Growth and photosynthetic responses following defoliation and bud removal in eucalypts

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ABSTRACT

CABALA, a productivity model for temperate plantation eucalypts, accounts for the impact of eucalypt defoliation on growth but does not yet account for differences in damage type. Consideration of both leaf and bud damage may result in a more realistic representation of growth outcomes for sites with different pest ecologies. We tested whether bud, as compared to leaf damage, elicited similar responses in two commercially important eucalypt species. Growth, biomass and physiological responses of young pot-grown plants to artificial removal of approximately 40% of leaf area (L treatment) or both leaves and buds (LB treatment) was assessed over a 4 month period of recovery. We identified that responses to defoliation were similar between the two species (*Eucalyptus globulus* and *Eucalyptus nitens*). Time series analysis highlighted that growth (height and stem diameter) was significantly reduced by defoliation during the study, which was more pronounced following LB treatment than L alone. At the end of the study, leaf area, stem height and diameter increment were not significantly affected by treatment, but total above-ground, stem biomass and foliar N were. This suggests that changes in patterns of biomass allocation occurred to maintain leaf area and capacity for light interception. Increased photosynthetic rate, which occurred for plants of both defoliation treatments but to a greater extent for the LB than L treatment, also contributed to recovery following defoliation. There was no evidence that photosynthetic rate increase was driven by changes in foliar nitrogen or chlorophyll, as there was not a statistically significant and strong relationship between the two factors. These results give us confidence that the process-based models used to predict the impacts of defoliation on productivity (1) can assume similar responses to defoliation for *E. globulus* and *E. nitens* and (2) should account for differences in physiological responses to foliage and bud damage.

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1. Introduction

Forest plantations are a managed ecosystem where plant primary productivity is optimized through understanding and potentially controlling those multiple abiotic and biotic stresses which limit growth and quality. Trees are subject to many types of biotic damage in typical growing environments, including insect, mammal and pathogen pests. Pest ecology varies due to many factors and the complement of pests may differ from region to region and even site to site, presenting site-risk considerations which can be based on empirical knowledge (Walsh and Wardlaw, 2011) or spatio-temporal models (van Staden et al., 2004; Pinkard et al., 2010a,b). The impact of damage on growth depends on the type of damage, e.g. defoliation, sap-sucking (Baldwin, 1990; Quentin et al., 2009; Zvereva et al., 2010), the type of tissue

damaged (Lavinge et al., 2001; Li et al., 2002; Schwenk and Strong, 2011) and many other variables including abiotic conditions (Anttonen et al., 2002; Pinkard et al., 2007; Wise and Abrahamson, 2007; Eyles et al., 2009), season of damage (Pinkard et al., 2006; Palacio et al., 2008) and ontogeny (Boege, 2005). While many studies have focused on leaf loss, bud loss may occur selectively, e.g. moose damage on maples (Schwenk and Strong, 2011), or combined with leaf loss, as is common in eucalypts, e.g. leaf beetles (Loch and Floyd, 2001).

A mechanistic understanding of response to defoliation is required to model its impact on productivity. Differences in growth response following damage of either leaves or buds has been related to source:sink relationships in conifers (Honkanen et al., 1994; Li et al., 2002). In evergreen trees, buds are a carbon sink while expanded leaves are a source. Many studies have shown that increased photosynthetic rate often follows foliage loss in trees (Pinkard et al., 2007; Eyles et al., 2011), but fewer studies have examined physiological compensation associated with bud loss, and those have only been for conifers. In spruce, photosynthetic

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increases occurred following debudding and foliar N was not altered compared to control plants (Ozaki et al., 2004). In Scots pine, removal of apical buds led to positive growth effects compared to removal of needles, which was probably related to new growth following release of suppression of lateral buds (Honkanen et al., 1994). Therefore, this is the first study that examines the physiological mechanisms of response to bud and foliage loss (not including pruning) in a broad-leaved tree species.

Globally, *Eucalyptus globulus* is a major and widespread hardwood plantation species of some temperate regions (e.g. southern USA, southern Europe, India, Brazil), and is also a favoured species (representing 62%) of Australian hardwood plantations (Bureau of Rural Sciences, 2010). *Eucalyptus nitens*, a closely related species, is preferred for colder areas, representing 19% of the Australian hardwood plantation estate (Bureau of Rural Sciences, 2010) and is also planted in other parts the world (e.g. Europe, South Africa, Chile and New Zealand). The main causes of defoliation in these eucalypt plantations include insect pests and fungal pathogens, and while the range of damaging agents may differ in various countries, themes emerge regarding damage patterns. Some insect pests typically only cause loss of mature foliage, e.g. autumn gum moth (*Mnesampela privata*) larvae and caterpillars of gum-leaf skeletoniser (*Uraba lugens*), which are pests of both eucalypt species in Australia (Farrow, 1996). However, in some cases when pest pressure is high, those insects that ordinarily only cause leaf loss will also cause bud damage, e.g. *M. privata* in *E. nitens* (Battaglia et al., 2011). Some pests cause damage to both leaves and buds at all times and the most notorious example is eucalyptus weevil (*Gonipterus* spp.) which can be a pest of both *E. globulus* and *E. nitens*. This is a widespread pest, including reports from Australia (Loch and Matsuki, 2010), Spain (Fernandez et al., 2011), South Africa (Newete et al., 2011) and Chile (Lanfranco and Dungey, 2001). The most damaging fungal pathogen of tropical eucalypts outside of Australia is *Phaeophleospora* (previously *Kirramyces*) *destructans*, which causes foliar and bud blight (Andjic et al., 2007). However for *E. globulus* and *E. nitens* the most damaging pathogens are the mycosphaerella leaf blotch pathogens (*Teratosphaeria nubilosa* and *Teratosphaeria cryptica*) which particularly infect young expanded leaves but do not infect buds (Carnegie et al., 2011). At high altitude sites, there is evidence that defoliation of *E. nitens* caused by mycosphaerella leaf disease can lead to development of buds which do not "harden" and then succumb to frost damage (T. Wardlaw, pers. comm.), possibly due to insufficient carbohydrate supplied to the developing buds. Therefore, interactions between biotic and abiotic factors can lead to additional damage to buds.

