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GENETICS OF EUCALYPTS: TRAPS AND OPPORTUNITIES

1. INTRODUCTION

Eucalypts are amongst the most planted hardwoods in the world (Doughty 2000). They are native to Australia and islands to its north (Ladiges *et al.* 2003) where they occupy diverse ecological habitats ranging from sea level to the alpine tree line, from high rainfall to semi-arid zones, and from the tropics to latitudes as high as 43° south (Williams and Woinarski 1997). In habit they vary from shrubs and multi-stemmed mallees, to giant trees (Hickey *et al.* 2000; Nicolle 2006), and include the tallest flowering plants on earth (*Eucalyptus regnans* – 99.6 metres, <http://www.gianttrees.com.au/>). They are generally sclerophyllous, and adapted to low nutrient soils and fire (Ashton 2000; Eldridge *et al.* 1993; Florence 1996). In the broad-sense, eucalypts encompass species of the genera *Eucalyptus* L'Hérit., *Corymbia* Hill and Johnson and *Angophora* Cav. (Ladiges 1997; Appendix 1). A key feature of the majority of *Eucalyptus* (*sensu stricta*) and *Corymbia* (bloodwoods) is the fusion of either the petals and/or sepals to form an operculum from which the eucalypts derive their name (Eldridge *et al.* 1993; Ladiges 1997). The latest formal taxonomic revision of eucalypts (Brooker 2000) recognizes just over 700 species that belong to 13 main evolutionary lineages (subgenera/genera; Appendix 1), and EUCLID (Euclid 2006 - an important electronic resource for practitioners) lists 894 eucalypt taxa. The major subgenera exhibit different ecological and reproductive characteristics (Florence 1996; Ladiges 1997; Harwood 2011 this volume) and closely related species are usually ecologically differentiated (Florence 1996; Williams and Woinarski 1997).

Most eucalypt species belong to the subgenus *Symphyomyrtus*, and it is mainly species from three sections of this subgenus that are used in plantation forestry world-wide (Appendix 1; see Hardwood this volume). This is certainly the case in Australia where there has been a major expansion of the eucalypt plantation estate in the last two decades. This eucalypt plantation estate reached 0.92 million ha in 2010 and is approaching the area of softwoods (Gavran and Parsons 2011). Most Australian eucalypt plantations occur in temperate regions and the estate is dominated by *Eucalyptus globulus* (58.4%; i.e. 538,000 ha) and *E. nitens* (25.5%, i.e. 235,000 ha) (Gavran and Parsons 2011). There are breeding and deployment programs in Australia and overseas for both *Eucalyptus globulus* (Potts *et al.* 2004) and *E. nitens* (Hamilton *et al.* 2008). These species are mainly grown for pulpwood.

However there is increasing interest in producing solid wood products (e.g. sawn timber, veneer, composites) from these plantations (Nolan *et al.* 2005; Beadle *et al.* 2008; Wood *et al.* 2009; Washusen 2011; Welsford and Henson 2011). At least 7% of the broadleaf plantations are managed for this purpose (Gavran and Parsons 2011), which includes Forestry Tasmania's solid wood estate of approximately 19,655 ha of *E. nitens* and 5,462 ha *E. globulus* (Wood *et al.* 2009). We here overview some of the key genetic issues associated with the breeding and deployment of these industrial plantation species and recent research aimed at understanding the genetic opportunities for growing these species for solid wood products.

2. BREEDING OBJECTIVES

Tree breeding programs aim to improve the profitability and competitiveness of forest growers/processors through the genetic improvement of economically-important harvest-age traits. To maximize economic gains made through breeding it is important to i) identify the breeding objective (i.e. what you are breeding for), ii) identify the most important harvest-age traits affecting this objective (i.e. the objective traits) and iii) apply appropriate weights to each of these traits. This is best achieved through bioeconomic modeling of costs (land, establishment, management, silvicultural, harvesting, transport, processing) and revenues (potentially from different product classes of varying value) of production systems (Ponzoni and Newman 1989; Raymond and Apolaza 2004). Traits such as pest and disease resistance, adaptability traits (e.g. frost resistance, drought resistance) and survival are only important as far as they impact on one or more objective traits and their incorporation into breeding programs requires an understanding of the frequency, intensity and impact of the associated biotic and abiotic threats across the plantation estate (Dutkowski *et al.* 2007).

Breeding objectives, objective traits and economic weights evolve with changes in understanding of production systems and harvest-age traits, silviculture (e.g. seedling to coppice [Whitlock *et al.* 2004], pulpwood to long-rotation solid-wood), processing techniques/technology (e.g. backsawn vs quartersawn, changes in sawmilling and drying technology - Washusen 2011), environment (e.g. expansion into marginal zones prone to frost, drought, climate change - ABARES 2011; exhaustion of historic water and nutrient reserves; new pests/diseases [e.g. Myrtle rust] or changed frequency/intensity of outbreaks), markets and products (e.g. solid-wood, carbon trading, bioenergy - Whitlock *et al.* 2007). Some organizations have multiple objectives, reflecting the diversity of their estate and/or targeted products (e.g. cold and mild sites, disease-prone and less disease-prone sites, pulpwood and solid-wood silviculture). In such cases, targeted deployment is often preferred, as a lower cost alternative to maintaining multiple breeding populations, particularly in cases where objectives are closely aligned (i.e. favorably and strongly genetically correlated) or where some objectives are only relevant to a small proportion of the estate (i.e. it is not unusual for enterprises to have multiple 'deployment objectives',

while maintaining only one breeding objective and population) (Dutkowski *et al.* 2007).

Bio-economic modeling has identified volume production per hectare, wood density and pulp yield as key objective traits for vertically integrated enterprises producing eucalypt kraft pulp (Borralho *et al.* 1993; Greaves *et al.* 1996; Dutkowski *et al.* 2007). The economic weight placed on each of these traits varies amongst Australian growers. For example, some wood chip exporters do not place an economic weight on pulp yield as a premium is generally not paid for high pulp yield (Whitlock *et al.* 2007), although it may become a threshold trait affecting market access in the future. However, in Australia where *E. nitens* and *E. globulus* breeding may involve joint evaluation (McRae *et al.* 2004a; Hamilton *et al.* 2008) or cooperative breeding (e.g. through the Southern Tree Breeding Association - McRae *et al.* 2004b), such differences in objectives amongst growers are often applied at deployment. Secondary wood property traits of interest to pulp producers include the quantity or quality of extractives or lignin in the wood that affect the economic and/or environmental cost of pulping (Raymond and Apiolaza 2004; Stackpole *et al.* 2011).

