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Effects of Different Rates and Methods of Leaf Area Removal on Rain Forest Seedlings of Coachwood *(Ceratopetalum apetalum)*

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Abstract

Different ways in which insect herbivores may consume the same proportions of leaf area were compared experimentally in their effects on a host plant. Part of the leaf tissue was removed from seedlings of *Ceratopetalum apetalum*, a native Australian rain forest tree, and growth recovery was monitored. Seedlings maintained in a controlled environment were subjected to one of five defoliation treatments: 25% of each leaf removed; 50% of each leaf removed; one of every four leaves removed; one of every two leaves removed; control. Growth was stimulated beyond the rate of the controls in both types of treatments with 25% removal of whole leaves or of leaf tissue, but was suppressed to a greater degree with 50% tissue removal. Seedlings with all leaves partially clipped recovered more successfully than those with some leaves completely removed, and the implications of this are discussed in relation to the behaviour of herbivores.

Introduction

Feeding behaviour and biology of herbivorous insects in forest communities can readily be observed but it is more difficult to quantify the loss of tissues from the host plants. Losses of leaf surface area in forest communities are typically between 3 and 8% (Bray 1961, 1964; Reichle and Crossley 1967; Odum and Ruiz-Reyes 1970; Jordan 1971; Reichle *et al.* 1973). These values reflect the increment missing from the potential canopy overall, but it is difficult to assess their physiological effects on plant fitness both in terms of regrowth and ultimate reproductive capacities.

The effects of loss of leaf tissue on plant productivity are of great economic and ecological interest (see Rafes 1968; Franklin 1970; Kulman 1971). In trees, foliage removal can affect seed production (Rockwood 1974; Janzen 1976), leaf size (Duncan and Hodson 1958), radial growth (Wickman 1963; Wilson 1966; Morrow and LaMarche 1978) and epicormic branch growth (Embree 1967), and can also have indirect effects by altering inputs to the soil-litter system (Kimmins 1972) and by changing microclimate. Because foliage has a short cycle of replacement, rapid recovery from an insect outbreak is possible with relatively little deterioration in the host plant. The severity and frequency of removal of leaf tissue and the vigour of the host plant together determine the net effect of herbivory on the plant's physiological condition. In general, loss of leaf tissue directly decreases the amount of photosynthetically active tissue, which may indirectly lead to decreased wood production (Wickman 1963; Wilson 1966; Morrow and LaMarche 1978) and reproductive capacities (Rockwood 1974; Janzen 1976). In some cases, however, moderate defoliation has been shown to stimulate photosynthetic activity of the remaining leaf tissue, e.g. lucerne leaves (Hodgkinson 1974). Grasshoppers, when feeding on blue gama grass, appeared to secrete growth-promoting substances into the plant and thereby stimulate metabolic activity in the remaining plant tissue (Dyer and Bokhari 1976). In this way, herbivores may stimulate primary productivity (Mattson and Addy 1975; Owen and Wiegert 1976). Most studies of losses of leaf tissue and subsequent recovery of plant metabolism have been confined to annuals (Jameson 1963; Harris 1973; Hodgkinson 1974; Dyer and Bokhari 1976). However, herbivores may have an equally significant effect on longer-lived plants, and the results obtained from studies on annuals may not be applicable to longer-lived plants.

Coachwood (*Ceratopetalum apetalum* D. Don) is a predominant species in the warm temperate and subtropical rain forests of Australia. It often attains a canopy position and its tall, straight trunks give it great economic importance. Ecological research on the growth dynamics of Australian rain forest canopies during the last 3 years revealed an overall grazing rate of 21·3% leaf area removal from coachwood canopies, the majority of grazers being chrysomelid beetles (Lowman 1982). The majority of herbivores preferred young leaf tissue and tended to chew holes along the leaf edges, although with young leaves the entire leaf was often consumed. In addition to the interest generated from these observations on coachwood herbivory, there are several additional reasons why it was suitable for experimental studies. (1) It has opposite, elongate leaves that are easily measured and from which measured portions of tissue can accurately be removed; (2) it is one of the few rain forest species that has germinated profusely during the last several years, which have been fairly dry; (3) it is a common rain forest species, with economic as well as ecological importance.

The insect herbivores observed on coachwood canopies displayed a variety of patterns in terms of numbers present, amounts ingested and seasonality of feeding. However, the manner in which different herbivores feed may also be important in terms of recovery of the plant. Two major types of feeding behaviour were recognized, which served as the basis for this experimental study.

(1) 'Efficient eating': where the insect bites off and consumes small, continuous patches at the tip or edges of the leaf and works towards the vascular tissue. With this behaviour, no leaf tissue is wasted. It is either eaten or able to remain intact and functional as a partially defoliated leaf. This pattern was observed in phasmids (Phasmatodea) and weevils (Curculionidae) on coachwood leaves, whereby the remaining portions of leaves had a normal lifespan.

