The Physiology of Host Responses to Pest Attack in *E. globulus* Plantations

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Abstract: Partial defoliation and infection by foliar pathogens results in reductions in stem growth and an increase in undesirable stem and wood traits in *Eucalyptus globulus* plantations. In this paper, we examine growth responses to pattern, severity and frequency of defoliation or infection, the physiological processes governing those growth responses (including differential responses related to mode of pest attack), and management tools to prevent or offset the effects of pest attack on plantation productivity (specifically the role of fertiliser application).   It is concluded that insects and pathogens elicit different physiological responses in the host plant associated with changes in light interception and light use efficiency, and that the effects of pest attack can be moderated in the host by strategic applications of nitrogen fertiliser.

INTRODUCTION

Tree responses to pest attack are complex. The impact on growth is related to severity (Pinkard 2003), pattern (Collett and Neumann 2002) and frequency (Wills et al. 2004) of attack, and is influenced by the mode of action of the causal agent (pathogen or herbivore) (Ayres 1992). Ultimately it is the host's defensive and physiological responses that will govern the degree to which host growth is affected.

Pest attack can affect the host's crown light environment and light interception directly by way of reduced leaf area, and indirectly by way of changes in patterns of biomass allocation (Rossing et al. 1992).   Light use efficiency can be affected through changes in photosynthyetic processes and in patterns of resource (particularly nitrogen) allocation throughout the crown.   Damage to new buds has implications for patterns of apical dominance and capacity for new growth in the host. As well, some pest species are known to secrete metabolites into the host that are translocated away from the site of attack, thereby increasing the impact of the pest on host function (Ayres 1992).

The complexity of the system makes it difficult to predict the longer-term outcomes of foliar attack on host growth.   Dynamic models with a physiological basis have been used successfully to predict the long-term effects of silvicultural treatments and changing environmental conditions (Battaglia et al. 2004). Because these models link production to the amount and functioning of foliage, and link allocation of assimilated carbon to sink demands, they have the potential to predict the effects of defoliation on longer-term growth.

The eucalypt plantation estate in Australia comprises close to 720 000 ha, of which around 65% is *Eucalyptus globulus* Labill. (Parsons and Gavran 2005).   Insect defoliation and infection by foliar pathogens occurs to some degree in most plantations. The most serious foliar pathogens of *E. globulus* plantations in Australia are *Mycosphaerella* species, and in particular *M. nubilosa* and *M. cryptica* (Carnegie et al. 1997). Mycosphaerella Leaf Disease (MLD) is characterised by necrotic lesions, foliar discoloration and, in severe cases, tissue

blighting (Park 1988) followed by premature leaf senescence. The major insect pests of *E. globulus* plantations in Australia are eucalypt leaf beetles (*Chrysoptharta* spp. and *Paropsis* spp.), scarab beetles (*Heteronyx* spp.), eucalypt snout weevels (*Gonipterus scutellatus*), gumleaf skeletoniser (*Uraba lugens*) and autumn gum moth (*Mnesampela privata*) (Elliott and de Little 1984, Loch and Floyd 2001). These all attack the leaves and buds, and some, for example *Uraba lugens*, may cause tip dieback. Sapsucking psyllids are a problem in some areas.

The effects of these pests on *E. globulus* growth, and ultimately economic returns, are poorly understood. Most studies have been short-term in nature and restricted to a small number of sites with limited treatments in terms of severity, pattern and frequency of attack. In one study of the effects of MLD on young *E. globulus* growing in north-western Tasmania, Australia (Smith et al. Under review), an empirical growth model was used to project growth of infected and uninfected trees through to the end of rotation (20 years). The model predicted that a severe MLD epidemic at age 1 – 2 years would result in a 33% loss of usable wood products and a 40% loss of internal rate of return. While this is only indicative, because the modelling approach could not account for the dynamic nature of host/pest interactions and there is no long-term data with which to validate the model, it highlights the potential cost of pest attack to growers. Given the impracticality of developing an adequate empirical database to forecast pest impact, development of physiological models for exploring the longer-term implications of pest attack is a priority. As a first step it is necessary to understand the physiological processes governing specific host/pest systems.

