling survival (Lopez *et al.* 2003; Watson *et al.* 2001; Martins-Corder *et al.* 1998). Commercially available seedlots are frequently pooled from top selections and after sieving; small seed is often discarded which could mean a loss of specific germplasm of high genetic quality. Nevertheless, a study of a commercial *E. globulus* seed lot did not detect any difference in genetic diversity between seed size classes (Martins-Corder *et al.* 1998). Seed size also appears to be unrelated to outcrossing level within a tree (McGowen *et al.* 2004c). Maintaining seed in individual tree seedlots when grading by size and density will, to some extent, help nurseries achieve more uniform and synchronous germination of seed and subsequent seedling growth. However, the vast majority of the variation still occurs within graded seedlots (Watson *et al.* 2001), which may reflect numerous factors including maternal and direct environmental effects. Lopez *et al.* (2000) report an optimum temperature of 28°C for the germination rate and capacity of *E. globulus* seed. Germination was also reported to be very sensitive to water potential (0 to -0.75 MPa), with no germination occurring at potentials below -0.25 MPa.

Conclusion

In summary, the reproductive biology of *E. globulus* is one of the most-studied of any eucalypt species. Studies have been facilitated by its comparably large flower, and driven by the exploitation of large open-pollinated family trials during the 1990's coupled with a focus on deployment of seedlings rather than clones. Such studies have allowed a better understanding of the genetic composition of open-pollinated progenies and the accuracy of derived genetic parameters, as well as identifying ways to minimising the deleterious effects of inbreeding on growth. While further refinements are no doubt ahead, the integration of advances in canopy and flowering management with simple, but revolutionary procedures for controlled pollination have lead to major advances in *E. globulus* breeding and seed deployment systems over the last decade. The reduced cost of controlled crossing has allowed (i) increased selection intensities and improved accuracy of selection through the development of large, fully pedigreed breeding populations and (ii) opportunities to avoid inbreeding depression and capture non-additive genetic effects through large-scale production of elite full-sib families for deployment.

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