Defining breeding objective traits and economic weights is more problematic for solid wood systems than for pulpwood systems, due to:

- i) a lack of an established plantation-eucalypt solid-wood processing industry in Australia,
- ii) the array of products (e.g. sawn timber, veneer, residues), silvicultural regimes, processing systems, and product values to be accounted for, and
- iii) longer rotation intervals and associated uncertainty (Greaves *et al.* 2004a; Greaves *et al.* 2004b; Greaves *et al.* 2004a; Shield 2004; Washusen 2011).

In the face of such difficulties, eucalypt growers targeting solid wood products have, initially at least, focused on generic traits (adaptability, form, etc), although numerous wood properties are known to affect the recovery and value of sawn timber, veneer and composite wood products (Table 1). Wood properties can impact multiple products in a favorable or adverse manner. For example, improvement in a trait such as wood density is likely to be favorable for multiple product types, at least in *E. nitens* (Kube and Raymond 2005).

The yield of plantation logs suitable for solid-wood processing is strongly dependent upon silviculture (Washusen 2004; Nolan *et al.* 2005; Beadle *et al.* 2008) and there are few genetics trials of *E. globulus* and *E. nitens* that have been managed using solid-wood silvicultural regimes (e.g. thinning, pruning). This has restricted most genetic studies of potential solid wood traits to closely-spaced, unpruned trials (Hamilton *et al.* 2007; Hamilton *et al.* 2010c; Blackburn *et al.* 2010), which raises the possibility of genetic by silvicultural interactions for some traits (e.g. wood shrinkage and collapse - Hamilton *et al.* 2009). While key traits affecting the yield of logs suitable for a given processing system (e.g. survival, growth rate, forking, stem straightness, branch size, log taper) are usually under some degree of genetic

control (Hamilton and Potts 2008; Callister *et al.* 2011; Blackburn *et al.* 2010), their impact on profitability will in part depend on whether adverse genetic effects are alleviated through routine silvicultural treatments such as thinning and pruning. Green recovery, drying defects and product value from logs are, in turn, affected by wood properties (Table 1), many of which are also known to be under some genetic control (Kube and Raymond 2005; Greaves *et al.* 2004b; Hamilton *et al.* 2007; Hamilton *et al.* 2009; Hamilton *et al.* 2010a; Blackburn *et al.* 2010).

Table 1. Wood properties affecting recovery and value for different product types (see also Raymond 2002).

<i>Pulp and paper</i>	<i>Sawn timber</i>	<i>Veneer, plywood and laminated veneer lumber (LVL)</i>
Basic density, pulp yield/cellulose content, lignin content and composition, extractives content, fiber dimensions,	Green recovery (growth stress, log end splits, decay) Dried recovery and value (knot size, checking, shrinkage, collapse, board distortion, strength and stiffness, density, hardness, dimensional stability, durability, sapwood-heartwood ratio, colour and colour variation)	Green recovery (growth stress, log end splits, decay) Dried recovery and value (knot size, veneer splitting, shrinkage and shrinkage variation, density, strength and stiffness, bond strength and glue usage, roughness, colour and colour variation)

3. CHOICE OF SPECIES

Choice of species based on breeding objectives and breeding objective traits (Table 2) may have a major impact on breeding and deployment. There are large differences in reproductive biology, potential for vegetative propagation and silvicultural options between *E. globulus* and *E. nitens* (Table 2). For example, as *E. globulus* coppices well, many plantations are not replanted but are managed as a coppice crop (Whitlock *et al.* 2004). This option is not available with *E. nitens* which does not coppice as well (Little and Gardner 2003), and plantations are normally re-established using seedlings. Extensive studies of the reproductive biology and mating systems of these two species have been undertaken in order to optimise breeding and deployment (see *E. globulus* - Potts *et al.* 2008; *E. nitens* - Hamilton *et al.* 2008).

As with most eucalypts, *E. globulus* and *E. nitens* are animal pollinated, but the type and efficiency of pollinators may vary (Hingston *et al.* 2004c; Hingston *et al.* 2004b; Hingston *et al.* 2004a). For example, the large-flowered *E. globulus* is pollinated by both birds and insects, and the pollination behaviour of birds is thought to result in higher outcrossing in the upper canopies of both native and seed orchard trees in Tasmania. Birds were not observed feeding from the small flowers of *E. nitens* in Tasmanian seed orchards, and despite suggestions that the introduction of honey bee hives would increase outcrossing rates and seed set, honey bees were rarely observed feeding from small flowers of *E. nitens* in a study by Hingston *et al.* 2004a. Flowers however were consistently well pollinated by the suite of small native insects visiting the flowers.

Both *E. globulus* and *E. nitens* have a mixed mating system, but are generally preferential outcrossers. While average seed set is reduced following self pollination compared to unrelated outcrossing, open pollinated seed collected from native stand and seed orchard trees still contain significant proportions of self-pollinated seed. Averaged across 23 species the outcrossing rate in eucalypts in the wild is 0.74 (Byrne 2008), and recent native population estimates for *E. globulus* range from 65-89% (Mimura *et al.* 2009) and seed orchard estimates from 60 to 92% (Potts *et al.* 2008). Only seed orchard estimates of outcrossing rates have been published for *E. nitens* but these range from 0.75 to 0.87 (reviewed in Grosser *et al.* 2010). Both species exhibit severe inbreeding depression for growth and survival (Hardner and Tibbits 1998; Costa e Silva *et al.* 2010b; Costa e Silva *et al.* 2010a; Costa e Silva *et al.* 2011a). Virtually all *E. globulus* and *E. nitens* plantations in Australia are established using seed-derived plants and minimising the levels of self pollination has been an important objective. The cost of artificial pollination of *E. globulus* has been markedly reduced through the development of single-visit cut-style techniques (single-visit pollination, SVP - Williams *et al.* 1999; one-stop pollination, OSP - Harbard *et al.* 1999) which has allowed most breeding to be done through control pollination to provide full pedigree control. These techniques have also allowed the development of manual pollination techniques (e.g. mass

supplementary pollination; MSP) for large-scale seed production to minimise selfing and to allow deployment of elite full-sib or mixed families (Potts *et al.* 2008). Despite numerous attempts, the cut style technique has not been successful with *E. nitens* (Williams *et al.* 1999), making it relatively expensive to control pollinate. While improved *E. globulus* seed is produced from open-pollinated (OP) seedling or grafted seed orchards as well as mass supplementary pollination, the later option is not available with *E. nitens*.

Table 2. Characteristics which favour the planting of *E. nitens* or *E. globulus* in Tasmania.