The objective of this paper was to review the effects of infection and/or defoliation on temperate eucalypt plantation productivity, drawing heavily on the results of a large study conducted in southern Tasmania, Australia. In particular, we examined (1) growth responses to pattern, severity and frequency of defoliation or infection, and physiological processes governing those growth responses; and (2) management tools to prevent or offset the effects of defoliation events on plantation productivity, specifically the role of fertilising.

GROWTH RESPONSES FOLLOWING PEST ATTACK

What level of defoliation reduces eucalypt growth? There have been numerous studies examining this question (e.g. (Lückhoff 1967, Lundquist and Purnell 1987, Carnegie and Ades 2002, Collett and Neumann 2002, Pinkard et al. 2006b). In a study of the effects of *Mnesampela privata* defoliation on *Eucalyptus nitens* stem growth, Rapley (2005) found that approximately 50% defoliation was required before stem growth was significantly affected. As little as 10% defoliation by *Gonipterus scutellatus* reduced stem growth of 3-year-old *E. globulus* 12 months after defoliation (Figure 1), whereas 3-year-old *E. globulus* growing at a different site were largely unaffected six months after artificial defoliation removed 45% of leaf area from the upper crown (Audrey Quentin, unpublished data). Similar variability is found in response to foliar diseases such as MLD, one of the major foliar diseases of temperate plantation eucalypts (Lundquist and Purnell 1987, Carnegie et al. 1997, Carnegie and Ades 2002). This highlights the need for controlled experiments in order to understand host responses to foliar pests separate from site and environmental conditions.
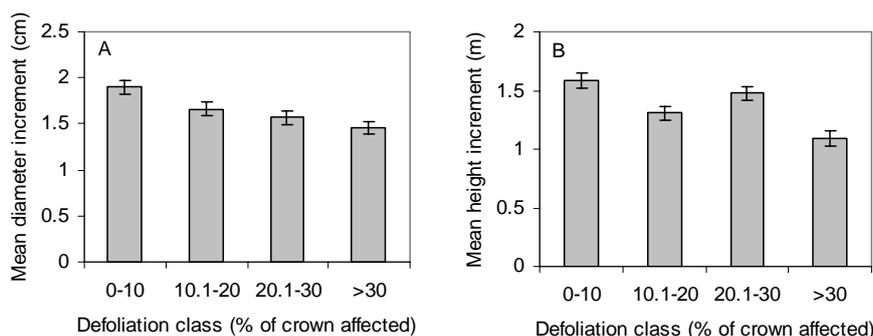

Figure 1. Effect of defoliation by *Gonipterus scutellatus* on 3-year-old *E. globulus* stem growth, 12 months after defoliation. Defoliation classes refer to the percentage of the crown affected in terms of incidence and severity of damage, as determined by the Crown Damage Index (Stone et al. 2003). From Pinkard et al.
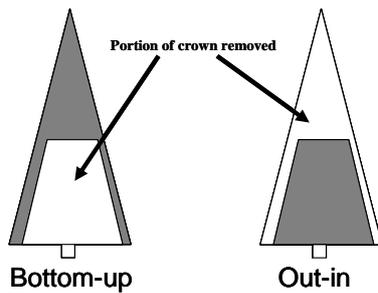
(2006b). Error bars indicate standard errors (P < 0.05).

Figure 2. Patterns of artificial defoliation applied in an experiment in *E. globulus* in southern Tasmania, Australia. Bottom-up defoliation involved removing all leaf area from the bottom 50% of crown length, excluding apical foliage. Out-in defoliation involved removing all leaf area from the top 50% of crown length, and including apical foliage in the lower 50% of crown length.

