

Impact of repeated defoliation on jarrah (*Eucalyptus marginata*) saplings

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Summary

In Australia, eucalypts frequently suffer defoliation due to insect herbivory or fire. Rapidly-applied 'shock' defoliation of eucalypts, characteristic of artificial defoliation experiments, is unusual under natural and plantation conditions, though the exception to this is defoliation by fire. The effect of 15 consecutive annual complete defoliations of jarrah (*Eucalyptus marginata* Donn ex Smith) saplings on diameter and survival of main stems is described. Within 3 y, this defoliation resulted in almost complete suppression of stem diameter growth. Despite up to 15 y of repeated defoliation, no plants died, although after 15 y about half the defoliated plants had died back to below 30 cm. Low mortality in *E. marginata* following complete defoliation is in contrast to effects on several other eucalypt species which have been subjected to defoliation experiments. Stem die-back did not appear to be related to less-than-usual winter rainfall in some years. Annual diameter growth of undefoliated plants was not correlated with preceding winter rainfall, probably due to the poor resolution of diameter measurements. The resilience to this defoliation, which is more severe than defoliation encountered in natural conditions, is evidence that understorey jarrah plants are capable of withstanding, for extended periods, defoliation by insects or fire. The degree and frequency of defoliation under current fire management regimes do not appear to threaten the persistence of jarrah saplings. Chronic defoliation by insect pests, while having a detrimental effect on growth, is unlikely to affect the persistence of jarrah saplings.

Keywords: regeneration; defoliation; growth rate; periodicity; persistence; *Eucalyptus marginata*; Western Australia

Introduction

The effects of defoliation on the growth of eucalypts have been investigated using two experimental strategies: exclusion of insect attack by application of insecticide (Lowman and Heatwole 1987; Fox and Morrow 1992; Stone 1993; Stone and Urquhart 1993; Stone and Bacon 1994, 1995; Stone 1996; Elek 1997; Stone *et al.* 1998; Floyd *et al.* 2002); and artificial defoliation which mimics, to some extent, the intensity, timing, frequency or location within canopy of natural defoliation (Mazanec 1966; Cremer 1972, 1973; Carne *et al.* 1974; Candy *et al.* 1992; Abbott *et al.* 1993; Wilkinson and Neilen 1995; Elek 1997; Neumann *et al.* 1997; Collett and Neumann 2002).

Insect herbivory of eucalypts usually results in partial defoliation over extended periods affecting particular parts of the canopy, often with annual or seasonal cycles of intensity. Defoliation by insects can be more or less complete for relatively short periods (e.g. Farrow *et al.* 1994) or remain chronic for decades (Mazanec 1974; Morrow and La Marche 1978; Abbott 1992). Thus comparisons of protected with unprotected foliage often consider confounded treatment effects, yet have the advantage of examining effects of insect damage. Reduced herbivory achieved by protection with insecticide results in significant growth increases, even when differences in damage between treated and untreated trees are small (Stone and Bacon 1994).

Rapidly-applied 'shock' defoliation of eucalypts, characteristic of artificial defoliation, is unusual under natural and plantation conditions, though the exception to this is defoliation by fire. Fire may cause rapid defoliation through combustion or canopy scorching, and be imposed relatively frequently. An advantage of artificial defoliation over insecticide protection as an experimental tool is that it can be quantified and applied at precise times during experiments (Candy *et al.* 1992; Abbott *et al.* 1993; Collett and Neumann 2002; Wildy and Pate 2002). Timing of application is important as there are differences between seasons in both abundance of regenerating shoots and production of shoot biomass (Wildy and Pate 2002).

Complete and repeated defoliation has severe consequences for eucalypt growth (Abbott *et al.* 1993; Collett and Neumann 2002), although mortality is rare in most cases (Landsberg and Cork 1997). Despite this, repeated defoliation for more than a few cycles has seldom been investigated. In an extreme case, Chattaway (1958) defoliated saplings at weekly intervals and found shoots were still produced on *Eucalyptus melliodora* after 21 defoliations, and on one plant of *E. hemiphloia*, after 26 defoliations.