<i>Eucalyptus globulus</i>	<i>Eucalyptus nitens</i>
Adaptive	
<ul style="list-style-type: none"> • More drought resistant¹ • Greater water use efficiency² • More resistant to <i>Phytophthora cinnamomi</i>³ • Less prone to copper deficiency³ 	<ul style="list-style-type: none"> • Generally more rapid site occupancy⁴ • Greater frost resistance and cold hardiness⁵ • Less prone to gum leaf skeletonizer³ • Greater resistance to Mycosphaerella leaf disease⁶
Pulping and paper making*	
<ul style="list-style-type: none"> • Generally greater kraft pulp yield^{7,8,9,10} • Higher wood basic density^{8,9,10,11} 	
Solid-wood, veneer and composite	
<ul style="list-style-type: none"> • Less internal checking in sawn boards^{12,13} • Greater wood strength, stiffness and hardness¹¹ • Better shedding of dead branches¹⁴ 	<ul style="list-style-type: none"> • Less prone to tension wood formation and associated drying defects¹³ • Better early-age stem straightness^{4,15}
Reproductive and deployment	
<ul style="list-style-type: none"> • Easier and quicker to grow seedlings in container nurseries (larger seed, easier to sow, grows 	<ul style="list-style-type: none"> • Easier to graft and less graft incompatibility^{14,22} • Open-pollinated seed orchards

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- larger seedlings in a shorter time)¹⁴
 - Stronger coppicing ability^{16,17}
 - Easier to artificially pollinate^{18,19} but exhibits unilateral cross incompatibility with smaller flowered taxa²⁰
 - Can be mass pollinated for deployment¹⁸
 - Easier to propagate by hardwood cuttings²¹
- easier to manage¹⁴:
- More flowers and seed per tree or hectare¹⁴
 - More overlap in flowering time^{23,24}

¹White *et al.* 1996; ²Honeysett *et al.* 1996; ³Wardlaw 2010 (but see Potter and Stephens 2005); ⁴pers. comm. D. Williams; ⁵Hallam *et al.* 1989; ⁶Mohammed *et al.* 2003; ⁷Beadle *et al.* 1996 ⁸Downes *et al.* 2006; ⁹Kibblewhite *et al.* 2000; ¹⁰Williams *et al.* 1995; ¹¹McKinley *et al.* 2002; ¹²Innes *et al.* 2008; ¹³Washusen 2011; ¹⁴pers. comm. K. Joyce; ¹⁵pers. comm. C. Harwood; ¹⁶Little and Gardner 2003; ¹⁷Whitlock *et al.* 2003; ¹⁸Venter and Silval 2007 ¹⁹Williams *et al.* 1999; ²⁰Gore *et al.* 1990; ²¹de Little 2004; ²²pers. comm. R. Griffin; ²³Jones *et al.* 2011; ²⁴Barbour *et al.* 2006.

* Other pulp and paper qualities of *E. globulus* and *E. nitens* are compared in Cotterill and Brolin (1997). While not cited as a consideration in Tasmania, overseas experience (pers. com. R. Griffin) suggests that *E. globulus* produces paper with higher tear strength and better porosity, whereas *E. nitens* is easier to refine and consumes less energy (see also Cotterill and Brolin 1997).

4. DEFINING THE GENEPOOL

The main breeding strategies used for genetic improvement of both *E. globulus* and *E. nitens* in Australia (McRae *et al.* 2004b; Li *et al.* 2007; Hamilton *et al.* 2008) and overseas (Griffin 2001) exploit genetic variability through single-species population genetic improvement. However taxonomically defining the base population used for genetic improvement is important (see for example Shepherd this volume) but has proved problematic in both species. Within species, marked genetic differentiation between populations is the norm rather than the exception (Pryor and Johnson 1971; Pryor and Johnson 1981; Potts and Wiltshire 1997). Genetic variation between populations in quantitative traits is often continuous and clinal, paralleling environmental gradients associated with changes in, for example, latitude, continent or altitude (Pryor and Johnson 1981; Potts and Wiltshire 1997; Dutkowski and Potts 1999; Butcher *et al.* 2009). Many recognized eucalypt species intergrade resulting in complexes of closely related species where no clear morphological discontinuity is apparent (see Shepherd this volume). This is the case with *E. globulus* which is part of a complex of four closely related taxa (*E. globulus*, *E. pseudoglobulus*, *E. bicostata* and *E. maidenii* - Brooker 2000) variously given species or subspecies

status (Jordan *et al.* 1993). The cores of these taxa are morphologically and geographically distinct, but linked by morphologically and geographically intermediate (intergrade) populations (Jordan *et al.* 1993; Jones *et al.* 2002). The main populations sampled for breeding programs around the world are core *E. globulus* and *E. globulus* intergrades (Jordan *et al.* 1993). Intergrade populations which are difficult to assign to a specific taxa caused problems in early seed collections where, for example, one collection locality was classified as *E. bicostata*, *E. globulus* and *E. pseudoglobulus* by different seed collectors (Jones *et al.* 2002). This issue is confounded by the fact that morphology often does not reflect underlying molecular affinities (Jones *et al.* 2002; Jones 2009). Three main molecular lineages have now been identified within the founder base population germplasm used in *E. globulus* breeding programs that strongly reflect geographic proximity (Jones *et al.* 2006; Steane *et al.* 2006). In the case of both *E. globulus* and *E. nitens* the broad-scale variation in the native gene pools has now been summarised using a hierarchy of geographic races, subraces and collection locality information based on quantitative genetic and geographic information (Dutkowski and Potts 1999; Hamilton *et al.* 2008).

In the case of *E. nitens*, two issues have complicated the exploitation of the base populations used for *E. nitens* breeding. Firstly, the founder native trees sampled in earlier collections encompassed phenotypes initially classified as *E. nitens* var *errinundra* by Pederick (1979), but subsequently classified as a separate taxon *E. denticulata* (Cook and Ladiges 1991). This taxon is mainly confined to the Errinundra region in eastern Victoria but some phenotypes are interspersed within predominantly *E. nitens* populations in central Victoria (Hamilton *et al.* 2008). More recent seed collections have avoided *E. denticulata*-like phenotypes (Dutkowski *et al.* 2001b), but their separation from *E. nitens* seed lots in data collected or reported from older trials has not always been possible (Hamilton *et al.* 2011). Secondly, further to characterising *E. denticulata*, Cook and Ladiges (1991), defined three genetically distinct races of *E. nitens* (i) Central and Northern NSW, (ii) Southern NSW and Mt Kaye, and (iii) Central Victoria. Dutkowski *et al.* (2001), later separated the Central Victorian race into three additional races - Northern, Southern and Connors's Plain. The boundaries of these new races do not correspond neatly to those of the previous provenance classification of the same area (Pederick 1979), making exact comparisons across studies challenging.