Artificial defoliation studies have demonstrated that the pattern of defoliation is very important in determining growth responses (Collett and Neumann 2002, Pinkard et al. 2006a) In a study in southern Tasmania (Pinkard et al. 2006a), young *E. globulus* (six months old at the start of the experiment) were subjected to either 1, 2 or 3 defoliation events, and to two patterns of defoliation (out-in or bottom-up; see Figure 2 for description). At the first defoliation event (autumn 2004, age 6 months), two severities of defoliation were applied (25% or 38% leaf removal from throughout the crown). The second (spring 2004) and third (autumn 2005) defoliation events removed leaves from 50% of the crown length. Out-in defoliation significantly reduced both height and diameter increment (Figure 3), whereas bottom-up defoliation had little effect for a single defoliation event. More frequent defoliation increased the effect on stem growth. A higher severity of bottom-up defoliation may have had a more noticeable effect on stem growth, as has been found in pruning studies in closed-canopy eucalypt plantations (Pinkard 2003, Pinkard et al. 2004)
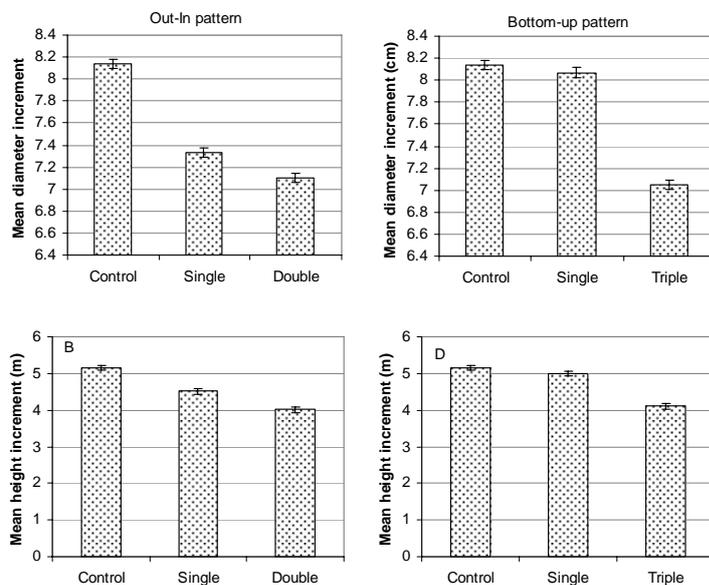

Figure 3. Mean diameter and height increment of *E. globulus* seedlings subjected to either out-in or bottom-up defoliation. Error bars indicate standard errors (P < 0.05).

HOST PHYSIOLOGICAL RESPONSES TO PEST ATTACK

Two factors are highly influential in determining plant responses to pest attack and have consequences for the rate of recovery of growth potential and therefore crop yield. The first is the extent to which unaffected leaves increase their unit levels of production, and the second is the dynamics of foliage retention and re-foliation. Both will be influenced by the mode of attack of the pest and by other environmental stresses such as those caused by current levels of nutrient or water availability.

In many species defoliation, due to pruning, artificial leaf removal or pest attack, results in changes in photosynthetic processes such that increased CO_2 assimilation occurs (Caldwell

