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Gene flow from *Corymbia* hybrids in northern New South Wales

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ABSTRACT

Some of the most productive taxa for forestry are interspecific F_1 hybrids grown as exotics in the tropics and subtropics. Attributes of resilience, adaptability and vigour which engender the hybrids for wood production, may also exacerbate the risk they present from gene flow to native species gene pools or to local ecologies as weeds. To determine the biological and genetic factors that influence the extent of hybridisation, we examine the distribution and genealogy of wildlings surrounding plantings of locally-exotic *Corymbia torelliana* (Section Cadageria) near native *C. henryi* (Section Maculatae) in northern New South Wales. Our study showed pre-mating and pre- and post-zygotic barriers were incomplete, with *in situ* generation and natural establishment of both F_1 hybrids ($n = 3$) and advanced generation hybrids under the disturbed conditions bordering native forest. As hybrids were located on alluvial flats exposed to frost, they also likely have an extended ecological range relative to native *C. henryi*. Despite the likely generation of large viable seed crops on F_1 trees at the site over many years, establishment success and survival of advanced generation hybrids may be low, as only 5 immature and no mature advanced generation hybrids were identified. Propagation and genetic analysis of a seed crop from one F_1 wildling showed early survival and vigour of seedlings in cultivation was high, and that at least for some F_1 in some seasons, backcrossing to the recurrent native *C. henryi* parent is favoured (60%), whereas selfing (10%) and crossing with other F_1 (30%) was less frequent. Transport of seed by stingless bees probably accounted for long distance dispersal from *C. torelliana*, but this mechanism does not appear to supplement gravity-dispersal of seed from the F_1. Coupled with other evidence from studies of bee behaviour, controlled pollination in *Corymbia* sp., and long-term fitness in second generation eucalypt hybrids, we anticipate gene flow via pollen rather than seed will be the greater challenge for managing the risk of introgression of *C. torelliana* ancestry into native species from the planted F_1 hybrid. If large sources of F_1 pollen become available to compete with native pollen, gene flow will probably be frequent and hybrids may establish in disturbed conditions and in habitats beyond the ecological range of their native parent. Further study is needed to determine the degree to which outbreeding depression and poor survival inhibits on-going gene flow.

1. Introduction

The translocation of tree species for wood and fibre production presents a challenge for forest managers because of the potential for alien species to become weeds or change the gene pools of cross-compatible native species through gene flow (Laikre et al., 2010; Larcombe et al., 2013; Potts et al., 2003). Although gene flow may be beneficial in some circumstances (e.g. reducing inbreeding depression in small populations), hybridisation may have negative effects where genetic distinctness is lost in rare populations due to pollen swamping, or where fitness in the recipient population is reduced due to outbreeding depression (Byrne et al., 2011; Rhymer and Simberloff, 1996). Forest standards and certification schemes increasingly require consideration of the consequences of gene flow in the planning and management of plantations, driving the need for the taxonomic, biological and geographic data to inform risk management frameworks (Australian Forestry Standard Limited, 2007; Byrne et al., 2011; Programme for the Endorsement of Forest Certification schemes, 2010).

Around the world, hybrids have become of local importance for plantation forestry in a number of countries (e.g. *Acacia* hybrids in Vietnam (Kha, 2001), *Pinus* hybrids in Australia (Nikles and Robinson, 1989), *Eucalyptus* hybrids in South America (de Assis, 2000), and *Populus* in North America (Stettler et al., 1996)). These hybrids are often preferred over pure species because they have

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increased performance due to hybrid vigour, greater plasticity enabling them to be planted over a wider range of environments, or because they combine desirable agronomic, growth and resilience characteristics in one background (Potts and Dungey, 2004). Many of the most successful hybrids are grown as exotics, however, and the same attributes of adaptability and resilience that contribute to their success in a production context, may also contribute to their success as weeds, or following transfer of alien genes to cross-fertile natives, endow an introgressive with a greater capacity to establish and reproduce (Allendorf et al., 2001; Richardson, 1998). Furthermore, during the development of a commercially-viable hybrid, intervention is often required to overcome pre and post-zygotic reproductive isolation factors (contributing to both low seed set and hybrid inviability) that would normally operate to prevent gene flow and the establishment of hybrids in nature (Barbour et al., 2008). Hence, the planting of large numbers of exotic hybrids may facilitate the transfer of novel adaptations between an exotic and native by circumventing barriers that might normally operate to isolate the parental species.

Corymbia (bloodwoods) hybrids are one of the few hybrid eucalypt taxa with promise for forestry to emerge in Australia in recent decades (Lee, 2007; Lee et al., 2009). A native of the rainforest margins in north Queensland, *Corymbia torelliana* (Section Cadagaria) naturally hybridises with *C. citriodora subsp. citriodora* (Section Maculatae) were they co-occur (Hill and Johnson, 1995; Parra-O et al., 2009). All combinations of hybrids between *C. torelliana* and spotted gums (Section Maculatae, *C. citriodora* subspecies *citriodora* (CCC); *C. citriodora* subspecies *variegata* (CCV), *C. henryi* (CH) and *C. maculata* (CM)) are possible, and have been developed and tested for use in production forestry in recent years (Dickinson et al., 2012, 2010; Lee, 2007; Lee et al., 2009). The hybrids are preferred because of their faster growth, broad adaptation, tolerance to a range of biotic and abiotic stresses, and amenability to vegetative propagation (Lee, 2007; Lee et al., 2009; Nahrung et al., 2010). With a plantation area of around 20,000 ha, *Corymbia* species and their hybrids are now the single most important group for hardwood plantations in the subtropical Australia (Barbour et al., 2008).

