



Survival and recovery of *Eucalyptus globulus* seedlings from severe defoliation



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ABSTRACT

Catastrophic damage that occurs at the early establishment stage of eucalypts, such as decapitation by browsing mammals, may have deleterious effects on survival, growth and tree shape. Such damage may result in a significant loss of productivity from planted forests, as well as represent a major selective force shaping patterns of adaptation in natural forests. An important recovery strategy of many eucalypts is to re-sprout from basal lignotubers, which contain a proliferation of dormant buds as well as stored carbohydrates. We investigated the genetic variation in seedling recovery following decapitation of two *Eucalyptus globulus* populations that differ in the extent to which they appear to allocate resources to foliar defence as opposed to recovery traits.

The two contrasting populations studied were from the continuous eastern distribution of *E. globulus* on the island of Tasmania. One population, from the wet southern forests, has relatively small lignotubers but high foliar defences; whereas the other from the dry northern forests, has relatively large lignotubers but low foliar defences. Seedlings of 10 families from each population were subjected to artificial decapitation treatments in the nursery at 6 months old, planted in a replicated field design and assessed up to 32 months after treatment.

The two populations differed significantly in their initial response to decapitation, with seedlings from the population with the larger lignotubers and stem base having greater survival and more shoots. Decapitation above the cotyledonary node had a more deleterious effect on survival than decapitation above the first seedling node. The surviving plants exhibited genetic stability not only in constitutive differences, but in the way they changed in response to decapitation. After 20 months of growth in the field, there were no lasting treatment effects on important growth traits, with genetic-based population differences overriding the initial treatment effects. These results are consistent with differential resource allocation being part of the adaptive response of *E. globulus*, and show that early-age decapitation has little long-term impact on the expression of inherent population differences in growth strategies and foliar chemistry.

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1. Introduction

Resprouting is a key strategy for many plants faced with unavoidable disturbance or damage, such as fire, wind or herbivory (Karban and Baldwin, 1997; Bond and Midgley, 2001). Like many plant traits, resprouting can exhibit inter- and intraspecific genetic variation and identifying such variation will not only help our understanding of the evolutionary processes that shape recovery strategies in plants (Bond and Midgley, 2003; Moreira et al., 2012; He, 2014; Shibata et al., 2014; Aparicio et al., 2015), but also inform how the long-term consequences of resprouting may affect

plant population dynamics (Bond and Midgley, 2001) and associated community assemblages (Hrbar and Du Toit, 2014).

Eucalypts are renowned for their capacity to recover from catastrophic damage by producing coppice (Noble, 2001; Noble and Diggle, 2014). High intensity biomass loss initiates re-sprouting from an organ at the base of the trunk called a lignotuber that is comprised of dormant buds (Vesk and Westoby, 2004; Burrows, 2013) and are a store of non-structural carbohydrates (Walters et al., 2005a, 2005b). These structures are related to the axillary buds in the cotyledonary axils and the axils of first few true leaves, and serve as a large source of stored buds linked to roots that supply stores of non-structural carbohydrates (Burrows, 2013; Clarke et al., 2013). Such recovery mechanisms are important particularly during early establishment as damage during this vulnerable stage

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may have significant fitness costs to the plant, such as reduced survival and seedling growth rate, and altered tree shape (Bulinski, 1999; Close et al., 2010; O'Reilly-Wapstra et al., 2012; Borzak et al., 2015a). The extent of eucalypt recovery may depend on timing, frequency, severity and pattern of defoliation (Noble, 2001; Pinkard, 2003; Wills et al., 2004; Pinkard et al., 2006; Noble and Diggle, 2014).

Eucalypts are noted for their high level of intraspecific genetic variation in morphological, reproductive and chemical traits (Potts and Wiltshire, 1997; Hamilton et al., 2011; Jones et al., 2011; O'Reilly-Wapstra et al., 2014; Padovan et al., 2014; Borzak et al., 2015b). Sprouting from enlarged lignotubers is no exception, exhibiting genetic-based variation in several species (Walters et al., 2005a, 2005b; Gauli et al., 2015). One species of eucalypt, *Eucalyptus globulus* has been the focus of much quantitative genetic research to address fundamental ecological and evolutionary questions in eucalypt systems (Jordan et al., 2000; Whittcock et al., 2003; Rapley et al., 2004; Stackpole et al., 2011; Wallis et al., 2011; Costa e Silva et al., 2013; Hamilton et al., 2013). While genetic-based recovery from lignotubers has been investigated in felled adult stumps of *E. globulus* (Whittcock et al., 2003), and recovery from epicormic buds following partial defoliation has been studied (Barry and Pinkard, 2013), the genetic basis of plant recovery after catastrophic browsing has not been examined at the vulnerable seedling stage. This is an important life history stage in this species, and in competitive field trial environments, early growth is significantly correlated with the probability of later age survival (i.e. size dependent mortality; Chambers et al., 1996) and growth (e.g. Stackpole et al., 2010). This information will provide a better ecological and evolutionary understanding of eucalypt recovery mechanisms, and how seedling-herbivore interactions can impact community composition and structure (Barton and Hanley, 2013). *Eucalyptus globulus* is a globally important plantation species (Dutkowski and Potts, 1999) and understanding the impact of severe mammalian browsing damage on plant survival and growth consequence also has applied relevance by enabling prediction of tree productivity after a browsing event, and the implementation of strategies to manage herbivory, such as the use of genotypes with improved recovery.