et al. 1981, Senock et al. 1991, Ayres 1992, Hoogesteger and Karlsson 1992, Harbinson 1994). It is widely acknowledged that changes in source-sink ratios drive such photosynthetic upregulation (Neales and Incoll 1968, Wareing and Patrick 1975). Hence more severe pest attack would be expected to result in a higher rate of photosynthesis than less severe pest attack. This was observed in response to defoliation in *E. globulus* (Figure 4A) (Pinkard et al. 2006c). In contrast to defoliation, the presence of a foliar disease such as MLD reduced light-saturated CO_2 assimilation as disease severity increased (Figure 4B) (Pinkard and Mohammed 2006). Foliar disease may also reduce the photosynthetic capacity of asymptomatic tissue (Ayres 1992, Shtienberg 1992, Meyer et al. 2001), thereby increasing the overall effect of the disease on carbon assimilation.
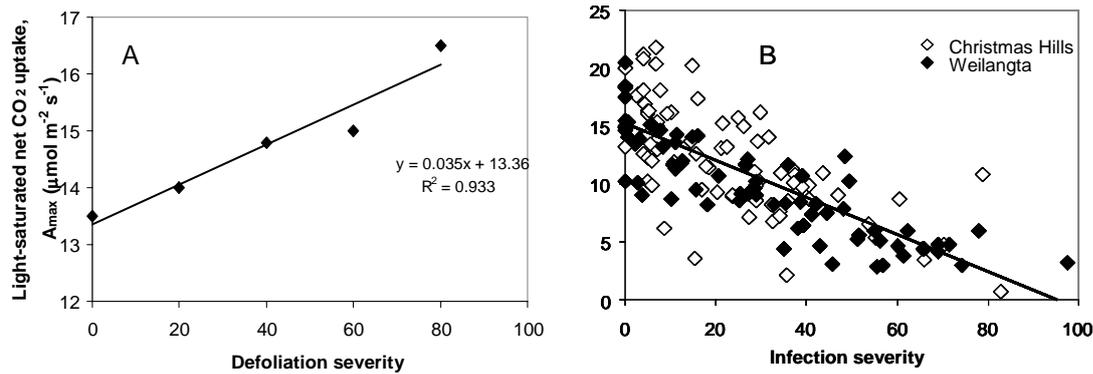

Figure 4. Relationship between light-saturated CO_2 assimilation and (A) defoliation severity (Pinkard 2003) or (B) MLD infection severity (Pinkard and Mohammed 2006), for *E. globulus* of between 2 and 3 years of age.

While severity of defoliation influences the degree of photosynthetic response, this is not always the case for the pattern of defoliation. In the artificial defoliation experiment described above, a similar level of photosynthetic upregulation occurred irrespective of defoliation pattern (Figure 5) (Pinkard et al. 2006c). However, measurements were made under light-saturated conditions, and therefore did not account for the effects of defoliation pattern on the crown light environment. A light interception model was developed to explore the effect of defoliation pattern on light interception and daily CO_2 assimilation in mid-winter and mid-summer (Battaglia and Sands, in Pinkard (2006a)). It was assumed that trees had a crown length of 3 m and diameter of 2 m, a leaf area density of 1 m^2 m^{-3} resulting in a leaf area index of 2 m^2 m^{-2}. Daily maximum temperature was assumed to be 22 ˚C and daily minimum temperature 10 ˚C with sinusoidal variation. The effects of bottom-up defoliation, and defoliation where leaves were removed from throughout the crown, were simulated, assuming 50% of leaf area was removed. The simulation suggested that the reduction in total CO_2 assimilation was not proportional to loss of intercepted radiation (Table 1).
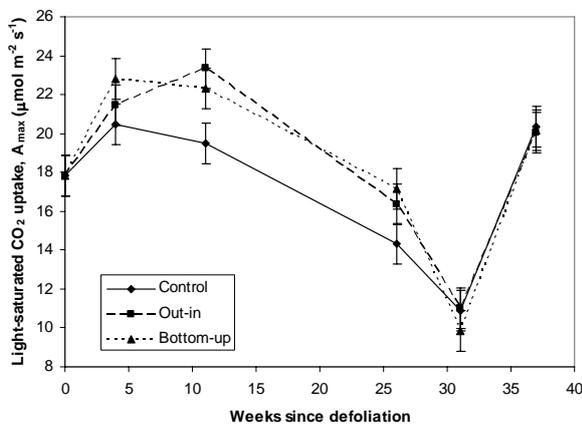

Figure 5. Mean light-saturated CO_2 assimilation measured in response to removal of 50% of the crown length by either out-in or bottom-up artificial defoliation (see Figure 2 for treatment description) (Pinkard et al. 2006c). Error bars indicate standard errors ($P < 0.05$).

