



Stability of genetic effects across clonal and seedling populations of *Eucalyptus globulus* with common parentage

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ABSTRACT

Eucalyptus globulus is widely planted in temperate regions of the world for pulpwood production and there are breeding programs in many countries. While breeding and deployment programs in Australia mainly use seedlings, in countries such as Chile, Portugal and Spain, a combination of seedlings and clones are used for genetic testing and plantation establishment. In the present study, we compared clones and seedlings produced from the same twenty open-pollinated families of the Jeeralang provenance of *E. globulus*, and randomised within the same field trial established in NW Tasmania. We specifically aimed to test whether mean performance, variance components, genetic parameters and breeding values estimated from the two propagule types were comparable. We studied the susceptibility of the juvenile foliage to leaf disease caused by *Teratosphaeria nubilosa*, the height at which the transition to the adult foliage occurred, as well as growth at selection and harvest ages. While the clones exhibited less disease damage, switched to the adult foliage at a slightly lower height and had less height and diameter growth than the seedlings, no significant differences in estimates of additive genetic variances and narrow-sense heritabilities between the two propagule types were detected. The additive genetic correlations estimated between the clonal and seedling populations did not differ significantly from one. The propagule type also had little effect on estimates of genetic correlations between traits. Thus, our results argue that while differences in trait means need to be taken into account, the propagation method is unlikely to affect the genetic architecture and predictions of breeding value in this species.

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1. Introduction

Eucalyptus globulus is the most widely planted eucalypt in temperate regions of the world for pulpwood production, and there are breeding programs in many countries (Potts et al., 2004). Most *E. globulus* plantations are established using seedlings derived from selected native stand provenances, open-pollinated seed orchards or, more recently, mass artificial pollination systems (Potts et al., 2008). While there may be additional costs involved in cloning, using clones instead of seedlings for testing, selection and deployment may potentially increase genetic gain due to an improvement in accuracy of selection (Shaw and Hood, 1985; Shelbourne, 1992; Isik et al., 2003, 2004; Snedden and Verry, 2004) and/or utilization of the total genetic variance (Mullin et al., 1992; Snedden and Verry, 2004; Baltunis et al., 2009), while reducing the time needed to deploy selected material in plantations (Matheson and Lindgren, 1985; Shelbourne, 1992; Snedden and Verry, 2004;

Kumar, 2006). However, *E. globulus* is not as readily vegetatively propagated as many of the subtropical species used in the world's eucalypt plantations (Turnbull and Booth, 2002; Potts, 2004), which may be attributed to the limited success of rooting using either micropropagation (Ruaud et al., 1999) or hardwood cuttings (Wilson, 1998, 1999a,b; Gaspar et al., 2005). Nevertheless, developments in the technology to vegetatively propagate *E. globulus* (Assis, 2001; Lopez et al., 2010) has led to the establishment of both seedling and clonal plantations in several countries such as Chile (Griffin, 2001), Portugal (Araújo et al., 1997; Gaspar et al., 2005) and Spain (Lopez et al., 2010), as well as replicating genotypes for genetic testing and research on genetic parameter estimation (Costa e Silva et al., 2004, 2005, 2009) and QTL detection (Freeman et al., 2009).

Although clonally replicated progeny may provide genetic information with greater efficiency (e.g. increase in accuracy of selection) than seedling progeny (Burdon and Shelbourne, 1974), a good relationship between the two propagation methods in field performance will be required to match testing and deployment systems. In this sense, estimates of breeding values and/or family means between propagule types need to be comparable in systems

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where selection is based on seedlings and plantation establishment uses clones, and vice-versa. Such information may be validated in trials where clones and seedlings of similar genetic background are tested, enabling evaluation of the effect of propagule type on both mean and genotype specific performances (Foster et al., 1987; Kageyama and Kikuti, 1989; Borralho and Kanowski, 1995; Frampton et al., 2000; Gaspar et al., 2005; Kumar, 2006; Baltunis et al., 2007; Cumbie et al., 2011; Reis et al., 2011; Dungey et al., 2012). Non-additive genetic and/or propagation effects are expected to influence the genetic information obtainable from vegetative propagules (Burdon and Shelbourne, 1974; Burdon, 1989), and thus affect the genetic correlation between related clones and seedlings.

