



Variable patterns of inheritance of ecologically important plant secondary metabolites in an inter-specific eucalypt hybrid



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ABSTRACT

Plant secondary metabolites (PSMs) play an important role in plant defense, and their patterns of inheritance may help explain the varying susceptibility of plant hybrids to herbivore and pathogen pests. Here, we studied the inheritance of PSMs in artificial hybrids between two temperate plantation species, *Eucalyptus globulus* and *E. nitens*, growing in a common environment field trial. Six different cross-types were compared: both pure species, F_1 , F_2 and both backcross classes. We sampled 190 13-year-old trees and assayed adult foliage for nine different PSM components: condensed tannins, total phenolics, total oils, 1,8-cineole, α -pinene, aroma-dendrene, β -eudesmol, sideroxylonal A and macrocarpal G. We found significant variation between the six cross-types for all but one compound (β -eudesmol). While discriminant analysis shows the hybrids are generally intermediate in their chemical profile, the overall inheritance of the chemical differences between the two eucalypt species was non-linear due to the non-additive inheritance of many compounds. The inheritance of five of the nine PSMs studied exhibited significant deviations from additivity in the F_1 's. Specifically, all hybrid classes had greater levels of sideroxylonal A and condensed tannins than either pure species suggesting heterosis; a relatively uncommon pattern of inheritance in PSMs. This increased expression of PSMs in the hybrids may have implications for the development of pest management approaches in planted forests for commercial or restoration purposes.

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1. Introduction

Hybridisation is common in plants, and changes in the phenotypic expression of traits in hybrids compared to the pure parental species can have significant ecological and evolutionary implications (Orians, 2000; Sakai et al., 2001). For example, variable patterns in plant traits in native hybrid stands can influence the distribution and feeding behaviours of a range of herbivores (Fritz et al., 1994, 2006), affect organisation of foliar arthropod communities (Dungey et al., 2000; Hochwender and Fritz, 2004) and have extended ecosystem consequences such as influence leaf decomposition, nutrient cycling and aquatic communities (Schweitzer et al., 2005; Whitham et al., 2006). Hybridisation also offers opportunities in species of high commercial value, where hybrids may offer the 'best of both worlds' by combining desirable traits from both parents (De Assis, 2000), offer increased expression in a desired trait (Storsberg et al., 2004; Savarese et al., 2009) or even express novel traits not present in the parents (Strauss, 1994; Stelkens and Seehausen, 2009).

Plant secondary metabolites (PSMs) are a diverse group of compounds, many of which are key plant traits due to their anti-herbivore properties. Levels of PSMs vary greatly both within (Hemming and Lindroth, 1995; Mann et al., 2012) and between plant species (Hjältén et al., 1996; Moore et al., 2004; Wallis et al., 2010) and this variability can translate to variable resistance to herbivores and pathogens (Fritz et al., 1999). Many studies have examined the genetic control of PSMs and the subsequent patterns of herbivory by investigating the inheritance patterns of PSMs in hybrids (Kirk et al., 2005; Nahrung et al., 2009). Inheritance patterns are not always predictable, and there are a range of possible inheritance outcomes (Fritz et al., 1999; Orians, 2000). For example, in willows, the hybrids of *Salix caprea* and *S. repens* exhibit intermediate expression of condensed tannins and phenolic glucosides to the parental plants (Hallgren et al., 2003). Alternatively, in *Eucalyptus citriodora* × *E. torelliana* hybrids, levels of monoterpenes and total phenolics were shown to be higher than in either parental species (Varshney et al., 2012). A recent review concluded that the most commonly reported patterns of inheritance of PSMs across a range of plant groups were: no difference between the parents and hybrids (29% of studies examined), intermediate expression of the hybrids compared to the parents (26%) and dominance towards the parent with the lower PSM levels (25%) (Cheng et al., 2011).

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Patterns of inheritance in advanced generation hybrids (F_2 and backcrosses to pure species) can be similar to first generation hybrids. However, due to genetic recombination, advanced generation hybrids may be more variable than parental plants and F_1 hybrids in their expression of PSMs and may also create new trait combinations (Hochwender et al., 2000; Orians, 2000; Kirk et al., 2010; Cheng et al., 2011). For example, in *Dubauti* hybrids, six of 20 flavanoids identified were novel in later generation hybrids (Crins et al., 1988). In natural systems, advanced generation hybrids further our understanding of the genetic control and evolutionary processes acting on traits through processes such as trait introgression (Hochwender et al., 2000). In commercial systems, advanced generation hybrids are also of interest due to possible exploitation of novel traits (e.g. PSMs) that may confer an advantage (e.g. resistance to pests). Despite this, it has only been in the last decade that the inheritance of PSMs in advance generation hybrids in natural systems has been investigated (Orians, 2000; Hallgren et al., 2003; Cheng et al., 2011), and relatively few studies have looked at tree species of commercial interest (Dungey et al., 2000; Varshney et al., 2012). Investigation of possible trade-offs (e.g. negative correlations) between multiple PSMs that may confer resistance to different pests and between PSMs and other traits of commercial interest (e.g. wood density and growth) is also important in determining how useful hybrids are commercially.

