

SHORT COMMUNICATION

Leaf damage does not affect leaf loss or chlorophyll content in the New Zealand pepper tree, kawakawa (*Macropiper excelsum*)S. Hodge, V. F. Keesing¹ and S. D. Wratten*

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Abstract: Kawakawa (*Macropiper excelsum*) is an understorey, forest tree which sustains conspicuous and substantial herbivory from the larvae of a geometrid moth, *Cleora scriptaria*. This study examined the relationship between leaf abscission and the amount of damage a leaf had sustained. In the field, kawakawa trees showed no increase in the rate of leaf shedding in response to experimental damage by *C. scriptaria* larvae or to artificial damage produced by a hole punch, even when 90% of the leaf area was removed. The tree did not compensate for a loss in leaf area by increasing the chlorophyll content of damaged leaves. Although herbivore damage is conspicuous and appears detrimental, the tree's leaf phenology does not appear to be affected. It is concluded that this plant species has evolved to tolerate frequent and severe feeding damage to its leaves.

Keywords: *Macropiper excelsum*; kawakawa; pepper tree; Piperaceae; herbivory; *Cleora scriptaria*; leaf abscission

Introduction

Kawakawa [*Macropiper excelsum* (Forst. f.) Miq.; Piperaceae] is a native New Zealand tree which sustains extensive herbivory by the larvae of a geometrid moth, *Cleora scriptaria* (Walker). Hodge *et al.* (1998) reported that, although leaf retention periods were short, there was no relationship between the rate at which leaves were shed and the amount of herbivory a tree sustained. Their experiments attempted to relate the number of leaves lost to the mean increase in grazing damage over the whole tree during a four month period. The aim of the experiments reported here was to follow the fate of individually labelled leaves and assess whether those sustaining higher levels of damage were shed in preference to relatively undamaged leaves.

Some plants are known to compensate for a decrease in leaf area by increasing the rate of photosynthesis per unit area of leaf tissue (Crawley, 1983; see also Williams and Carpenter, 1997). To examine whether this occurs in kawakawa, an

assessment was made of the chlorophyll content of leaves to determine whether damage initiated such a compensatory response.

Methods

Effect of damage on leaf loss

There can sometimes be a difference between a plant's responses to insect damage compared to those to artificial damage (see Karban & Myers, 1989). Therefore, in the first experiment, leaves were subjected to damage by *C. scriptaria* larvae or a mechanical hole punch. All field experiments were carried out between February 1997 and November 1998 in an area of mixed native broadleaf-podocarp forest in Okuti Valley (43° 47' S, 172° 50' E) on the Banks Peninsula, South Island, New Zealand. Undamaged kawakawa leaves of similar age (≤ 3 months) and initial size (c. 5 - 7 cm length along the midrib) were subjected to three damage treatments on 19 trees selected *ad hoc*. On each tree,

two leaves were each covered with muslin bags (controls), two were covered with bags containing two II / III instar *C. scriptaria* larvae (natural damage) and two were covered after being punctured five times (holes 4 mm diameter) using a mechanical hole punch (artificial damage; representing around 5% of leaf area removed). All 114 leaves were individually labelled using cardboard tags tied around the petioles. The bags were removed from the leaves after 48 hours, allowing sufficient time for the *C. scriptaria* larvae to cause feeding damage to the leaves (mean \pm SE leaf area consumed = $28\% \pm 3.2$). The survival of these leaves on the trees was monitored over a 60-day period.

The second experiment investigated how the amount of artificial damage affected the rate of leaf loss. Forty-four trees were selected and 20 newly-emerged undamaged leaves on each tree were labelled as before. The labelled leaves were subjected to one of four levels of artificial damage using a mechanical hole punch, so each damage treatment was replicated 11 times, using 880 leaves in total. The damage levels used were: 0% (controls), c. 1% (1 hole), c. 5% (5 holes) and c. 90% (multiple holes leaving only a small leaf-blade fragment attached to the petiole). The presence of each leaf was checked once every two months for 12 months.

Effect of damage on chlorophyll content

To examine if there was a compensatory response in leaves after they were damaged, a measure of the chlorophyll content of leaves was carried out using a portable chlorophyll meter (SPAD - 502, Minolta Camera Co. Ltd., Japan). The meter consists of a micro-spectrophotometer and uses light absorption to produce a relative measure of the amount of chlorophyll present in the leaf. Five readings were taken for each leaf and the mean calculated.

Two age-classes of leaf were examined on trees at Okuti Valley; new leaves at the tip of the stem and older leaves, one node further down the branch. For each age class, 15 leaves without insect damage and 15 with insect damage were assessed for chlorophyll content. The data collected were analysed using a balanced ANOVA to examine the effects of leaf age and the presence of damage on chlorophyll content.