Diversification of morphological traits among populations of *E. globulus* presents an opportunity to explore recovery strategies based on resource allocation theory. Many plants employ a range of both resistance and recovery mechanisms (Mauricio et al., 1997) to cope with multiple herbivore damage across all life stages (Nunez-Farfan et al., 2007; Fornoni, 2011). Despite the lack of support for trade-offs between resistance and recovery mechanisms (Muola et al., 2010; Tucker and Avila-Sakar, 2010; Oduor et al., 2011), we may expect a stronger association between these factors at the vulnerable and resource limited seedling stage (Boege and Marquis, 2005; Hanley et al., 2007). In the case of *E. globulus*, there are specific population differences that may signal a resource allocation trade-off between growth, storage and defensive chemistry, whereby populations representing the low and high extremes of genetic resistance to marsupial browsing in Tasmania (St Helens and Blue Gum Hill; O'Reilly-Wapstra et al., 2004) have respectively large and small lignotubers (Whittcock et al., 2003). Theory predicts the existence of trade-offs between defence and growth that could maintain the genetic variation for resistance and recovery observed in plant populations (e.g. Fritz and Simms, 1992; Strauss and Agrawal, 1999; Agrawal, 2011). An important question in the interaction between *E. globulus* and its herbivores is, does this difference in resource allocation impact on tree recovery from browsing damage?

Here we investigated intraspecific variation in seedling resprouting from lignotubers after severe artificial browsing in two *E. globulus* populations, St Helens and Blue Gum Hill. We also

report on foliar physicochemical properties after 12 months growing in the field, subsequent lignotuber and stem base diameter up to 20 months, and plant growth and shape up to 32 months. Specifically, we asked the following questions:

- (1) Are genetic-based differences between *E. globulus* populations in seedling lignotuber development reflected in their re-sprouting response following catastrophic browsing damage?
- (2) Does basal re-sprouting have long-term effects on plant growth, shape and foliar physicochemical profile and do these effects differ between *E. globulus* populations?

2. Methods

2.1. Experimental design and assessments

Eucalyptus globulus has been classified into 13 genetically differentiated broad geographical groupings (Fig. 1; Dutkowski and Potts, 1999). Populations within these groups are trees growing within 10 km of each other (Potts and Jordan, 1994), and family is progeny derived from open-pollinated seed collected from a native tree within a population. Ten families from two native Tasmanian *E. globulus* populations (i.e. total of 20 families) were selected to represent two geographically and genetically different populations in Tasmania (Fig. 1). These populations also represent the extremes of browsing resistance. The population from St Helens has relatively low foliar defensive chemistry, and originates from a distinct geographic area in north-eastern Tasmania (latitude 41°15'S, longitude 148°19'E) characterised by low rainfall and dry forests. The population, Blue Gum Hill, is in the wet southern forests of Tasmania (latitude 43°03'S, longitude 146°52'E) and has relatively high foliar defensive chemistry (O'Reilly-Wapstra et al., 2004, 2005). Seedlings used were from a previous experiment where they were harvested at the stem base at six months of age for a feeding trial (these seedlings became the decapitation treatment for the current study and unharvested seedlings were used as controls). Initially, families were randomly arranged in individual trays and seedlings were grown in 50 6×7 cell plastic seedling trays filled with slow release fertiliser potting mix (Premium + CRF, low P; Table 1). They were grown for five months in a glasshouse where each tray was manually randomly allocated a position and moved monthly to reduce potential environmental effects. The trays were then transferred to an outdoor nursery for four weeks to allow seedling leaves to harden. At six months of age, the seedlings of each family were subjected to three different treatments:

- Control (C): Uncut seedlings.
- Treatment 1 (T1): Stem cut above node 1 (leaving two nodes remaining).
- Treatment 2 (T2): Stem cut above the cotyledonary node 0 (leaving one node remaining; most severe damage).

Treatments were manually randomly allocated across trays in an unbalanced design, since the seedlings were used from a previous experiment. Complete trays of seedlings were cut to either node 0 or node 1, and entire trays of uncut seedlings served as controls. There were between 76 and 360 seedlings spread across 10 families per population in each treatment (St Helens controls n = 313, T1 n = 115, T2 (cotyledonary node) n = 360; Blue Gum Hill: controls n = 145; cut above node 1 n = 76, cut above node 0 n = 274). Following the decapitation treatments, the seedlings resprouted from lignotubers (T1 and T2; Fig. 2). Seedlings remained in the outdoor nursery with automated irrigation. Short-term recovery was assessed five months later using the following measures: mortality, relative lignotuber size at the

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