Bond and Midgley (2001) coined the term 'persistence niche' to describe characteristics of plants that persist *in situ* in the face of disturbance. Where severe defoliation is a disturbance, persistent species typically have surviving meristems from which new foliage growth is initiated (Bellingham and Sparrow 2000) and the new growth is sustained, at least initially, by stored carbohydrate reserves (Bowen and Pate 1993; Wildy and Pate 2002). In eucalypts the meristems are axillary and epicormic, and in some cases lignotuberous tissues (Jacobs 1955; Burrows 2002). The leaf removal process of Abbott *et al.* (1993), removing only leaves

and petioles, left most of the axillary and epicormic meristems undamaged. Foliage regrowth during the 3-y period reported in Abbott *et al.* (1993) was likely to have been influenced by carbohydrate stored before the initial defoliation, leading to the questions:

- how persistent is this influence on growth of jarrah saplings?
- how many cycles of defoliation can these plants survive?

We report here the continuation of the experiment on jarrah (*Eucalyptus marginata* Donn ex Smith) initially reported after three defoliation events by Abbott *et al.* (1993). The original experiment investigated the effects of intensity and repetition of artificial summer defoliation on sapling diameter. Stem diameter growth declined proportionally to the intensity and frequency of defoliation. Three consecutive years of complete defoliation resulted in diameters about half those of undefoliated plants.

The experiment was then continued for a total of 15 consecutive annual applications of complete defoliation, with one objective: to examine the resilience of jarrah saplings subjected to extreme defoliation.

Materials and methods

Treatment details are those already reported for the 3 y of experimental data from a regenerating stand of *E. marginata* in Holmes forest block (32°43'55"S 116°6'E) near Dwellingup, Western Australia (Abbott *et al.* 1993). The stand was thinned in 1984 and contained abundant saplings and dynamic ground coppice. Saplings are defined as having a height greater than 1.5 m and a stem diameter less than 15 cm (Abbott and Loneragan 1986). Stand basal area averaged 16 m² ha⁻¹ after thinning. Defoliation treatments were initially applied in December 1987 (summer) and defoliation was repeated annually in December. Defoliation was effected by removal of whole leaves by hand, starting from the apex of the crown and encompassing all foliage in the crown. All plants were defoliated on the same day.

Initially the experiment was set up with 15 replicates of each treatment. Each treatment was a combination of defoliation intensity (0%, 25%, 50%, 75% or 100% defoliation) and frequency (1, 2 or 3 defoliation events). The results of this initial phase, reported in Abbott *et al.* (1993), have been summarised above. Measurement and defoliation of the partial defoliation treatments were discontinued after the initial 3-y study. Illegal logging in 1988 resulted in the death of 15 saplings, leaving 11 saplings in the undefoliated treatment and 13 saplings in the treatment subjected to ongoing complete annual defoliation.

The two most extreme treatments, no defoliation and annual complete defoliation, were continued for a total of 15 y on the main stem of the same saplings. Stem diameters were measured 30 cm above ground level using a diameter tape. Defoliation and measurements of individual stems were continued until the measured stems were dead at the point of measurement.

Annual growth was standardised against the diameter in the previous year using the formula 'Relative growth = ln ((diameter for year T)² × (diameter for year T - 1)⁻²)', with units cm²cm⁻². Defoliation treatments were compared within years using Mann–Whitney *U* tests.

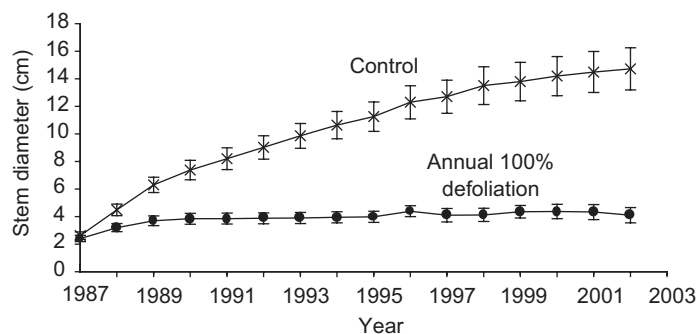


Figure 1. Mean diameters of stems remaining alive at the measuring point. Error bars are standard error of mean. Within-year treatment means are all significantly different ($P \leq 0.01$, Mann–Whitney *U* tests) except for the initial pair.

Results

The mean diameters of undefoliated and defoliated treatments were not significantly different at the beginning of the experiment but were significantly different ($P \leq 0.01$, Mann–Whitney *U* test) a year after the initial defoliation (Fig. 1). At the termination of measurements, average stem diameter of undefoliated saplings was 3.6 times larger than that of defoliated saplings. Two phases of growth were apparent from relative growth data — an initial phase where relative growth rate was high but declining rapidly, and a second phase where relative growth was lower but also declining slowly (Fig. 2). During the initial phase of rapid growth, relative growth of defoliated plants was always significantly less than that of intact plants ($P \leq 0.01$, Mann–Whitney *U* tests). Within 3 y of the initial defoliation, annual 100% defoliation resulted in almost complete suppression of stem diameter growth (Abbott *et al.* 1993; Fig. 2).