(2) 'Inefficient eating': insects that chew petioles, leaf bases or vascular tissue, thus killing the rest of the leaf, albeit uneaten; or insects that eat patches throughout the leaf in a manner that causes the remaining portions to die. This feeding behaviour renders portions of leaves both unproductive and uneaten, since they die and fall off. Inefficient eaters observed on coachwood included miners which bored along the mid vein, causing leaf abscission, and several weevils which ate very young leaves but the uneaten sections desiccated and died.

Since more coachwood herbivores exhibited the efficient eating behaviour, I hypothesize that this manner of leaf loss may be less detrimental to the host plant in terms of growth recovery. To test this, seedlings were subjected to different methods of defoliation, both partial and complete leaf loss to simulate efficient and inefficient herbivory respectively. Two questions were addressed in this experiment.

(1) Does the manner in which an insect consumes a portion of leaf tissue affect the plant's ability to recover (e.g. is there a difference between taking one entire leaf out of every four and taking 25% of every leaf)?

(2) Does loss of some leaf tissue stimulate growth of rain forest seedlings as it does for some annual species?

Methods

A total of 130 seedlings of coachwood was transplanted from simple notophyll vine forest at Royal National Park, N.S.W. into a controlled environmental cabinet. The seedlings had germinated 6 months previously, and were approx. 5 cm tall with cotyledons still attached and the first pair of leaves expanded. They were set out in individual pots with a rich soil mixture of 2 parts peat, 1 part sand and 1 part perlite. The soil was enriched with a full Hoagland's solution every 2 weeks and kept fairly moist. The environment was controlled at 12-h dark/light cycles, with 600 μE m^{-2} s^{-1} light, 60% humidity and 15/25°C night/day ambient temperature.

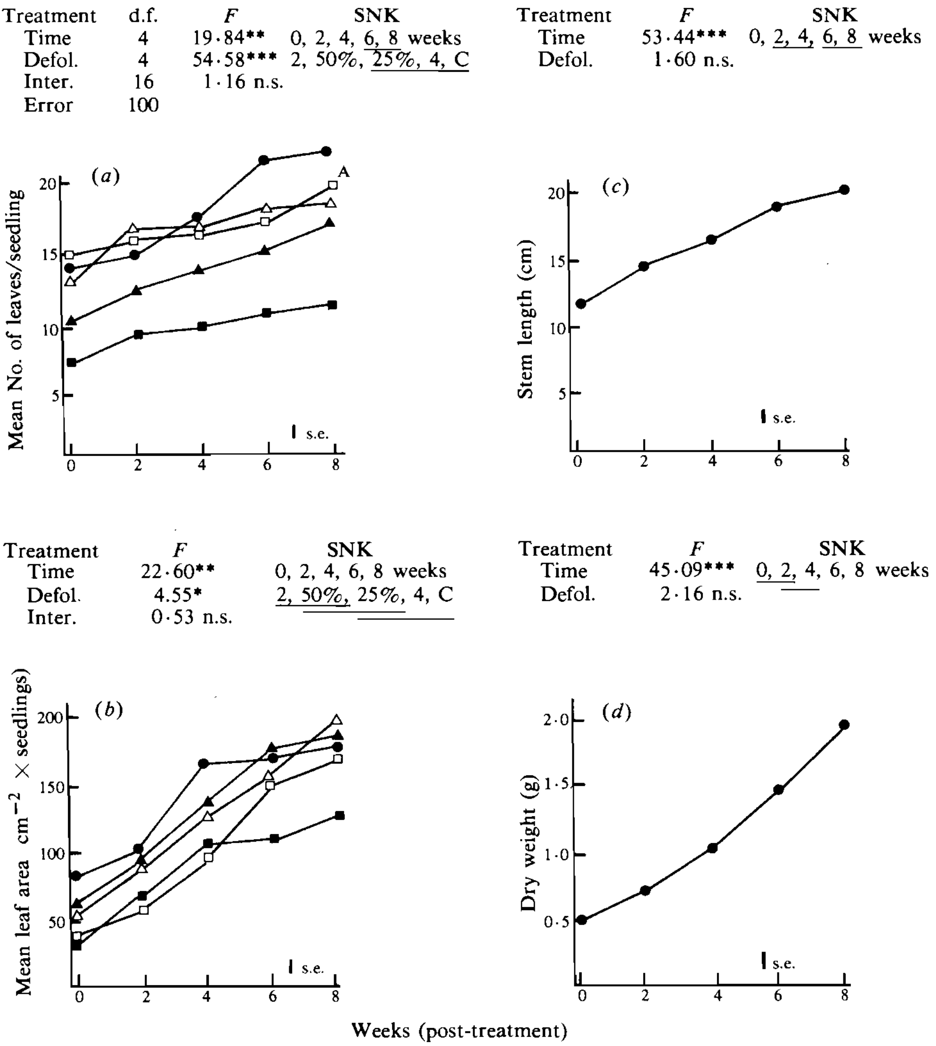
The experimental treatments commenced after 4 months in the cabinet when each seedling had at least five pairs of fully expanded leaves. All leaves were morphologically homogeneous along the stems; the lower leaves were slightly older but, since the plants were very young, no sun or shade leaf characteristics had developed. Five seedlings were harvested initially, to use in determining growth rates. The remaining 125 seedlings were divided into 5 groups of 25, using a randomized block design to ensure equal distribution of larger and smaller plants in each group. The seedlings in each group were treated as follows: (1) control; (2) every fourth leaf removed; (3) 25% of each leaf removed; (4) every second leaf removed; and (5) 50% of each leaf removed. All leaves within a treatment were cut in a homogeneous manner to eliminate shape of the removed portion as a factor of variability. For 50% of leaf removal the top half was removed with a straight cut; for 25% of leaf removal the top right corners were removed using the mid vein as a boundary (but not cutting into it). Since the number of leaves per seedling varied, removal of every fourth leaf may have resulted in slightly more or less than a 25% removal of leaves, especially where leaf numbers were not multiples of 4. This error was minimized by having replication, and also by excising leaves of the most appropriate size to approximate 25%. Since leaf size varied both within and among seedlings, it was possible to exercise latitude in counting every fourth leaf, i.e. from top to bottom of plant, right to left or vice versa.