While 50% defoliation was predicted to reduce light interception by 40 – 50%, the effect on total assimilation was less than 30 – 40%. Upregulation of photosynthesis by 26% (the level observed in the field) came close to removing the gross assimilation differences between defoliated and undefoliated trees. The pattern of defoliation had a small effect on radiation interception and CO_2 assimilation, with less radiation intereception associated with bottom-up than throughout-crown defoliation.

Table 1. Simulated values of intercepted radiation and total assimilation per tree under different defoliation scenarios mid-winter and mid-summer.

Treatment	Mid-summer intercepted radiation (MJ d^{-1})	Mid-winter intercepted radiation (MJ d^{-1})	Total assimilation mid-summer (g[CH$_2$O] tree^{-1})	Total assimilation mid-winter (g[CH$_2$O]tree^{-1})
No defoliation	78	30	28.3	8.3
50% removal throughout, no up-regulation	48	18	19.0	5.8
50% removal throughout, 26% up-regulation	48	18	23.0	6.1
50% removal bottom-up, no up-regulation	46	16	17.9	5.5
50% removal bottom-up, 26% up-regulation	46	16	21.7	5.7

Foliar nitrogen (N) concentrations, and the influence of patterns of biomass allocation on light interception, are key factors determining tree productivity (Jarvis and Leverenz 1983, McMurtrie 1991, Hollinger 1996, Le Roux et al. 1999). While there is some understanding of nitrogen dynamics (Saur et al. 2000) and patterns of biomass allocation in *E. globulus* (Pinkard and Beadle 1999, Pinkard 2002), the effects of pest attack on patterns of resource allocation in this species have received scant attention. Quentin (2005) examined the effects of artificial defoliation and infection with the foliar pathogen *Kirramyces eucalypti* on *E. globulus* seedling growth. She found that branch and leaf dry mass increased in the lower crowns in response to both defoliation and infection, while seedlings produced considerably less stem, branch and leaf dry mass in the crown zone produced following defoliation (upper) than did control or infected plants (Table 2). Branch diameter, and leaf area per unit branch diameter, were greater in the lower crowns of treated seedlings compared to the control, whereas in the portion of the crown produced following treatment, defoliation resulted in a lower specific leaf area (SLA) and smaller mean branch diameter. In other studies (Pinkard et al. 2006a) *E. globulus* SLA has been found to increase in response to defoliation and infection. In another pot experiment Pinkard et al. (2006a) observed remobilisation of nitrogen from the roots to the leaves of *E. globulus* seedlings that had been artificially defoliated or infected with *K. eucalypti*, and preferential partitioning of new nitrogen entering the plant to leaves. Both remobilisation of existing plant nitrogen and uptake of new nitrogen from the soil occurred in response to infection, whereas nitrogen uptake was more important than remobilisation in response to defoliation. These sorts of changes in patterns of resource allocation within trees subjected to pest attack are likely to influence both light interception and light use efficiency.

MANAGEMENT OPTIONS FOR PREVENTING OR OFFSETTING EFFECTS OF PEST ATTACK ON PLANTATION PRODUCTIVITY

Managing leaf diseases and insect browsing in plantations is very difficult. Chemical control is usually cost-prohibitive and may be associated with environmental problems. Selection for genetic resistance is possible, as resistance to some foliar pathogens and to browsing is under strong genetic control (O'Reilly-Wapstra et al. 2002, Rapley et al. 2004, Milgate et al. 2005). However it is known that genetic resistance may break down under certain growth

Table 2. Mean dry mass apportioned to stem, branches and leaves, leaf specific leaf area (fresh area:dry mass), and mean branch diameter of *E. globulus* seedlings 12 weeks after they were subjected to either artificial defoliation to remove the upper 50% of crown length or infection with a conidial suspension of 200 000 *Kirramyces eucalypti* conidia mm^{-3}. The lower crown zone refers to the lower 50% of crown length at the start of the experiment; the mid crown zone refers to the upper 50% of crown length at the start of the experiment; the upper crown zone refers to all growth subsequent to the start of the experiment. * indicates significantly different from control value ($P < 0.05$) (Quentin 2005).

