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HERBIVORE DAMAGE AND LEAF LOSS IN THE NEW ZEALAND PEPPER TREE (‘KAWAKAWA’; *MACROPIPER EXCELSUM*; PIPERACEAE)

Summary: The pattern of herbivore damage on the New Zealand pepper tree (kawakawa; *Macropiper excelsum*) caused by its main insect herbivore (*Cleora scriptaria*) was investigated in the field and laboratory. In the field, only a small proportion of kawakawa leaves had no herbivore damage and *C. scriptaria* typically produced a number of small holes in each leaf. Leaves were shed at a rapid rate but leaf shedding was not increased by higher levels of herbivore damage. Some older leaves had less damage than would be expected for their age, possibly suggesting some variation in leaf susceptibility to herbivory. The effect of previous leaf damage on subsequent herbivory was examined in the field and laboratory. On no occasion did artificial leaf damage, or herbivory by larvae of the same or another species, affect the edibility of leaves to *C. scriptaria*. The results suggest that leaf shedding by kawakawa was not primarily a response to herbivore damage and induced defences against herbivores could not be demonstrated in this system.

Keywords: *Cleora scriptaria*; Geometridae; *Macropiper excelsum*; Piperaceae; kawakawa; herbivory; induced defences; abscission, insect-plant interaction.

Introduction

Kawakawa (the New Zealand pepper tree; *Macropiper excelsum* (Forst. f.) Miq.) is a small tree, usually between 1 and 3 m in height. It is commonly found in the sub-canopy of New Zealand coastal forests, scrub and damp mixed bush (Smith, 1975). The species has a narrow geographic range, occurring only in New Zealand and a few surrounding islands (Smith, 1975).

Kawakawa is a member of the Piperaceae - a family which is known to contain a number of bioactive chemicals - and possesses a range of anti-insect properties. Burning leaves emit a toxic fume and this was used by Maori to protect crops from insect pests (Brooker *et al.*, 1987). Leaf material is toxic to house-fly (*Musca domestica* L.) larvae (Russell *et al.*, 1972) and a leaf extract deters feeding in some insects (Russell and Lane, 1993). Novel lignins and substances mimicking the action of insect juvenile hormones occur in the leaves and these may also have an insecticidal effect (Russell and Fenimore, 1973; Nishida *et al.*, 1983; see also Bowers, 1980).

Despite this potential complex of ‘defences’, the leaves of kawakawa are conspicuously grazed by larvae of a geometrid moth, *Cleora scriptaria* (Walker). This herbivore commonly produces a large number of holes in most leaves, and these holes are ubiquitous enough for this character to have been

suggested as a diagnostic feature of the plant (Beever, 1987). Although *C. scriptaria* feeds on some other host plants (Spiller and Wise, 1982) and kawakawa is host to a few other herbivore species (Spiller and Wise, 1982; Clare and Singh, 1988), kawakawa is the primary host plant of *C. scriptaria* larvae (Hudson, 1928) and this herbivore is its main grazer.

This paper examines two processes by which the plant may lessen the effects of herbivore damage; leaf shedding and wound-induced chemical responses. Preliminary observations have indicated that kawakawa trees may shed leaves at a rapid rate. Although shedding leaves may reduce the photosynthetic capacity of the plant, shedding damaged leaves may be of an overall benefit by reducing levels of microbial infection and preventing depression of transpiration and photosynthesis in undamaged tissue (Grime, 1979; Addicott, 1982).

The holes in kawakawa appear to have a ‘regular’ spatial pattern and may fit a model of herbivory based on wound-induced plant defences (Edwards and Wratten, 1982; Edwards *et al.*, 1995). In these systems, it is hypothesized that herbivory induces the plant to produce antifeedant compounds which accumulate at the site of damage. The herbivore feeds until the concentration of these compounds becomes so high that the animal is forced to move away. This process produces a series of small, uniformly spaced, areas of damage such as those seen in the leaves of kawakawa.

This study examined the distribution of herbivore damage between kawakawa leaves, the relationship between leaf damage and leaf age and whether the rate of leaf shedding was related to the level of herbivory. The feeding responses of *C. scriptaria* larvae to leaves of different ages and to leaves that had had prior herbivore damage were examined.