Propagation effects may comprise non-genetic sources of covariance common to ramets of the same clone (i.e. genotype), and those specific to ramets within a clone (Burdon and Shelbourne, 1974). However, they could also arise from genotype by propagation method interactions at higher levels (e.g. additive or family levels) through, for example, genetic-based differences amongst genotypes in their ability to be propagated clonally. The simulation study of Borralho and Kanowski (1995) compared the importance of among- and within-clone propagation effects and their covariance with additive genetic effects on the relationship between clonal and seedling performance. They showed that the relative performance of families was mainly affected by propagation effects among clones. These effects common to ramets of individual clones could reduce significantly the genetic correlation between clones and seedlings, particularly in the presence of a negative covariance with additive effects. This is certainly possible in *E. globulus* where genetic variation in rooting ability at the family and provenance levels occurs (Borralho and Wilson, 1994; Ruaud et al., 1999; Cañas et al., 2004). Sasse and Sands (1997) reported that the quality of the root system initiated during propagation has an impact on the development of *E. globulus* stem cuttings, and observed important differences between cuttings and seedlings in the structure of root systems. These differences were associated with reduced initial growth of cuttings compared with seedlings (Sasse and Sands, 1997). Nevertheless, for growth and wood quality traits measured in field trials of *E. globulus*, Gaspar et al. (2005) did not detect significant differences between cuttings and seedlings in mean performance, nor a significant interaction between family and propagule type. However, field studies in other eucalypt species suggested that propagation effects could be involved in reducing clonal mean performance and/or affecting the relationship between genetically related clones and seedlings (Kageyama and Kikuti, 1989; Reis et al., 2011). In view of these results, further studies will be needed to ascertain whether the propagule type differentially influences genotypic performance in *Eucalyptus*, a genus in which reports comparing clones and seedlings of similar genetic background are still scarce.

Mycosphaerella leaf disease is one of the major foliar diseases of *E. globulus* and is caused by a fungi of the genus *Teratosphaeria* (known previously as *Mycosphaerella*; Crous et al., 2007), which infects eucalypts growing in native forests as well as plantations around the world (Mohammed et al., 2003; Balmelli et al., 2012; Pérez et al., 2012). *E. globulus* undergoes a dramatic ontogenetic change in leaf phenotype, and is a well-known example of a heteroblastic plant. In this context, juvenile foliage is more susceptible to *Teratosphaeria nubilosa* than adult foliage (Milgate et al., 2005), as well as to other pests and pathogens (such as: *Ctenarytaina eucalypti*, Brennan et al., 2001; *Mnesampela privata* [Autumn gum moth], Rapley et al., 2004; and *Paropsisterna agricola*, Lawrence et al., 2003). Thus, early heteroblastic transition may represent a means of “escape” from the most severe impacts of these pests and pathogens. Furthermore, differences between juvenile and adult foliage may be of adaptive significance in the absence of

pests and diseases, given the diverse abiotic environments occupied by the species (Jordan et al., 2000). In *E. globulus* plantations, the ontogenetic transition to adult foliage normally occurs between 2 and 4 years of age, and the height of transition is under strong genetic control (Dutkowski and Potts, 1999; Jordan et al., 1999). Moderate to strong genetic control has also been reported for *Mycosphaerella* leaf disease (Milgate et al., 2005). However, there are no studies evaluating the effects of propagule type on disease susceptibility and development traits in *E. globulus*.

The present study examines the effect of propagule type on growth, disease susceptibility to *Mycosphaerella*, and height of ontogenetic transition to adult foliage, measured over a 12-year period in a *E. globulus* field trial. Specifically, we aimed to: (i) compare the mean performance, as well as additive genetic and residual variance estimates, between clones and seedlings for the target traits; (ii) estimate the genetic correlation between propagule types for a trait; and (iii) assess whether the propagule type impacts on the genetic correlation between traits, and between selection and harvest ages for growth.

2. Materials and methods

2.1. Genetic material and field trial

The genetic material used in the present study consists of a random sample of twenty families obtained from open-pollinated seed lots, which were collected at the Jeeralang locality as part of the 1987/88 CSIRO base population collection of *E. globulus* (Dutkowski and Potts, 1999). Individuals from these families were cloned and grown as seedlings, so that each family was represented by unique genotypes as both seedlings and cuttings. The vegetative propagules were derived from the study of Ruaud et al. (1999), and details of the cutting production are given there in.

The sampled families and propagation material within families were planted in a field trial located at Blandens, South Ridgley, Tasmania (latitude 41° 15', longitude 145° 48'). The trial site was ex-pasture with a clay loam kraznozom soil and located at an altitude of approximately 280 m. The site was mound ploughed and sprayed with herbicide prior to planting. Trees were located in the trial on a regular rectangular grid, with a spacing of 2.5 m within planting rows and 3.5 m across planting rows. The field trial was planted at the same time as the adjacent trial studied by Milgate et al. (2005), with both trials being infected at the same age by *Mycosphaerella* leaf disease caused by *T. nubilosa*.

The experimental layout of the trial was a randomized block design with 18 replicates. Each replicate comprised usually one seedling and one clone (of an independent sample of seedlings) from each family, with the single-tree plots being arranged in a completely random manner with respect to both family and propagule type. The number of ramets per clone ranged from 1 to 4, with ramets of the same clone being randomly allocated to different replicates. This layout will allow a direct comparison of the performance of the families as clones and seedlings. Nevertheless, for some families, the numbers of available seedlings and/or clones were insufficient to allow a complete distribution across all the replicates. In this sense, the missing positions within replicates were allocated to filler trees. The average numbers of seedlings and clones per family were 14 and 11, respectively.

2.2. Trait measurements

The traits assessed comprised the susceptibility of the juvenile foliage to *Mycosphaerella* leaf disease (MLD), the height at which the transition to the adult foliage occurred (HPC), total tree height (HT) and over-bark diameter at breast height (DBH). MLD was

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