To assess experimentally whether there was a response in leaf chlorophyll, five nursery-reared plants each had five leaves allocated to each of three damage treatments; five holes made with a hole punch, leaves damaged by pressing them into a metal file and a no-damage control. Each leaf was individually labelled as above. The chlorophyll content was measured prior to damage, three days after damaging the leaves (to investigate short-term responses) and one month after damage (to investigate the longer term response). Data

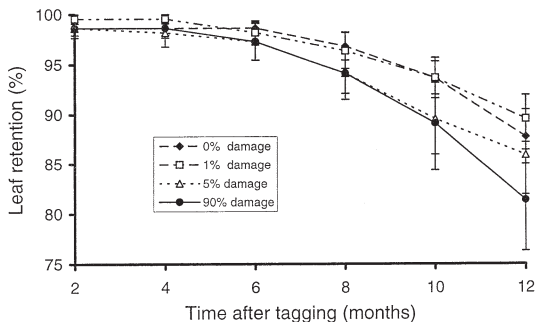


Figure 1. The pattern of leaf retention in kawakawa after different levels of simulated herbivory were made using a mechanical hole-punch. Vertical bars are two standard errors.

were analysed using a repeated-measures ANOVA to examine differences in chlorophyll content between plants, treatments and the interaction between treatment and sampling occasion.

Results

Effect of damage on leaf loss

In the first experiment, only three of the 114 labelled leaves had been lost (two in the hole-punch treatment and one where leaf damage was caused by *C. scriptaria* larvae) after 60 days. Therefore, artificial damage or damage by the *C. scriptaria* larvae did not induce abscission of new leaves over this period.

In the second experiment, there was a gradual loss of leaves over the twelve-month monitoring period, but leaf retention rates remained generally high (Figure 1; mean leaf retention \pm SE = $86.1\% \pm 0.37$; $N = 44$). Although leaves with the greatest damage were, on average, shed slightly sooner than those of the controls, the number of leaves retained by trees in the different damage treatments was not significantly different after 12 months ($F_{3,40} = 0.75$, $P > 0.50$).

Effect of damage on chlorophyll content

For field trees, although the older leaves had a higher chlorophyll content than the young ones (mean \pm S.E. for relative light absorption: old leaves, 40.0 ± 0.7 ; young leaves, 35.5 ± 1.0 ; $F_{1,56} = 14.4$, $P < 0.001$), there was no significant difference between the grazed leaves and the undamaged leaves in each age class ($P > 0.05$).

In the nursery-reared kawakawa, there were no differences in the chlorophyll content of leaves on different plants or between sampling occasions. Damaging the leaves with a hole punch or a file did not

induce a significant change in chlorophyll content (mean \pm S.E. for relative light absorption: control, 42.0 ± 1.0 ; holes, 43.0 ± 1.3 ; file, 39.3 ± 1.3 ; $F_{2,66} = 1.12$, $P > 0.30$).

Discussion

In some species of plants there is a direct relationship between leaf abscission and the extent of leaf damage (Simberloff and Stiling, 1987). However, in this investigation leaf abscission in kawakawa was not influenced by natural or artificial damage nor was it related to the extent of artificial damage. This supports the findings of Hodge *et al.* (1998) who reported no difference in the average rates of leaf loss between trees with high levels of insect herbivory, compared with those with low grazing levels.

The high retention of leaves in these experiments differs from the suggestion made in Hodge *et al.* (1998) that young leaves are shed relatively rapidly. Their suggestion arose from using a 'static' image of the foliage age-profile as a 'life-table' to derive the dynamics of leaf survival. The kawakawa foliage they examined was dominated by young leaves and it was suggested that to maintain this age-class distribution many of the young leaves must be shed before each stem produced even younger foliage. However, as the results of the current investigation indicate that new leaves are not shed rapidly, we believe that the age-class profile of the foliage is produced by the pattern of leaf production, rather than a mechanism based on leaf loss. New leaves are borne in pairs, so are twice as abundant as the previous leaf cohort. This produces a foliage age-profile which is dominated by young leaves with a geometric halving in leaf frequency with age-class [Frequency = $(0.5)^{\text{age} \times 1.059}$; based on data in Hodge *et al.*, 1998].

It can be speculated that the *C. scriptaria* / kawakawa system is one of coevolved tolerance. *C. scriptaria* is the primary insect herbivore on this plant and seems able to tolerate the various anti-insect compounds in kawakawa tissue (Russell and Fenemore, 1973; Nishida *et al.*, 1983; Russell and Lane, 1993; Hodge *et al.*, 1998). The plant does not compensate for a decrease in photosynthetic capacity due to a loss in leaf area by increasing the chlorophyll content of the remaining leaf tissue and it appears able to function

adequately with consistent and regularly distributed damage to its leaves (see also Baird, 1983).

Acknowledgements

We would like to thank Mandy Barron, Nadine Berry, Nancy Clarkson, Kay Cocker, Vanessa Hepplethwaite, Linda Hills, Janna Kirchoff, Beverly Smith, Mick Whittle and Cor Vink for helping with field work. Thanks to Chris Frampton for his advice on statistical and mathematical issues. The British Ecological Society (Small Project Grant No. 1504) provided funding for this project.

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