Methods

Field sites

The main field site was an area of mixed native broadleaf-podocarp forest at Okuti Valley on the Banks Peninsula, South Island, New Zealand, at a latitude of 43°47'S (longitude 172°50'E), which is close to the southern limit of kawakawa distribution (Smith, 1975).

The other three sites used in the initial parts of this investigation were Flock House Agricultural Centre, Bulls (40°10'S, 175°23'E), Bledisloe Park in Palmerston North, (40°23' S, 175°36' E), on the North Island, and Scott's Beach, near Karamea (41°05' S, 172°06' E), on the South Island. These sites all consisted of areas of native forest where the understorey was dominated by kawakawa.

Age profile and herbivore damage in kawakawa leaves

To examine the age profile of extant leaves, the age-classes of all leaves on five trees in the Okuti Valley were recorded. Leaf age-classes were determined by classifying apical leaves at the tip of a branch as 1, the next leaf down the stem as 2, then 3 and so on. Although there will undoubtedly be a positive relationship between age-class and the real age of the leaf on each shoot, this method of designating leaf age-classes does not produce a linear relationship between class and absolute time, as the rate of leaf production may change throughout the year or from site to site. Observations by the authors suggest that new leaves tend to be synchronously produced on all the shoots of a particular tree, and within a localized area, at the same time. Thus, within a site at least, these leaf age-classes give a fair indication of the relative time the leaves have been exposed to herbivores.

At each of three field sites (Okuti Valley, Flock House & Scott's Beach), between twenty and thirty trees were selected at random. Each leaf up to 2 m above the ground was scored for herbivore damage, estimating by eye, to the nearest 5 %, the proportion of the leaf area removed. Each leaf was scored by two different people and the two values averaged.

To assess the relationship between herbivore damage and leaf age, leaves in age-classes 1 to 5 were assessed for damage in the Okuti Valley and at Bledisloe Park. Rather than use leaves randomly, a deliberate attempt was made to find large samples of leaves in each age-class at each site (*n* for each age class at each site ranged from 60 to 215).

The effect of herbivory on leaf damage and leaf loss

Sixteen randomly selected kawakawa trees in the Okuti Valley were sprayed to run-off with acephate (as Orthene, a systemic insecticide) up to a height of 2.5 m at the rate of 0.78 g active ingredient per litre. A further sixteen trees in the same plot of trees were assigned as controls and sprayed with water. Before spraying, all leaves on each tree were counted and the youngest leaves (age-class 1) were scored for herbivore damage. Spraying of the trees was repeated twice more, at 14 day intervals. Damage assessments were repeated after 50 and 130 days from the date of spraying.

The effect of leaf damage on subsequent herbivory in the field

Six leaves of the youngest age class were selected randomly on each of 20 kawakawa trees at Okuti Valley. The leaves were individually labelled using cardboard tags tied loosely onto the petiole. The six leaves from each tree were grouped into pairs and one pair of leaves from each tree was subjected to one of the following three treatments;

- i) Individual leaves were covered using a muslin bag (10.5 cm x 14 cm; with a mesh size of approximately 0.7 mm) which contained two *C. scriptaria* larvae (instar II/III). These larvae had been caught in the Okuti Valley and had been fed on kawakawa plants in the laboratory.
- ii) Four holes (4 mm diameter) were punched into the leaf which was then bagged.
- iii) The leaves were bagged undamaged.

Respectively, these treatments were to compare the effects of larval leaf damage, artificial damage and no damage on subsequent leaf herbivory. To minimise effects caused by regional induction of defences between leaves (Wratten *et al.*, 1984), each pair of leaves allocated to one treatment was separated from the others by being located on a different major shoot of the tree.

The bags and larvae were removed 48 h later - adequate time for the initial *C. scriptaria* larvae to damage the leaves sufficiently for any defence induction to occur - and the damage on the leaves

scored by eye. The leaves were then scored for additional herbivore damage at intervals (see results) over the following two months.