Eucalyptus is a dominant tree genus in Australia with over 700 species (Brooker, 2000) some of which are widely planted for commercial forestry. *Eucalyptus globulus* is planted throughout temperate regions of the world due to its fast growth, high pulp yield and wood density (Volker et al., 2008). This species is quite susceptible to frost damage, and is often replaced by the more frost tolerant *E. nitens* in colder climates and/or higher altitudes in Australia (Tibbitts et al., 1991). There is interest in breeding and deploying hybrids to combine the superior growth of *E. globulus*, with the frost resistance of *E. nitens* (Espejo et al., 1995; Volker et al., 2008). To date, however, breeding trials have shown that survival, disease resistance and browsing resistance are all poorer in the *E. globulus* × *E. nitens* hybrids than parents (Dungey et al., 1997; Potts and Dungey, 2004; Costa e Silva et al., 2012).

Eucalypts are rich in PSMs and some of these have anti-herbivore properties against a range of mammalian and invertebrate herbivores (Lawler et al., 1999; Floyd and Foley, 2001; Marsh et al., 2003a; Andrew et al., 2007). Little research has examined the inheritance of PSMs in this ecologically and commercially important genus (O'Reilly-Wapstra et al., 2005; Andrew et al., 2007; Varshney et al., 2012), and we believe this is the first study to examine inheritance in advanced generation hybrids. Here, we use a synthetic advanced generation hybrid trial of *E. globulus* and *E. nitens* to examine the patterns of inheritance of a range of different PSMs in first and later generation hybrids.

2. Materials and methods

We used an advanced generation hybrid trial located at Tyenna in Southern Tasmania (42°43'S 146°39'E), planted in 1995 (Lawrence et al., 2003; Costa e Silva et al., 2012). The trial was a randomized, complete block design of seven replicates containing 126 families in single tree plots. Each replicate contained 132 plants (11 rows 3 m apart; where each row had 12 individuals, 2.5 m apart); the more common families were represented more than once within each replicate. Plants were from full-sib families derived from unrelated crossing amongst *E. globulus*, *E. nitens*, and their F_1 hybrids to produce six different cross-types: the two parental species, *E. globulus* and *E. nitens*; the F_1 hybrid; outcrossed F_2 's (F_1 × F_1); backcrosses to *E. nitens* (BCn = *E. nitens* × F_1 or F_1 × *E. nitens*); and backcrosses to *E. globulus* (BCg = *E. globulus* × F_1 or

F_1 × *E. globulus*). These six genetic classes provided a complete genetic continuum between the two parental species.

Most *E. globulus* grandparents were from the King Island and Taranna provenances (where provenance is a population of trees growing within 10 km of each other) that represent different races of *E. globulus*, but grandparents from four other races were also represented in the crossing (Dutkowski and Potts, 1999). The *E. nitens* grandparents were from the Torongo provenance (Hamilton and Potts, 2008). Due to the difference in flower size between *E. globulus* and *E. nitens*, the F_1 hybrids can only be produced using the small-flowered *E. nitens* as the female parent (Gore et al., 1990). The backcrosses to *E. globulus* were mainly derived from using F_1 's as the female parent and the backcrosses to *E. nitens* were mainly derived from using the *E. nitens* as the female.

Adult foliage was sampled from 190 trees in the trial in January 2008 (summer), when trees were 13 years old and approximately 15 m high (Table 1). Table 1 summarises the pedigree representation of the sampled trees across three generations. Trees were sampled from replicates throughout the trial in a blocked manner, where at least one representative of each type of cross was growing in close proximity to each other. The choice of trees in each area was made to maximise parental and family diversity represented in each cross-type and, apart from avoiding unhealthy trees, sampling was otherwise random. We aimed to collect 40 each of g×g, n×n, F_1 and F_2 , and 20 each of the backcrosses. Due to differential numbers in planting, differential mortality in the field and extra samples that were collected for g×g and F_2 , there are different numbers of trees representing each cross type. We conducted several analyses on data collected in earlier years from the full trial of 924 plants to ensure that the sub-set of 190 trees in this trial are representative of the full trial with regards to foliage chemistry and not biased due to factors such as previous browsing and mortality. Results (not shown) indicate there was no selective survival of trees that were un-browsed and therefore potentially higher in defensive chemistry. Branches were shot down on the northern side of each tree and individual branchlets were placed into zip-lock bags and put in cool storage in the field; they were then frozen (−20 °C) upon return to the laboratory.

2.1. Foliage chemistry

Chemical analysis was performed on all samples. Components assayed were: condensed tannins, total phenolics, total oils, 1,8-cineole, α -pinene, aroma-dendrene, β -eudesmol, sideroxylonal A and macrocarpal G (two formylated phloroglucinol compounds; FPCs). Many of these compounds affect rates of herbivory by many marsupial herbivores and structure foliar arthropod communities (O'Reilly-Wapstra et al., 2004; Barbour et al., 2009; Moore et al., 2010). Healthy, current season and fully expanded leaves were selected for chemical analysis. Six frozen leaves were randomly sub-sampled from each bag for oil analysis and another six leaves were randomly selected from each bag and freeze-dried for total phenolics, condensed tannins and formylated phloroglucinol analysis. Oils (total oils, 1,8-cineole, α -pinene, aroma-dendrene, β -eudesmol) were assayed using frozen foliage by gas chromatography-mass spectrometry (GCMS) following O'Reilly-Wapstra et al. (2011). Total phenolics and condensed tannins were assayed with a modified Prussian blue assay for total phenolics using gallic acid standards (Graham, 1992), and the acid butanol assay for condensed tannins using purified sorghum tannin standards (Porter et al., 1986). Foliage for these assays was prepared and extracted following the method outlined in Hagerman (2002). Sideroxylonal A and macrocarpal G were assayed by high performance liquid chromatography (HPLC) following Wallis and Foley (2005).

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