After treatment, five seedlings from each treatment were havested at 2-week intervals. Seedlings were analysed for leaf area, number of leaves, stem length and dry weight. Two-factor analyses of variance were performed with time and leaf treatments as random and fixed factors respectively. (Unfortunately, rates of leaf production per seedling over time could not be compared, since the experimental design required destructive sampling at each harvest to maintain the independence required for analyses of variance.)

Results

Removal of leaf tissue, either as segments or whole leaves, affected the recovery of total leaf area and the number of leaves the plants subsequently carried (Fig. 1). Where only leaf segments were removed the recovery of the leaf area to that of its initial value took place in about 2 weeks. Where whole leaves were removed this period was doubled (Fig. 1*b*); thereafter, leaf area rapidly increased until week 6, after which its rate of increase slowed considerably (Fig. 1*b*). The number of leaves showed a similar pattern, with an initially more rapid increase which eventually slowed (Fig. 1*a*). The treatment of removing every second leaf caused a cessation in growth of new leaves after 4 weeks (Fig. 1*a*), although the areas of remaining leaves continued to expand (Fig. 1*b*).

Defoliation treatments did not cause significantly different changes in total dry weight or stem height measured at each harvest, although both were gradually increasing between harvests with continued growth of the plants. Presumably, the apparent absence of differential responses in dry weight was due to the overall fast growth rates in seedlings, and also to the fact that the roots (which made up a large proportion of the dry weight) remained intact regardless of defoliation treatment. Stem growth is probably a lower priority in seedling growth strategies than leaf area, and thus did not respond to defoliation treatments as rapidly and as obviously as replacement of leaf material.



Treatment	d.f.	*F*	SNK
Time	4	19·84**	0, 2, 4, 6, 8 weeks
Defol.	4	54·58***	2, 50%, 25%, 4, C
Inter.	16	1·16 n.s.	
Error	100		

Treatment	*F*	SNK
Time	53·44***	0, 2, 4, 6, 8 weeks
Defol.	1·60 n.s.	

Treatment	*F*	SNK
Time	22·60**	0, 2, 4, 6, 8 weeks
Defol.	4.55*	2, 50%, 25%, 4, C
Inter.	0·53 n.s.	

Treatment	*F*	SNK
Time	45·09***	0, 2, 4, 6, 8 weeks
Defol.	2·16 n.s.	

Fig. 1. Growth recovery of coachwood seedlings after defoliation treatment, as reflected by changes in (*a*) number of leaves, (*b*) leaf area, (*c*) stem length and (*d*) dry weight. Results of analyses of variance and Student-Neuman-Keuls rankings (SNK) are given, with all statistically similar treatments underlined. In (*a*) and (*b*) ● control; □ 50% of leaf removed; △ 25% of leaf removed; ▲ every 4th leaf removed; ■ every 2nd leaf removed. In (*c*) and (*d*) ● $\bar{x}$ of all treatments. A Snedecor and Cochran (1967): $*P = 0·05$; $**P = 0·01$; $***P = 0·001$; n.s., not significant.