Experience with the base populations of *E. globulus* and *E. nitens* has emphasised the importance of maintaining information on founder tree morphology as well as precise geographic origin. Such information is now easily collected and maintained with digital photographs (of tree habit and morphology) and accurate GPS information. Given the costs of field sampling and reducing costs of DNA studies, the collection and storage of foliar samples from trees sampled for seed collection is also warranted for assessing relationships (Shepherd this volume), future quality control (Vaillancourt *et al.* 1998; Faria *et al.* 2010) and potential use in molecular breeding (Section 8).

5. CHOICE OF PROVENANCE

Base populations for breeding *E. globulus* and *E. nitens* have been established from large-scale single-tree, open-pollinated seed collections from many localities within their native ranges (Eldridge *et al.* 1993; Potts *et al.* 2004; Hamilton *et al.* 2008). In many cases, these collections have been distributed across breeding organisations leading to numerous trials with shared pedigrees, and possibilities for joint analyses (Costa e Silva *et al.* 2006), cooperative breeding (McRae *et al.* 2004b) and/or joint evaluation (McRae *et al.* 2004a; Kerr *et al.* 2008). Genetic evaluations of base populations account for spatial genetic structure in the founder generation using genetic groups. Genetic groups are traditionally reported as “provenances” in forest tree studies, but in the case of both *E. globulus* and *E. nitens* where the native gene pools have been extensively studied, it is the race or subrace classification which is usually used (see Section 4).

Numerous studies of the quantitative genetic variation within *E. globulus* and *E. nitens* have been published from base-population trials (reviewed for *E. nitens* by Hamilton and Potts 2008 and for *E. globulus* by Dutkowski and Potts 1999; Potts *et al.* 2004; see also Stackpole *et al.* 2010b; Stackpole *et al.* 2011; Hamilton *et al.* 2010b). These studies provide information on the genetic architecture of the native forest gene pools as well as the basic information required for genetic improvement. As with most eucalypt species studied (Potts and Wiltshire 1997), there is considerable provenance (race/subrace) variation within *E. globulus* and *E. nitens* which impact on all stages of breeding and deployment from reproduction to product value. For example, during the rapid expansion of the *E. globulus* estate in Australia in the 1990’s large amounts of seed were obtained directly from native forest due to the shortage of improved seed-orchard seed. As the subraces differ significantly in breeding objective traits for pulpwood production, Apiolaza *et al.* (2005) estimated that choice of subrace could alter Net Present Value (NPV) of plantations by as much as AU\$2129 per hectare, effectively the difference between profit and loss. Notable examples of where genetic-based difference amongst native stand races or subraces impact the forest production system are given below.

5.1. Reproduction

Studies of the reproductive biology (including pollination ecology) and breeding systems have been important for understanding the limits to genetic evaluation using open-pollinated seed lots as well as development of efficient pollination and deployment systems for these species (see Hamilton *et al.* 2008 and Potts *et al.* 2008 for references prior to 2008). These include studies of the pollination ecology, breeding system (outcrossing rates and gene flow - Groszer *et al.* 2010; Mimura *et al.* 2009), self-incompatibility (McGowen *et al.* 2010), flowering time (Jones *et al.* 2011) and abundance, pollination techniques, as well as seed production (Suitor *et al.* 2008; 2009a; Suitor *et al.* 2009b; Suitor *et al.* 2010) and seed germination (Nair *et al.* 2009; Rix *et al.* 2011).

While flowering time in *E. nitens* orchards is relatively synchronous, this is not the case for *E. globulus*. There may be up to 8 months difference in the peak flowering time amongst *E. globulus* genotypes, largely due to genetic-based differences between subraces (Gore and Potts 1995; Jones *et al.* 2011). This asynchrony has the potential to significantly reduce mating opportunities within open-pollinated seed orchards. A classic example relates to the two Bass Strait island races, King Island and Furneaux, which in early trials were grouped together into the same subline (Orme 1988) with a view to conversion to open-pollinated seedling orchards. These races have subsequently been found to differ in numerous traits (Dutkowski and Potts 1999) and the peak flowering of the King Island race is nearly 100 days later than Furneaux (Gore and Potts 1995). Genetic information is now available on flowering time which has subsequently been used to better synchronize flowering within seed orchards. Flowering time limitations to cross pollination are one of the advantages of mass supplementary pollination as opposed to relying on open-pollination in *E. globulus*. There is also evidence to suggest that subraces of *E. globulus* may differ in their degree of inbreeding depression (Costa e Silva *et al.* 2011a), which may differentially affect their performance under open pollination. Choice of provenance may also affect propagation costs. The subraces of *E. globulus* differ in flower and capsule size, as well as their reproductive output and seed characteristics in seed orchards. For example, one of the more favoured subraces - Strzelecki Ranges –has the smallest flowers and capsules, and in a seed orchard studied produced the smallest seed and lowest whole tree seed output (McGowen *et al.* 2004). This subrace has also been reported to be amongst the more difficult to propagate by hardwood cuttings (Cañas and Toval 2004).

5.2. Adaptability

Growth and survival are fundamental to successful plantations, regardless of the product objective (Teulière *et al.* 2007). The longer the rotation and the greater the investment in plantation silviculture, the more important it will be to have well adapted germplasm. Often genetic effects may take several years to become evident following plantation establishment (Lopez *et al.* 2003; Costa e Silva *et al.* 2010b). While adaptive differences may be manifest early in the life cycle (e.g. frost susceptibility - Tibbits and Hodge 2003; Tibbits *et al.* 2006), there is increasing evidence of their ongoing expression, particularly with increasing competition following canopy closure and the onset of genetic-based size-dependent mortality (Chambers *et al.* 1996; Stackpole *et al.* 2010a; Costa e Silva *et al.* 2011a). Key pests and disease have been shown to impact growth and survival of both *E. nitens* and/or *E. globulus* (Battaglia *et al.* 2011), and when severe defoliation occurs their impacts will be embodied in later growth and survival measures both at a phenotypic (Rapley *et al.* 2009) and even genetic (Raymond 1995; Milgate *et al.* 2005; Jordan *et al.* 2002) level.

5.2.1 Abiotic threats

Large differences exist amongst the races of *E. globulus* and *E. nitens* traits associated with adaptation to the abiotic environment, and differences in susceptibility to factors such as frost and drought are evident. In *E. nitens* the more frost sensitive northern NSW races (Tibbits and Hodge 2003) grow better in summer rainfall zones, whereas the Victorian races perform better in winter rainfall zones (Hamilton *et al.* 2011). The races of *E. globulus* differ in drought resistance (Dutkowski 1995), which in part explains their differential performance in trials across southern Australia (Costa e Silva *et al.* 2006).