The response of *E. globulus* to simulated or insect-derived defoliation in young (Abbott and Willis, 1996; Pinkard et al., 2006, 2007; Eyles et al., 2009; Barry et al., 2012) and older trees (Loch and Matsuki, 2010; Quentin et al., 2011) has been well studied and generally loss of up to 50% leaf area can be tolerated with no eventual reduction in growth. In the short-term, growth may be adversely affected if defoliation is continuous (Loch and Matsuki, 2010), occurs in autumn (Abbott and Willis, 1996; Eyles et al., 2009) or when N is low (Pinkard et al., 2007). While most studies of growth recovery in eucalypts have focussed on leaf defoliation, information on how response is altered when combined with bud damage is lacking. Two previous field studies have highlighted the significant impact of bud loss on growth when combined with leaf loss, in 3 year old *E. nitens* (Elek, 1997) and 6 year old *Eucalyptus regnans* (Candy et al., 1992a).

Increased understanding of the physiological mechanisms that enable recovery from defoliation of *E. globulus* has led to the integration of defoliation as an "event" (Pinkard et al., 2010a,b; Battaglia et al., 2011) into the stand productivity model CABALA (Battaglia et al., 2004). This model allows users to input defoliation

as a percentage of leaf area in each of three vertical crown zones, as defoliation in upper crown zones leads to greater impact on growth (Pinkard et al., 2006). The model assumes similar responses to defoliation between *E. globulus* and *E. nitens* (Battaglia et al., 2011), however this has not been tested. The model performed poorly when severe defoliation of *E. nitens* was caused by *M. privata* and it was proposed that this was due to significant damage to buds, which was not accounted for in the model (Battaglia et al., 2011). Therefore, more information on response to bud damage is required for *E. globulus* and *E. nitens*.

In the present study we investigated two variables of response to defoliation; (1) differences between closely related plant species, 92) different types of defoliation. We focussed on leaf loss alone or leaf and bud loss combined as these are the most common damage patterns in young eucalypts (i.e. bud loss alone is less common). The aims of this study were to:

- Determine if there was a significant difference in growth responses (height, stem diameter, leaf area) between *E. globulus* and *E. nitens* following artificial defoliation.
- Determine if there was a significant difference in mechanisms of growth recovery (increased photosynthetic rate, crown recovery) between *E. globulus* and *E. nitens* following artificial defoliation.
- Compare growth responses and mechanisms for recovery between leaf removal alone (L) and the combination of leaf and bud defoliation (LB), for *E. globulus* and *E. nitens*.

Based on previous research in eucalypts and other evergreen genera, we hypothesised that:

(1) There will be no difference due to species in any aspect of the growth response or physiological mechanisms for recovery.
(2) Growth will be reduced more when plants are subject to LB, compared to plants that experience L.
(3) Physiological responses (specifically the rate of photosynthesis) will be stronger for plants experiencing LB than those with L.
(4) There will be different patterns of biomass allocation between plants that are subject to LB, compared to plants that experience the L treatment (including an increase in branching associated with debudding).

2. Materials and methods

2.1. Plant material

Open-pollinated seedlings (as used in commercial Tasmanian plantations) of *E. globulus* and *E. nitens* were obtained (Woodlea Nursery, Tasmania) and potted in to 200 mm diameter pots in March 2008. They were repotted to larger pots (300 mm diameter × 270 mm depth) in November 2008. The experiment began in December 2008 (early summer) when plants were approximately 12 months old. Plants were maintained in an open growing area. Automatic watering was delivered by drippers and slow release fertilizer (Osmocote Native Gardens, N:P:K of 17.9:0.8:7.3, Scotts Australia) provided continuous nutrition.

2.2. Experimental design and defoliation treatments

A total of 24 plants of each species were used in the study (48 in total). This sample size was designed to adequately capture variation in growth and physiological responses based on previous field studies, where lower replicate numbers were used (Barry et al., 2012). Six randomly selected plants of each species were used for