Crown zone	Treatment	Dry mass (g)			Specific leaf area (m^2 kg^{-1})	Branch diameter (cm)
		Stem	Branches	Leaves		
Lower	Control	38.1	5.8	13.1	2.31	2.63
	Defoliated	41.3	17.4*	20.7*	2.49	3.23*
	Infected	49.2	12.7*	26.7*	2.57	3.34*
Mid	Control	17.3	11.5	29.7	1.86	2.81
	Defoliated	13.1	12.9	21.1	1.27	2.89
	Infected	20.7	14.6	37.7	2.20	2.91
Upper	Control	7.2	6.4	21.4	1.30	2.10
	Defoliated	1.3*	1.1*	4.3*	0.89*	1.55*
	Infected	8.3	6.0	20.3	1.38	2.29

conditions (eg. high soil fertility) (O'Reilly-Wapstra et al. 2005). There is some evidence that better nutrition may help prevent or offset the effects of infection or defoliation (Carnegie and Ades 2001, Stone 2001), although silvicultural treatments, such as fertilising, that are intended to improve tree vigour may also directly influence herbivore populations and hence future browsing (Bruyn et al. 2001, Lou and Baldwin 2004, Prudic et al. 2005). However maintaining an optimal nutrient status is perhaps the silvicultural option with the most promise for preventing or offsetting stem growth losses following foliar attack. Where nutrient supply from the soil limits growth, fertiliser application, in the absence of other site limitations, can promote crown development (Smethurst et al. 2003).
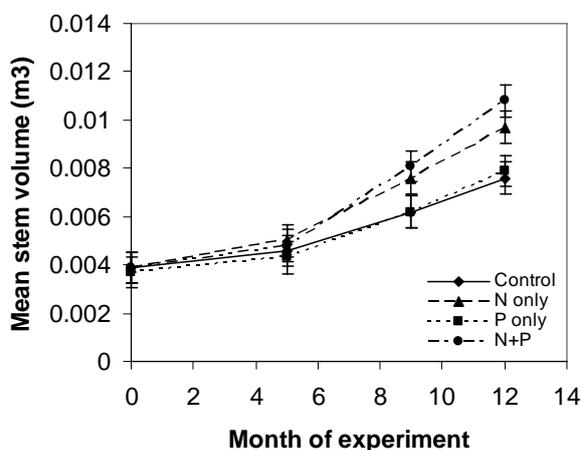

Figure 6. Mean stem volume of 3-year-old *E. globulus* defoliated by *G. scutellatus*. Following the single defoliation event, fertiliser was applied, either as nitrogen at 300 kg ha^{-1} (N only), or phosphorus at 100 kg ha^{-1} (P only), or the combination of nitrogen and phosphorus (N+P). From Pinkard et al. (2006a). Error bars indicate standard errors ($P < 0.05$)