5.2.1 Pests and diseases

Variation in pest (insect and mammals) and disease risk occurs both temporarily and spatially across the plantation estates of *E. globulus* and *E. nitens* in Australia (e.g. Mohammed *et al.* 2003; Pinkard *et al.* 2010), as well as following silvicultural treatments such as pruning (Pinkard *et al.* 2004; Wiseman *et al.* 2006). Many of the Australian pests of these species have also become established overseas, including the brushtail possum in New Zealand (O'Reilly-Wapstra and Cowan 2010). Plantations within Australia are also at risk from introduced pests and diseases, no better exemplified by the recent introduction and spread of Myrtle Rust (*Uredo rangellii*) in Australia (<http://www.dpi.nsw.gov.au/biosecurity/plant/myrtle-rust>). This newly described pathogen of the family Myrtaceae has close links to the eucalypt guava rusts of South America which affects plants belonging to the family Myrtaceae, including eucalypts.

Provenance differences in susceptibility to pests (e.g. insects - Jordan *et al.* 2002, mammals - O'Reilly-Wapstra *et al.* 2002; Miller *et al.* 2011), diseases (e.g. Mycosphaerella leaf disease (MLD) caused by *Teratosphaeria* species - Milgate *et al.* 2005; Carnegie and Ades 2005) and susceptibility to wood decay have been reported in *E. globulus* (Poke *et al.* 2006; Hamilton *et al.* 2007). Decreased wood decay in one study (Poke *et al.* 2006) was associated with increased wood extractives at the provenance level (Stackpole *et al.* 2011). At an holistic community level, genetic-based differences between races of *E. globulus* have been shown to affect the composition of insect and fungal communities that develop on canopy foliage (Barbour *et al.* 2009c), under trunk bark (Barbour *et al.* 2009b) and even in decaying litter beneath trees (Barbour *et al.* 2009a).

Adverse genetic effects arising from such biotic factors can potentially contribute to genotype by site interactions and make some provenances unsuitable for planting in high risk areas. For example, the low defensive chemistry of the St. Helens provenance of *E. globulus* appears to account for its atypically high susceptibility to marsupial browsing (O'Reilly-Wapstra *et al.* 2002; O'Reilly-Wapstra *et al.* 2004; O'Reilly-Wapstra *et al.* 2005) and unsuitability for growth in southern Tasmania (Volker and Orme 1988). Several approaches are being used to reduce marsupial

browsing damage in plantations, including seedling protection with stockings or repellent (Miller *et al.* 2008). However, genetic based differences in susceptibility are more persistent and there are direct and indirect (defensive chemistry) screening approaches for genetic improvement (Miller *et al.* 2009; Miller *et al.* 2011).

5.3. Pulpwood traits

There are numerous studies demonstrating significant variation between the races of *E. globulus* and *E. nitens* in wood property traits affecting the pulpwood breeding objective. The key breeding objective traits related to wood properties are basic density and percentage pulp yield for both species. A review of published results from 11 trials (Hamilton *et al.* 2011) indicated that the significant differences in basic density between the *E. nitens* races were mainly due to the extreme low and high basic density of southern and northern NSW races, respectively. There was no consistent difference in basic density between the three Victorian races which are the focus of *E. nitens* breeding for the winter rainfall zones in Australia. In *E. globulus* there is significant subrace variation within the base population for basic density with the mainland subraces tending to have higher basic density than King Island and most Tasmanian subraces (Dutkowski and Potts 1999; Stackpole *et al.* 2010a; Stackpole *et al.* 2010b). This has led to a focus on the mainland subraces of *E. globulus* for breeding (Jones *et al.* 2006). There are few published studies of the genetic variation in pulp yield in either species (e.g. *E. nitens* - Williams *et al.* 1995; Tibbits and Hodge 1998; Hamilton *et al.* 2011; *E. globulus* - Williams *et al.* 1995; Stackpole *et al.* 2010b). However, a recent study of an *E. globulus* base-population trial has shown significant variation in pulp yield between subraces with the highest pulp yield observed in the King Island and southern Tasmanian subraces (Stackpole *et al.* 2010b). Such large-scale information has not been previously available and if shown to be consistent at other sites will mean that the economic value of germplasm from these subraces may have been underestimated. This finding demonstrates the importance of large-scale studies, the potential changes in the economic value of germplasm which can occur as more information is obtained, and the value in long-term maintenance of base population trials.

5.4. Solid-wood traits

There are few studies of the genetics of traits in *E. globulus* and *E. nitens* which are specific to a solid wood objective. Nevertheless, the few available suggest that the choice of provenance will not only affect solid wood product recovery but also quality. Recovery from trees or logs will be affected by stem straightness, forking, branchiness and taper. The three key Victorian races of *E. nitens* (Northern, Southern and Connors Plains) differ in stem straightness, log taper and predicted green board recovery, with the Southern race best on all traits (Blackburn *et al.* 2011a). A processing study also showed that the Connors Plain race produced boards of lower stiffness (Blackburn *et al.* 2010). While no significant race differences were detected for basic density, or board checking in Blackburn *et al.*

(2010), studies of cores suggest that the *E. nitens* races do differ in the propensity for shrinkage (total volumetric) and collapse (McKimm 1985; Hamilton *et al.* 2011). Tension wood is one of the main factors believed to cause drying defects in *E. globulus* boards (Washusen 2011), and a study of 10-year old trees reported a higher proportion of tension wood and collapse in the Jeeralangs, one of the races with high basic density that is most favoured for pulpwood plantations, compared with the low density King Island race (Washusen and Ilic 2001). Board properties are altered by sawing pattern and in a study of 15-year old trees, Hamilton *et al.* (2010c) showed significant differences among races in the internal checking observed in quartersawn but not backsawn boards. Nevertheless, these genetic studies have been undertaken on unpruned and unthinned trials and the repeatability of observed differences in collapse, shrinkage and checking remain to be determined on other sites and under different silviculture regimes.