The effect of leaf damage in the field on subsequent herbivory by *C. scriptaria* in the laboratory

A bioassay was carried out to investigate the effect of damage on subsequent feeding by *C. scriptaria*. Leaves on trees in the Okuti Valley were assigned to one of the three ‘damage’ treatments described above for the field experiments. There was also a fourth treatment which used leaf roller larvae (*Ctenopseustis obliquana* (Walk.), obtained from Mount Albert Research Centre, Auckland, N.Z.) to damage leaves in the field. This was to assess whether feeding by another species of herbivore would influence subsequent feeding by *C. scriptaria*. The mesh bags and larvae were removed after 48 hours. The leaves were cut off the branch at the base of the petiole, stored between damp tissue paper inside an insulated polystyrene container and returned to the laboratory. The leaves were used in experiments within 4 hours of being removed from the trees.

The petiole of each leaf was wrapped in damp tissue paper and sealed with “Parafilm”. Leaves were placed abaxial side upwards in 9 cm diameter plastic Petri dishes with a moistened filter paper in the base. A single *C. scriptaria* larva was added to each dish and the dish inverted so that the abaxial side of the leaf was above the larvae, mimicking the feeding position of *C. scriptaria* in nature. The Petri dishes were kept in a darkened room and maintained at room temperature and humidity. Initially 10 replicates per treatment were set up but this was reduced to between 5 and 7 replicates per treatment as some larvae did not create any initial damage and some *C. scriptaria* larvae died before the assay was completed.

Damage by *C. scriptaria* larvae was monitored over four days. Leaves were photocopied and the leaf area eaten by the caterpillars was measured using a video image analysis package [Joyce Loebble Magiscan, Version 4.6, Applied Imaging, U.K.].

The effect of leaf age on subsequent herbivory by *C. scriptaria* larvae in the laboratory

Eight age-class 1 and eight age-class 2 leaves were collected from kawakawa trees at the Okuti Valley field site. The leaves were returned to the laboratory and an assay set up to assess any differences in *C. scriptaria* feeding rates on ‘old’ and ‘young’ leaves. Damage caused by the larvae was monitored over six days by taking photocopies of the leaves once every 24 h. The leaf area which had been removed

by the larvae was measured by using a grid (divided into 1 mm² squares) printed on a transparent plastic sheet.

Statistical analysis

All proportional leaf damage data were arcsine square-root transformed before analysis. Individual trees were used as replicates to help control for the inherent variation in susceptibility between trees to herbivores (Fowler and Lawton, 1985; Neuvonen and Haukioja, 1985; Wagner, 1988). To avoid ‘pseudoreplication’, data from leaves on the same plant from the same experimental treatment were averaged and the averages used as replicates.

Data were analysed using repeated measure analyses of variance (von Ende, 1993) using SYSTAT (Version 5.2, Evanston, Illinois, USA). The variables measured in many of these investigations (such as leaf damage and leaf loss) are expected to change over time. Therefore, the important component in these analyses is the interaction between time and treatment and this term is presented in the Results.

Results

Age profile and herbivore damage in kawakawa leaves

Young leaves dominated the kawakawa foliage (Figure 1). The loss of leaves was rapid with approximately half the leaves being lost before they reached age-class 2 and only 4.4 % of leaves were found to be age-class 5 or over.

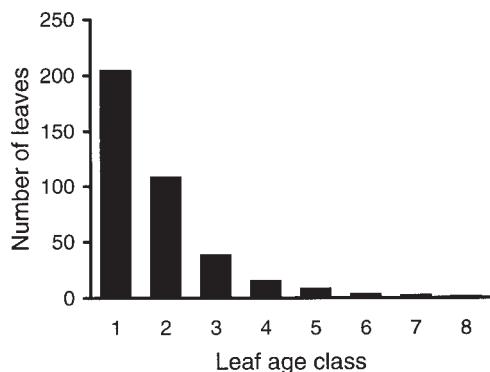


Figure 1: The age profile of leaves on kawakawa trees at Okuti Valley. Age-class is designated by position of leaf down the stem; leaves at the tip of the stem being designated as age-class 1, the next leaf down stem as age-class 2 and so on.

The trees at the three sites showed similar patterns of leaf damage (Figure 2). Almost all leaves had at least a small amount of herbivore damage. The most frequent damage class was 1-5 % of leaf area missing, with the frequency of subsequent categories decreasing steadily. Very few leaves (3.1 % overall) had no damage.