After 8 weeks, both types of 25% removal treatments showed the greatest leaf areas. Their rate of leaf area growth recovery exceeded the growth rate of the controls (Fig. 1*b*), although not significantly. In contrast, the 50% removal treatments did not show similar rapid growth recovery and gained significantly less leaf area than did the other treatments.

In general, the removal of entire leaves had a more severe effect than partial clipping of each leaf. Partial defoliation of leaves appeared to stimulate growth, and in none of the leaves where only a portion was removed did the remaining leaf die afterwards. At the final harvest, seedlings receiving 25% defoliation per leaf had significantly greater leaf area than seedlings losing one of every four leaves; and those with 50% tissue loss per leaf had greater leaf area than seedlings losing every second leaf, although not statistically so owing to the extent of interaction through time (Fig. 1*b*).

Discussion

Removal of leaf tissue is usually regarded as a setback to the plant, and large numbers of herbivores are considered detrimental to a plant community in terms of net primary productivity and subsequent biomass accumulation. This may not necessarily be the case.

Removal of up to 25% of the leaf tissue stimulated growth in the coachwood seedlings, and similar reactions are documented for annual plants as well. Such moderate amounts of tissue removal promoted higher growth rates beyond the normal rate of controls for at least up to 8 weeks under these conditions. In addition to this effect on an individual plant, moderate herbivory may have important consequences for the entire community in terms of nutrient cycling. Material ingested by herbivores re-enters the system soon afterward as frass, which is already well broken down. Conversely, uneaten leaf tissue eventually undergoes senescence and recycles more gradually through the decomposition pathway. For coachwood, the turnover time of fallen, uneaten leaf tissue through decay is well over 1 year (Lowman, unpublished data), a surprisingly slow re-entry time for a rain forest species (cf. Nye 1961; Ewel 1976). The severity of effects of herbivory to both the individual plant and the entire plant community depends in part upon season. Plant leaf tissue may be more vulnerable at certain times of year, and removal of young leaves may reduce the net photosynthetic activity significantly. Also, the decay rates of leaf material are faster during the warmer, moister months of spring and summer, and presumably this holds true for frass. It is not known whether it is the removal of young emerging leaf tissue in spring or of fully expanded leaves later in the growing season which represents the greater loss to the plant, but the seasonality of phytophagous activities will influence the impact of the herbivory.

In addition, grazing on seedlings situated in the shade may be more detrimental than that on individuals situated in the sun, since growth is slower in the shade. Within mature tree canopies, coachwood leaves were grazed more heavily in shade than in sun, with 35·3% and 9·4% leaf area losses respectively (Lowman 1982). However, seedlings have not been similarly measured. The nutrient content and toxicity of shade versus sun leaves, as well as young versus old leaf tissue, may also contribute to variability in herbivory. These aspects will be discussed in a future publication.

In this comparison of partial versus entire leaf removal in coachwood seedlings the original hypothesis was upheld: seedlings with portions of leaves removed (the pattern of an efficient eater) recovered more successfully than the seedlings suffering loss of whole leaves in the manner of an inefficient eater. In addition, plants from which 25% of leaf area was removed showed a stimulated rate of growth recovery compared with the controls.

This study sought to simulate the behaviour of insects as observed in the natural community, but also stimulated many further questions concerning plants and herbivores. For example, do insects secrete substances that may affect the leaf's ability to recover? Or do particular types of damage induce chemical reactions within the leaf tissue (e.g. Carroll and Hoffman 1980)? One cannot extrapolate from seedlings to adult rain forest trees, so the effects of different types of leaf removal in a mature canopy may be different. In particular, the seasonality, intensity and manner of herbivore feeding may have long-term effects on the reproductive capacities of adult trees. Nonetheless, seedlings are most amenable to the rigours of statistical analysis. Seedling survival dictates the ultimate composition and ecology of a rain forest community, and studies of their herbivory provide a better understanding of mechanisms controlling diversity and plant–animal relationships.

Summary

Coachwood (*Ceratopetalum apetalum*) seedlings were subjected to a range of types and degrees of leaf area removal to observe the effects of different levels and manners of herbivory. Moderate removal of leaf tissue (25%) stimulated leaf growth rates above the level of controls, but 50% defoliation did not. Seedlings with portions of each leaf removed recovered their leaf area more quickly than seedlings with entire leaves removed, even though the total area removed was the same for both treatments. These methods of leaf area removal reflect observations of how insects feed in the rain forest: some act efficiently, in that portions of leaves are consumed and uneaten portions remain alive and photosynthetically active; others are considered inefficient because their eating behaviour causes uneaten portions of the leaf to die, rendering them useless in terms of either insect food supply or photosynthetic activity. In this study, seedlings given treatments simulating efficient patterns (i.e. where portions of all leaves were removed but no leaves were completely removed) exhibited more vigour in recovery than did seedlings with entire leaves removed as occurs with inefficient eating patterns.

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