6. EXPLOITING VARIATION WITHIN PROVENANCES

While large and rapid genetic gains can often be made from exploiting the natural genetic variation which exists amongst provenances of a species (e.g. subraces/races - the genetic groups used in statistical analyses), substantial genetic variation also resides within provenances which can also be exploited for genetic improvement (Eldridge *et al.* 1993). From a quantitative genetics perspective, this variation may include both additive and non-additive genetic components. Only the additive genetic component can be exploited for ongoing population improvement but the non-additive genetic component in any one generation can be captured for deployment, along with the additive component, by cloning or use of full sib-families (e.g. mass supplementary pollination) (Eldridge *et al.* 1993). For base populations, the additive component of genetic variation is usually assessed from the pooled within-provenance variation amongst open-pollinated families and is assumed to represent the additive genetic variation which exists within a random mating population in the wild. The narrow-sense heritability (h^2) of a trait derived from such a partition represents the proportion of the phenotypic variation within provenances which is under additive genetic control. When the narrow-sense heritability has been estimated based on open-pollinated progeny the symbol h^2_{op} is used to indicate that the calculations make assumptions regarding the average relationship amongst open-pollinated sibs (i.e. they are not all unrelated half-sibs).

The reported heritabilities for a given trait may vary depending upon numerous factors, but meta-analyses are revealing a generalised picture of h^2_{op} within base population trials of both *E. globulus* (Potts *et al.* 2004) and *E. nitens* (Hamilton and Potts 2008). While most traits and most trials tend to exhibit statistically significant h^2_{op} , on average the heritability of growth, survival, animal browsing and tree architecture traits tend to be lower than that of wood property, reproductive and developmental traits. For example, in *E. nitens* the average heritabilities for growth traits (e.g. average h^2_{op} = 0.26 for diameter) were generally lower than those for

wood property traits (e.g. average $h^2_{op} = 0.51$ for basic density) (Hamilton and Potts 2008). Breeders also need knowledge of the stability of this genetic variation across ages (age-age correlations) and across sites (genotype x environment interactions – GxE) as well as an understanding of the genetic association amongst traits (Eldridge *et al.* 1993; Callister *et al.* 2011). This knowledge is usually obtained from calculating the additive genetic correlations (r_a) for the same trait measured at different ages or on different sites as well as between different traits. Age-age correlations for growth and wood density are relatively high (Borralho *et al.* 1992; Stackpole *et al.* 2010a; Hamilton *et al.* 2010c) and four-year DBH is commonly used as an early selection trait (Borralho *et al.* 1992). Additive genetic correlations across sites estimated from open-pollinated families also tend to be relatively high in both *E. globulus* – (MacDonald *et al.* 1997; Costa e Silva *et al.* 2006; Callister *et al.* 2011) and *E. nitens* (reviewed in Hamilton and Potts 2008), arguing that selections undertaken on one site will be reasonably suited for another site. However, in *E. globulus* lower genetic correlations have been reported for growth at the subrace level suggesting significant genotype by environment interaction (see section 4.2).

Large-scale assessments are required to obtain robust genetic parameter estimates, particularly for genetic correlations. While this is feasible with many traits obtaining large sample sizes for traits which are technically difficult or expensive to assess is problematic and often leads to relatively imprecise estimates (see discussions in Stackpole *et al.* 2010b; Hamilton and Potts 2008). Nevertheless, this situation is rapidly changing with the advances in phenotyping, such as near-infrared (NIR) spectroscopy (Downes *et al.* 2010a; Downes *et al.* 2010b) and acoustic (Blackburn *et al.* 2010) technologies that can now be used non-destructively on standing trees to predict traits relevant to pulpwood and solid-wood value (e.g. Blackburn *et al.* 2010; Stackpole *et al.* 2010b). For example, NIR models have recently allowed large-scale non-destructive studies of genetic variation in pulp yield (Stackpole *et al.* 2010b) and wood chemical traits (lignin, cellulose, extractives, lignin and its syringil to guacin ratio [S/G] – Stackpole *et al.* 2011) in *E. globulus*. Technologies for assessing wood colour have also been tested with *E. nitens* (Raymond and Bradley 2002). In addition, despite increasing efficiencies in sampling wood cores for density and other measurements (Raymond *et al.* 1998; Stackpole *et al.* 2010a), Pilodyn penetration is still being used as a rapid, indirect measure of wood density (MacDonald *et al.* 1997; Raymond and MacDonald 1998; Callister and England 2010).

Sample size has certainly limited genetic studies of solid-wood objective traits. Nevertheless, efficiencies have been made in tracking tree and log identities through processing systems (Blackburn *et al.* 2011b), allowing board and veneer properties to be linked to tree pedigrees and potential selection traits. Already, a recent study of 496 trees has shown the stiffness and checking of *E. nitens* boards are under strong genetic control and amenable to genetic improvement (Blackburn *et al.* 2010). Wood stiffness and checking traits were more-or-less genetically independent, surface and internal checking were only moderately positively

correlated, but while basic density was positively correlated with stiffness it was adversely correlated with surface check length. NIR models for predicting specific solid wood traits from standing tree samples are yet to be developed. Nevertheless, in *E. nitens*, standing tree acoustic wave velocity is proving useful. It is strongly genetically correlated with board stiffness and moderately positively genetically correlated with basic density (Blackburn *et al.* 2010). While associations with non-destructive techniques are yet to be identified, a strongly positive genetic correlation between internal board checking and checking in wedges taken from disks removed from felled trees has been shown in *E. nitens* (Blackburn *et al.* 2010). However in *E. globulus*, board checking has yet to be shown to be significantly genetically correlated with potential selection traits assessed from standing trees (Hamilton *et al.* 2010c).

As is typical of eucalypt species, most reported estimates of genetic parameters in *E. globulus* and *E. nitens* are derived from base population trials. Base population trials tend to be more numerous, and have large numbers of individuals and founder parents than trials comprising control pollinated families. However, there are inaccuracies associated with parameter estimates from the open-pollinated families due to the unknown male parentage. Open-pollinated families may comprise variable levels of selfing, biparental inbreeding and unrelated outcrosses (Eldridge *et al.* 1993; Hardner *et al.* 1998). The performance of open-pollinated families may thus be affected not only by the additive genetic worth of the female, but also the outcrossing rates and patterns, and the females' inherent propensity for inbreeding depression (Costa e Silva *et al.* 2010a; Bush *et al.* 2011). In *E. globulus*, outcrossing rates tend to be higher in seed collected from the upper canopy compared with the lower canopy (Patterson *et al.* 2001; Hingston and Potts 2005). There is also marked tree-to-tree variation in outcrossing rates (Patterson *et al.* 2004), which tend to be lower in fragmented (low density) than continuous forest (Mimura *et al.* 2009). Self-incompatibility (McGowen *et al.* 2010) is likely to be a key determinant of tree-to-tree variation in outcrossing rates, and assessing self-compatibility through controlled pollination and collecting seed from self-sterile trees is one option to avoid inbreeding in deployment seed lots. While progress has been made in terms of accounting for average selfing rates in genetic evaluation of open-pollinated progenies of eucalypts (Dutkowski *et al.* 2001a), it is difficult to account for variable outcrossing rates without parentage analysis (Burgess *et al.* 1996; Gea *et al.* 2007; Bush *et al.* 2011). Even then the impacts of variable inbreeding depression at the individual level will be difficult to predict (Costa e Silva *et al.* 2010a; Costa e Silva *et al.* 2010b). In addition, there is some evidence to suggest that inbreeding depression may induce site stability in open-pollinated family performance that has resulted in an underestimation of the importance of environment x genotype interaction from an additive genetic perspective (Costa e Silva *et al.* 2011a). However, the effects of inbreeding depression appear to be more an issue for growth and survival traits (e.g. Costa e Silva *et al.* 2010a) and more reliable predictions of genetic parameters and breeding values are likely with other traits of economic interest (e.g. wood properties, disease susceptibility – Potts *et al.* 2004).