During the second phase of low relative growth, relative growth of defoliated plants was also always significantly less than that of intact plants, except for the year 1996 when poor measurement

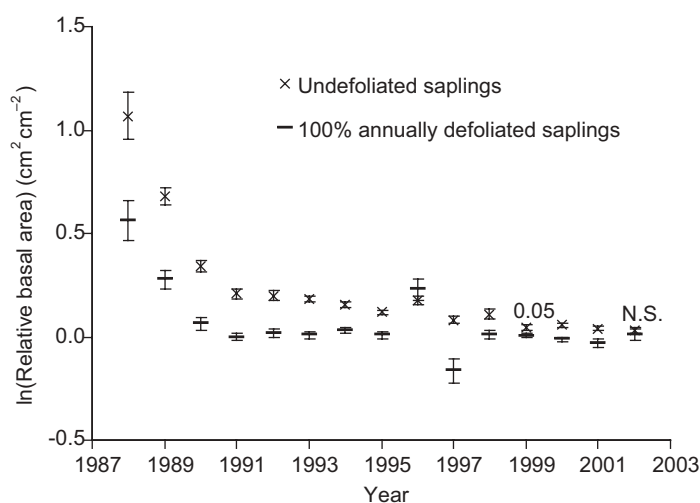


Figure 2. Relative growth rates of stems remaining alive at the measuring point. Within years treatment means are significantly different ($P \leq 0.01$, Mann–Whitney *U* tests) except where noted above data points on the graph. Error bars are standard error of mean.

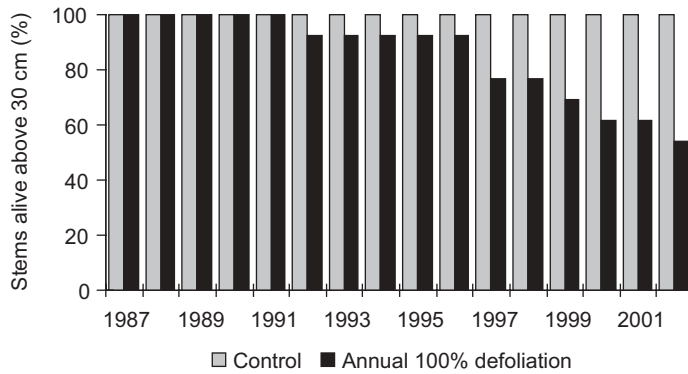


Figure 3. Fraction of stems remaining alive above the measuring point (initially there were 11 Control plants and 13 100%-defoliated plants)

technique resulted in defoliated plants apparently having the greater growth rate, and 2002 when relative growth rates of intact and defoliated plants were not significantly different (Fig. 2).

Despite 15 y of repeated defoliation no plants died. In some cases the main stems, from which measurements were taken, died back over time, but the progress of die-back was not measured. After 15 y about half the defoliated main stems had died back to below the measuring point (Fig. 3). Die-back of stems to below the measuring point was not related to the level of winter rainfall (Table 1), and was as likely in years of higher-than-average as lower-than-average April to October rainfall (Table 1). This was also the case for rainfall in the winter prior to the growing year.

The second phase of low relative growth was also investigated for any correlation between April to October rainfall and relative growth of undefoliated plants, with year as a covariate to accommodate the declining trend in relative growth. The diameter tape measurements appear to have been too crude to reveal any relationship.

Discussion

Jarrah ground coppice appears to be extremely resilient to repeated defoliation. Defoliated saplings managed to produce new foliage each year, although stem diameter growth was suppressed and in some cases stem die-back occurred. Despite this, no plants died after 15 y of defoliation. This result is consistent with that of Carne *et al.* (1974) who found no mortality of *E. grandis* after seven defoliations of 75–80% intensity, and that of Collett and Neumann (2002) who found 100% survival of *E. globulus* saplings after two complete summer defoliations. However, in *E. regnans*, Candy *et al.* (1992) found mortality rates of 5% (early summer defoliation), 60% (late summer defoliation) and 85% (early and late summer defoliation) after two consecutive years of complete defoliation events. Mortality after single defoliation events is seasonally variable in *E. regnans* and *E. obliqua* seedlings (Cremer 1973) and *E. delegatensis* saplings (Mazanec 1966), with summer defoliation resulting in greatest mortality. Wilkinson and Neilsen (1995) found the effects of defoliation on mortality still apparent up to 5 y after defoliation in 7-y-old stands of *E. regnans* and *E. nitens*, with *E. nitens* the more severely affected. In the current study, complete defoliation in summer did not result in mortality

Table 1. Categorisation of the 15 y of the study by the amount of winter rainfall and instances of death of the main stem of defoliated trees to below the 30 cm measuring point. The average winter rainfall for the period was 1061 mm.