In a plantation with 3-year-old *E. globulus* experiencing defoliation by *G. scutellatus*, a 2 x 2 factorial N x phosphorus (P) experiment was established, using 300 kg ha^{-1} N and/or 100 kg ha^{-1} P, in a single broadcast application in the autumn following defoliation (Pinkard et al. 2006b). While there was little response to P alone 12 months after fertiliser application, stem volume of trees increased considerably in response to N alone, or the combination of N and P (Figure 6). The artificial defoliation experiment outlined earlier examined the responses of defoliated plants to two rates of N application (100 or 300 kg ha^{-1}). Applying even 100 kg ha^{-1} N increased diameter increment of defoliated trees to the level of undefoliated, unfertilised trees (Figure 7). The strong relationship between stem diameter and leaf area in *E. globulus*
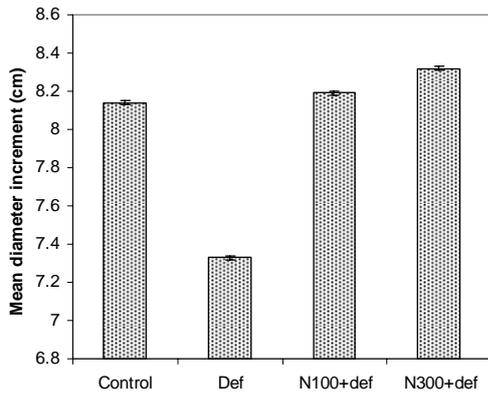
(Pinkard 2003) suggests that N application promoted crown recovery after defoliation on that site. N application also increased CO_2 assimilation rates, particularly in defoliated trees

Figure 7. Effect of application of 100 or 300 kg ha^{-1} N to undefoliated *E. globulus* and trees experiencing spring out-in defoliation (See Figure 3), on mean diameter increment 12 months after treatment. From Pinkard et al. (2006a). Error bars are standard errors (P < 0.05)

(Figure 8). This explains to some extent the increased growth rates observed in defoliated and fertilised trees.

Responses to fertiliser application of *E. globulus* experiencing MLD were examined at a site in north-western Tasmania (Wardlaw, in Pinkard (2006a)). Fertiliser, in the form of 100 kg N ha^{-1} and 70 kg P ha^{-1}, was applied both before and after the start of a MLD epidemic. Application prior to the epidemic resulted in higher levels of the blighting-type infection (i.e. entire leaves, buds and branch tips affected) that causes out-in defoliation. This was most likely a consequence of fertilised trees producing more new-season's foliage that is susceptible to the blighting-type damage. Counteracting the heightened susceptibility to blighting-type infection, however, was evidence that the trees fertilised before the epidemic displayed more rapid crown recovery than trees fertilised after the epidemic.
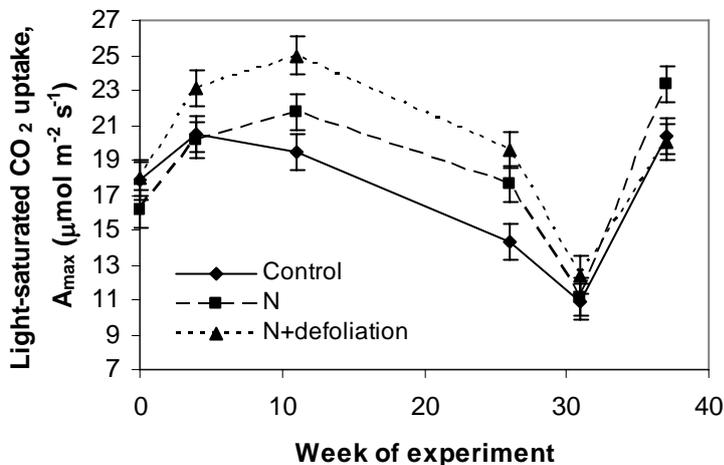

Figure 8. Effect of applying N at 300 kg ha^{-1} on light-saturated CO_2 uptake of undefoliated *E. globulus* and trees subjected to artificial defoliation to remove 30% of leaf area from throughout the crown. From Pinkard (2006a). Error bars indicate standard errors (P < 0.05).

CONCLUSIONS

Quantifying the physiological responses to pest attack is necessary to improve the precision of rotation-length growth modelling. The current level of understanding of physiological processes in *E. globulus* is such that physiologically-based models can be developed to examine this question. Research to date has focused on relatively stress-free environments, and in order to validate models for a range of site and environmental conditions, further research is required into the effects of abiotic stresses such as water or nutrient limitation, on responses to pest attack. The effects of pest attack on resource pools (nutrient, carbohydrate) within the tree, as related to time of year, severity and frequency of attack and tree age, also requires further investigation.

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