The non-additive (dominance, epistasis and maternal) components of genetic variation can only be captured through family or clonal deployment and estimation of these effects requires crossing designs with full-pedigree control. Understanding the relative importance and nature of non-additive genetic effects is now possible, particularly with *E. globulus* where control-pollinated (CP) trials are increasing in number and size. This information is required, for example, to help decide whether to shift from open-pollinated seed orchards to more expensive clonal and full-sib family deployment strategies. For growth traits, studies of control-pollinated trials in *E. globulus* have indicated that open-pollinated heritability estimates are inflated compared with control-pollinated estimates (Hodge *et al.* 1996; Volker 2002; Costa e Silva *et al.* 2010a), but to date this trend is not evident in *E. nitens* (Hamilton and Potts 2008). In *E. globulus*, breeding values for growth traits are poorly correlated between control- and open-pollinated populations (Hodge *et al.* 1996; Volker 2002; Costa e Silva *et al.* 2010a). Significant dominance variation has also been reported within many (Volker 2002; Li *et al.* 2007; Callister *et al.* 2011), but not all (Lopez *et al.* 2003; Costa e Silva *et al.* 2004), *E. globulus* populations studied. Non-additive effects for growth have also been reported for inter-provenance F₁ crosses of *E. globulus* which are positive, ranging from mid-parent (Volker *et al.* 2008) to better parent (Lopez *et al.* 2003) heterosis, and may partly reflect mild levels of inbreeding in local populations (Hardner *et al.* 1998). However the pattern of expression of inter-provenance F₁ heterosis needs to be better understood. It is also unclear whether these positive effects of inter-provenance crossing will persist in subsequent generations due to the possibility of outbreeding depression (see Shepherd this volume).

7. HYBRIDISATION

The major eucalypt subgenera do not hybridise but barriers to hybridization between species within subgenera are often weak (Griffin *et al.* 1988; Potts *et al.* 2003). Natural hybridization and introgression between recognized taxa is relatively common (Griffin *et al.* 1988; Potts and Wiltshire 1997; Butcher and Williams 2002; Field *et al.* 2011), and in some cases only detectable at the molecular level (McKinnon *et al.* 2001; McKinnon *et al.* 2004).

Artificial hybridisation has been widely used as a breeding strategy in eucalypts in subtropical and tropical regions of the world but to a lesser extent in temperate regions (Potts and Dungey 2004; see also Harwood this volume). While there has been extensive research on artificial hybridisation of *E. nitens* and *E. globulus* in Australia (Potts *et al.* 2000; Potts and Dungey 2004; Tibbits 2000; Meddings *et al.* 2003; Lopez *et al.* 2000), high costs of development and clonal propagation have meant that such germplasm has generally not been developed commercially in

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Australia. An exception is the ‘Saltgrow’ hybrids involving *E. globulus*, which have been developed for environmental plantings (Dale and Dieters 2007; Hardner *et al.* 2011).

While F₁ hybrid clones between *E. globulus* and *E. nitens* have been developed in Chile (Griffin 2001), attempts to develop such hybrids in Australia have not come to fruition, partly due to difficulties in clonal propagation (Tibbits 2000). However the genetics of this hybrid combination have been well-studied. In the early 1990’s large crossing programs were undertaken by both CSIRO and North Forest Products Ltd (now part of Gunns Ltd) to develop hybrids between these two species with the aim of developing germplasm with the pulpwood qualities of *E. globulus* which could be planted on higher altitude colder sites. The first generation hybrids were expensive to produce as the cross could only be obtained using the small-flowered *E. nitens* as the female parent. This unilateral barrier appeared to be physical and due to the pollen tubes of *E. nitens* being unable to grow the full length of the large *E. globulus* style (Gore *et al.* 1990). The set of F₁ hybrid seed was low, high levels of abnormalities were observed in the nursery, the F₁’s exhibited increased susceptibility to possum browsing and poor survival in the field, although the success of hybridisation varied between the two *E. globulus* provenances tested (Dungey and Potts 2001; Volker *et al.* 2008). This crossing program is noteworthy as it used a relatively large number of parents of each species, and compared the performance of the hybrids against selfs, open-pollinated and unrelated outcrosses of the parental species. However, as the hybrids and pure species were planted in separate plots within each replicate of the field trial, high mortality of the hybrids resulting in a lower competitive environment for survivors biased later-age cross-type comparisons. Second generation hybrids (backcrosses and outcrossed F₂’s) which were later produced and planted along with F₁ and pure species crosses at two sites, but using a single-tree plot design to avoid survival biasing cross-type means. At both sites the F₂’s exhibited poor mean survival compared to the pure species and the backcrosses were intermediate (Potts *et al.* 2003; Costa e Silva *et al.* 2011b) and at both sites the top families at age 14 were from the pure species (B. Potts unpubl. data). These hybrid populations exhibited severe outbreeding depression which increased with age, and appeared to be mainly due to adverse additive x additive epistasis (Costa e Silva *et al.* 2011b).

Another attempt to develop hybrid germplasm to extend the planting of *E. globulus* into colder areas involved crossing with the frost resistant species, *E. gunnii* (Potts *et al.* 2000). In this case trials were established along an elevation gradient. The F₁ hybrids in this case exhibited less abnormality and survival problems than the *E. nitens* x *globulus* hybrids but only outperformed *E. globulus* at the highest altitude site where the pure species was heavily damaged by frost. However at this highest altitude site, the performance of the F₁ hybrids were well below the routine *E. nitens* plantation seedlings included as a control.