Winter rainfall category (mm) (Apr.–Oct.)	Total number of years in rainfall category	No stem die-back in <i>n</i> y	Stem die-back occurs in <i>n</i> y
<1061	9	6	3
>1061	6	4	2

in jarrah saplings. In addition to seasonal variation within eucalypt species, it appears that there is large inter-specific variation in mortality following complete defoliation.

Measurements of diameter of defoliated stems revealed two phases of growth in the 15 y of treatment. In the first phase, lasting for 3 y after the initial defoliation, the relative growth rate was high though declining. Cessation of stem height or diameter growth is not apparent in results of other studies of repeated defoliation (Carne *et al.* 1974; Candy *et al.* 1992; Collett and Neumann 2002), though in none of these studies was defoliation continued for more than 2 y.

In the second phase, stem diameter growth of defoliated plants had virtually ceased. It appears that during this phase sufficient carbohydrate was stored in each year to allow a flush of new leaves to develop after subsequent total defoliation, but an optimum balance between allocation of new photosynthate to storage and allocation to new growth was not necessarily reached, as stem die-back occurred in some cases. Stem die-back would reduce respiration costs by reducing the amount of non-essential tissue.

In natural conditions two agents, herbivory and fire, alone or in combination, are capable of imposing repeated defoliation which can approach the frequency and intensity applied artificially in this study. Chronic and extensive outbreaks of gumleaf skeletoniser, *Uraba lugens*, have caused moderate to severe defoliation across extensive tracts of jarrah forest lasting about 6 y (Abbott 1992; Farr 2002). The jarrah leafminer, *Perthida glyphopa*, has also been in outbreak across extensive areas of jarrah forest for more than three decades (Abbott 1992). Defoliation by jarrah leafminer, however, is rarely complete.

Periodic fire is likely to result in complete defoliation of understorey plants across tracts on a scale of one to tens of square kilometres. Intervals between the return of fire have usually exceeded 1 y but rarely 15 y, even before European settlement when low-intensity understorey fires were apparently more frequent than after European settlement (Burrows *et al.* 1995). Modal fire frequency was about three per decade before European settlement and is now at about one per decade in forest managed under a policy of fuel reduction burning (Ward *et al.* 2001).

Fire is likely to modify the impact of vertebrate browsing on understorey *E. marginata* since kangaroo and wallaby populations are large in the first year after fire and decline within 3 y of fire (Christensen and Kimber 1975). Defoliation due to the combination of fire and browsing would be expected to have a

duration, following fire, of about 3 y, with the browsing intensity being variable during this time.

The intensity of defoliation due to vertebrates, insects and fire appears to be much less than that of the artificial defoliation imposed in this experiment. Neither historical nor contemporary fires have been annual events, thus allowing some recovery in the intervals between them. Insect defoliation is either incomplete though chronic, as with jarrah leafminer, or nearly complete for only a short period, as with the gumleaf skeletoniser. Given the resilience demonstrated under repeated artificial defoliation, understory jarrah plants would appear to be capable of withstanding natural defoliation, by fire or herbivores, for extended periods.

A limitation of the experiment was that defoliation was not continued after stems had died back below the measuring point. For some plants, defoliation resulted in multi-stemmed ground coppice (termed incipient ground coppice by Abbott and Loneragan 1986), effectively a regression to an earlier phase of crown development. Leaf biomass of some plants may have continued to decline and these plants may have died if the defoliation treatment had continued.

The origins of defoliation resilience in understory jarrah are likely to be complex. At the stand level, intra-specific competition is high, leading to development of an understory of suppressed jarrah. Strategies of carbon allocation that allow persistence of suppressed tree species in the understory could contribute to defoliation resilience by allowing flexible responses to defoliation (e.g. Kobe 1997; Kaelke *et al.* 2001). Despite the resilience of jarrah to defoliation, it remains vulnerable to introduced pathogens such as *Phytophthora cinnamomi* (Shearer and Tippett 1989).

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