It might be expected that, if feeding by caterpillars and leaf-shedding was random, that the older leaves would have the highest levels of damage simply because they had been exposed to herbivores for a longer time. However, this was not the case (Figure 3). The few leaves that persisted to reach age-class 5 were less damaged than those in age-classes 3 and 4 (polynomial relationships between leaf damage with age; Okuti Valley: mean damage = $3.1 \text{ age}^2 + 20.6 \text{ age} - 5.8$, $r^2 = 0.94$; Bledisloe Park: mean damage = $4.0 \text{ age}^2 + 27.9 \text{ age} - 6.5$, $r^2 = 0.99$). This result suggests that older leaves with high levels of damage are being shed more frequently than older leaves with low levels of damage, and thus the average damage for age-class 5 leaves is lower than that of the previous age class.

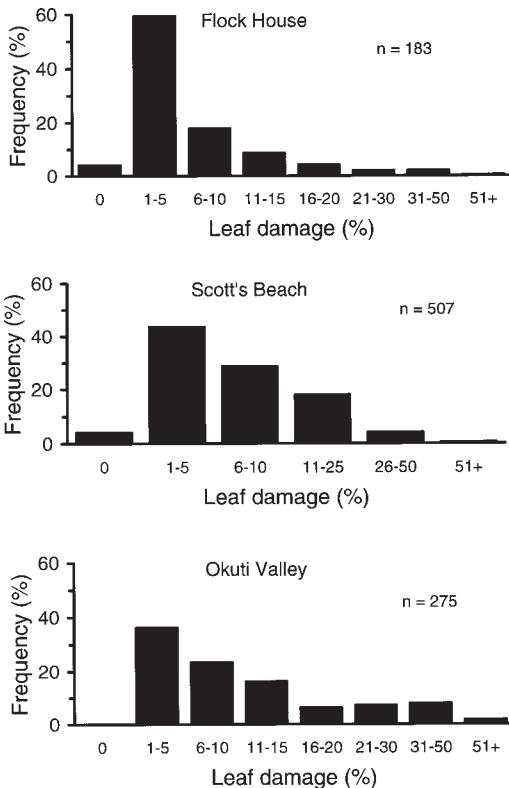


Figure 2: The frequency distribution of herbivore damage found on kawakawa leaves (to 2m in height) at three sites.

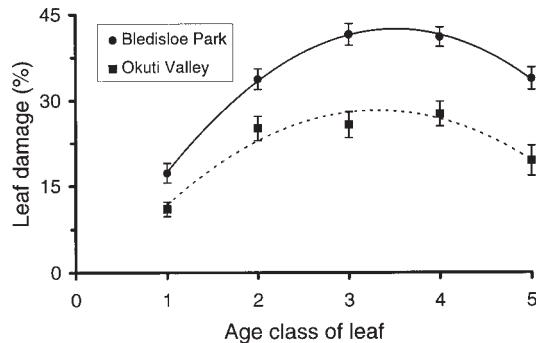


Figure 3: The distribution of leaf damage (mean \pm s.e.) on kawakawa leaves in different age-classes on trees at Bledisloe Park and Okuti Valley.

The effect of herbivory on leaf damage and leaf loss

This experiment examined the effect of spraying kawakawa trees with insecticide on subsequent herbivore damage and leaf loss. The control trees (sprayed with water) showed a greater increase in herbivore damage, to around 12 % of leaf area after 130 days, than did those sprayed with insecticide (5%) (Figure 4; treatment x time, $F_{1,30}=6.4$, $P<0.02$). This result confirms that the pesticide did prevent most herbivore damage as intended.

There was no significant difference between the proportion of the initial cohort of leaves shed from the trees sprayed with insecticide and those shed from the control trees (Figure 5; treatment x time, $F_{1,30}=1.77$, $P>0.15$). In both cases around 50 % of leaves had been lost after 130 days. Therefore, although the average level of leaf damage was higher on trees exposed to herbivores, the rate of leaf-loss did not differ.

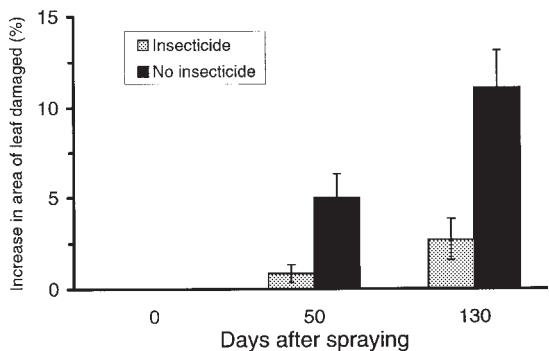


Figure 4: The effect of pesticide application on levels of leaf damage (mean \pm s.e.) found on kawakawa trees at Okuti Valley.