8. MOLECULAR BREEDING

There have been major advances in eucalypt genomics and marker technologies in the last year which are leading to a rapid increase in our understanding of the eucalypt genome and opportunities to link genes to phenotypic variation of adaptive and economic significance (Poke *et al.* 2005; Grattapaglia and Kirst 2008; Myburg *et al.* 2008; Mamani *et al.* 2010). Following acceptance of a proposal from the international eucalypt genetics network EUCAGEN (<http://web.up.ac.za/eucagen/>), an assembled genome of *E. grandis* was generated and released into the public domain by the US Department of Energy's Joint Genome Facility in April 2011 and an *E. globulus* genome has been re-sequenced (see <http://web.up.ac.za/eucagen/>). There has simultaneously been increasing release of other genomic resources for eucalypts into the public domain (e.g. Rengel *et al.* 2009; Mizrahi *et al.* 2010; Faria *et al.* 2011; Neves *et al.* 2011; Paiva *et al.* 2011). This expansion has been coupled with the recent development of the Diversity Arrays Technology (DArT) for eucalypts (Sansaloni *et al.* 2010; Steane *et al.* 2011). DArT has allowed cost-effective generation of high-density linkage maps (Kullan *et al.* 2011) to provide a framework for comparative mapping (Hudson *et al.* 2011), generation of a multi-species consensus map (C. Hudson unpubl. data), and the expansion and integration of quantitative trait loci (QTL) studies (Thumma *et al.* 2010) across multiple species. The sequenced DArT markers allow QTL to be linked to the *E. grandis* genome sequence to help identify candidate genes for association genetic and other genomic studies. Association genetic studies aiming to identify the molecular change (e.g. single nucleotide polymorphisms – SNP) underlying the phenotypic variation in many wood property traits are well advanced in both *E. nitens* and *E. globulus* (Thumma *et al.* 2009; Southerton *et al.* 2010; Thavamanikumar *et al.* 2011), although the stability of marker trait associations across pedigrees and environments is becoming a key research issue (Southerton *et al.* 2010). We are at the threshold of major advances which will see an increasing number of validated markers/trait associations available for traits of interest to breeders, and potentially the development of genome-wide strategies for selection (Grattapaglia and Resende 2011). An important challenge ahead will be to integrate this molecular information into current breeding programs in a manner which is cost efficient and competitive with advances in phenotyping technologies ({Kerr, 2011 #11540}). The near absence of non-destructive tests and high costs of phenotyping breeding objective traits associated with solid-wood products (e.g. board checking-Sexton *et al.* 2010) combined with the longer rotation time of such plantations, would no doubt make solid-wood objective traits prime targets for molecular breeding.

9. SUMMARY

In summary, clearly defined breeding objectives are required to efficiently exploit the vast amount of genetic diversity which resides within eucalypts at multiple levels. While such objectives and associated traits are relatively well defined for

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pulpwood production, technological changes in solid-wood products and production systems argues for an initial focus on the more generic objectives and traits. Species and provenance choices offer key opportunities for gains in the early phase of domestication, impacting on not only product quantity and quality, but breeding and propagation options. Understanding the genetic architecture and economic weights of traits is important for breeding, but requires assessment under appropriate silvicultural regimes.

10. ACKNOWLEDGEMENTS

We thank Rod Griffin (Griffin Tree Improvement Pty. Ltd.), Tim Wardlaw and Dean Williams (Forestry Tasmania), Kelsey Joyce (Gunns Ltd) and Chris Harwood (CSIRO) for their contributions to Table 2 as well as René Vaillancourt and Tony McRAe for their comments on the text. We also acknowledge support from the CRC for Forestry and the Australian Research Council Linkage Grant LP0884001.

11. APPENDICES

12.1. Appendix 1: Major evolutionary lineages within the eucalypts (modified from Myburg *et al.* 2007). The alignment of Pryor and Johnson's (1971) genera and subgenera with Brooker's (2000) subgenera. Pryor and Johnson's classification was informal, but widely used for 30 years. The number of species in each of Brooker's subgenera is indicated and examples of well-known forestry species are given. Most species used in plantation forestry (see Harwood this volume), particularly outside Australia are from Brooker's sections *Maidenaria* (e.g. *E. dunnii*, *E. globulus*, *E. nitens*), *Exsertaria* (e.g. *E. camaldulensis*, *E. tereticornis*) and *Latoangulatae* (e.g. *E. grandis*, *E. pellita*, *E. saligna*, *E. urophylla*) in the subgenus *Symphyomyrtus*.

Pryor & Johnson's subgenera/genera	Brooker's subgenera	No. of species	Examples of well-known forestry species
<i>Angophora</i> (genus)	<i>Angophora</i> ¹	7	
<i>Blakella</i>	<i>Blakella</i> ¹	15	
<i>Corymbia</i>	<i>Corymbia</i> ¹	67	<i>C. torelliana</i> , <i>C. citridora</i> , <i>C. variegata</i> , <i>C. maculata</i>
<i>Eudesmia</i>	<i>Eudesmia</i>	19	
<i>Gaubaea</i>	<i>Acerosa</i>	1	
<i>Gaubaea</i>	<i>Cuboidea</i>	1	
<i>Idiogenes</i>	<i>Idiogenes</i>	1	<i>E. cloeziana</i>
<i>Monocalyptus</i>	<i>Primitiva</i>	1	
<i>Monocalyptus</i>	<i>Eucalyptus</i>	110	<i>E. regnans</i> , <i>E. delegatensis</i> , <i>E. obliqua</i> , <i>E. marginata</i> , <i>E. fastigata</i>
<i>Symphyomyrtus</i>	<i>Cruciformes</i>	1	<i>E. guilfoylei</i>
<i>Symphyomyrtus</i>	<i>Alveolata</i>	1	<i>E. microcorys</i>
<i>Symphyomyrtus</i>	<i>Symphyomyrtus</i>	474	<i>E. camaldulensis</i> , <i>E. dunnii</i> , <i>E. exserta</i> , <i>E. globulus</i> , <i>E. grandis</i> , <i>E. nitens</i> , <i>E. paniculata</i> , <i>E. pellita</i> , <i>E. robusta</i> , <i>E. saligna</i> , <i>E. tereticornis</i> , <i>E. urophylla</i> , <i>E. viminalis</i> , <i>E. deglupta</i>
<i>Telocalyptus</i>	<i>Minutifructus</i> ²	4	

¹The subgenera *Blakella* and *Corymbia* had previously been treated as a separate genus *Corymbia* Hill and Johnson and the subgenus *Angophora* treated as a genus (Hill and Johnson 1995) and this approach has been adopted in the text

²A recent molecular study suggests that these species belong within subgenus *Symphyomyrtus* (Whittock 2003)

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