The potential of *C. torelliana* to become a weed has been established through experience with its use as an ornamental in southern Queensland and northern New South Wales over the past 40 (Slee et al., 2006). *C. torelliana* is a prolific seeder, and its ability to invade disturbed and undisturbed rainforest and wet sclerophyll forest is enhanced by an association with stingless bees (Wallace and Trueman, 1995). The bees forage for resin in the mature capsules of *C. torelliana* to use in nest construction and inadvertently carry seeds trapped in resin back to their nests where they are discarded (Wallace and Trueman, 1995). Seed has been found to be transported up to 1 km from the parent tree, far more than typical gravity-dispersal of seed in eucalypts (Wallace and Lee, 2010; Wallace and Trueman, 1995). Recent studies of bee behaviour predicts bee transport of seed from the *C. torelliana* F_1 hybrid should be less frequent than for *C. torelliana*; the F_1 are less attractive than pure *C. torelliana* (the bees rely on complex olfactory signals to recognise *C. torelliana*) and seeds are less accessible due to capsule structure (Leonhardt et al., 2014; Simmons et al., 2012). However, this prediction remains untested, and the applicability of these findings to large scale field plantings and advanced generation backcross hybrids remains unknown (Simmons et al., 2012).

The purpose of the present study was to gather information on the biological and genetic factors which influence gene flow between the *C. torelliana* hybrid and cross compatible native species in the zone where the hybrid is planted in northern NSW. We were interested in the degree to which pre-mating barriers (e.g. flowering asynchrony and lack of suitable pollen vectors) may prevent or bias gene flow between the F_1 and natives. Secondly, if gene flow occurs, do subsequent generations of hybrids establish and survive to maturity in the field? Second generation eucalypt hybrids may have lower fitness than their pure species grandparents, thus outbreeding depression may limit their long term viability and their potential to contribute to ongoing gene flow (Barbour et al., 2008). A third objective was to test whether bee transport will be important for seed dispersal from the F_1. Little monitoring of seed or pollen escape from experimental plantings of F_1 hybrids has been conducted as yet, as hybrids have only reached reproductive maturity in recent years. In order to study gene flow from mature F_1 hybrids, therefore, the present study was conducted at a locality representative of the environment where *Corymbia* plantations have been established in northern NSW, but where spontaneous hybridisation had been occurring for decades between ornamental plantings of *C. torelliana* and native *C. henryi*.

2. Material and methods

2.1. Site description and land use history

The study was conducted at the Bonalbo Common, a reserve adjoining the township of Bonalbo, west of Casino in northern NSW. Early surveys at the Common detected mature, putative F_1 hybrid individuals between *C. torelliana* and spotted gum as well as a larger cohort (>100) of immature *C. torelliana* wildings (i.e. their location suggested they were not planted), indicating the potential for spontaneous advanced generation hybridisation at the site (Fig. 1). Like many towns in Northern NSW and southeast QLD, *C. torelliana* had been planted widely around Bonalbo as a windbreak and amenity tree during the 1970s and 1980s. The Common was logged during the late 1800s and has been used for grazing and recreation since this time. Prior to the late 1990s, the Common had been burnt and/or slashed to promote pasture and manage weeds, since then, however, natural regeneration of forest cover had been encouraged, and weeds were removed by spot application of herbicide (Pers. Comm. T. Moody).

The Common encompasses a central forested hill (up to 300 m above sea level (ASL) dominated by spotted gum (*C. henryi*), with ironbark (*Eucalyptus siderophloia*), pink bloodwood (*C. intermedia*) and gum-topped box (*Eucalyptus moluccana*) associates. Census plots for mature *C. henryi* indicated there were around 1400 trees in the approximate16 ha of forested hill. Below the 190 m ASL contour, the surrounding alluvial flats have been largely cleared for grazing or urban development, with some remnant blue gum (*Eucalyptus tereticornis*), *E. amplifolia* (cabbage gum) and *E. moluccana* retained. Because of the relative isolation of the native stand of *C. henryi* at higher elevations, it has represented a most-likely point source for spotted gum pollen during the time *C. torelliana* has been established in plantings around the township.

2.2. Surveys and sampling of C. torelliana wildlings and parental taxa

An inventory was made of all identified *C. torelliana* wildlings ($n = 121$) in the Common or it surrounds during October–December 2009. Each accessible wilding was characterised for growth (height, basal stem diameter were estimated by comparison with a height stick) and leaf and crown morphology (i.e. crown shape (strong or weak apical dominance), leaf shape (cordate, ovate or lanceolate) and leaf hairiness (setose or glabrous) and was recorded along with their global positioning system (GPS) coordinates and a photograph. A sample of foliage was obtained from a subset of 77 of these individuals (including the 4 mature trees) for a botanical specimen and to allow DNA analysis, and is termed the *C. torelliana* test population (Test-CTW) (Supplementary