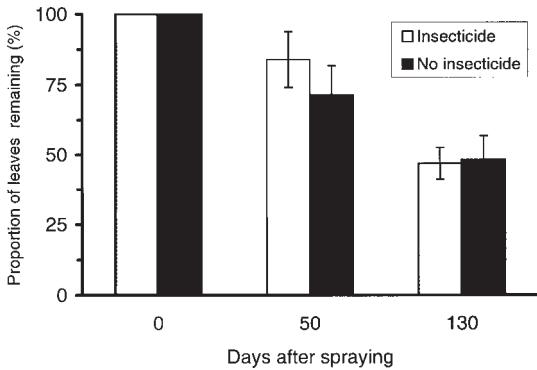


Figure 5: The effect of pesticide application on the proportion of leaves lost on kawakawa trees (mean ± s.e.) at Okuti Valley.

The effect of leaf damage on subsequent herbivory in the field

This experiment examined how herbivory was affected by previous damage to the leaves. The levels of herbivory in the field increased steadily over the study period but even after two months the average damage per leaf remained low (5 %) (Figure 6). A repeated measures ANOVA indicated that treatments differed (treatment x time, $F_{8,212}=2.12, P<0.05$) but the highest levels of subsequent damage occurred on leaves previously damaged by *C. scriptaria*. This counters the hypothesis that prior feeding, or artificial damage, induces effective ‘defences’ against this herbivore.

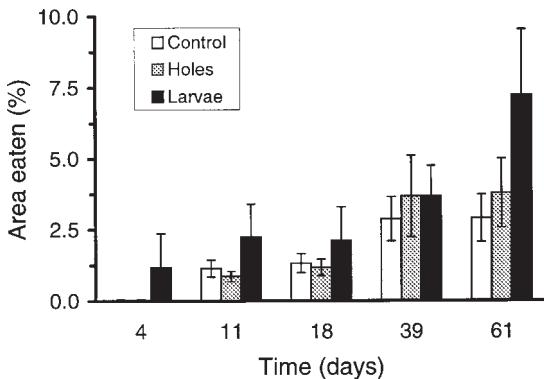


Figure 6: The effect of herbivore and mechanical leaf damage on subsequent naturally-occurring herbivory (proportion of leaf area eaten; mean ± s.e.) in the Okuti Valley.

The effect of leaf damage in the field on subsequent herbivory by *C. scriptaria* in the laboratory

This experiment examined how the amount of leaf material consumed by *C. scriptaria* larvae in the laboratory was affected by previous damage to the leaves caused by *C. scriptaria*, *C. obliquana* and a hole punch. Average levels of feeding damage were higher in the laboratory after only four days (~20 %) than those seen in the field after 2 months (Figure 7). This was presumably due to the higher density of the larvae per leaf in the laboratory (*pers. obs.* 1 larvae per leaf is much higher than densities seen in the field) and also because the larvae could not move between leaves. Feeding rates of *C. scriptaria* did not differ between damage treatments (treatment x time, $F_{6,40}=0.43, P>0.85$), indicating that the palatability of the leaves was not affected by artificial damage or previous herbivory by the same or another species of lepidopteran larvae.

The effect of leaf age on subsequent herbivory by *C. scriptaria* larvae in the laboratory

This experiment examined how the amount of leaf material consumed by *C. scriptaria* larvae was affected by the age of the leaf (age-class 1 or age class 2). Initially, it appeared that the younger leaves were more palatable than the older leaves (Figure 8a; treatment x time, $F_{5,70}=5.69, P<0.001$). However, this result was based on the proportion of leaf eaten and the difference was caused by the older leaves being systematically larger than the young leaves. When the actual amount of leaf tissue eaten was considered, this pattern disappeared (Figure 8b; treatment x time, $F_{5,70}=0.21, P>0.95$), suggesting that the older leaves were equally as palatable as young leaves.

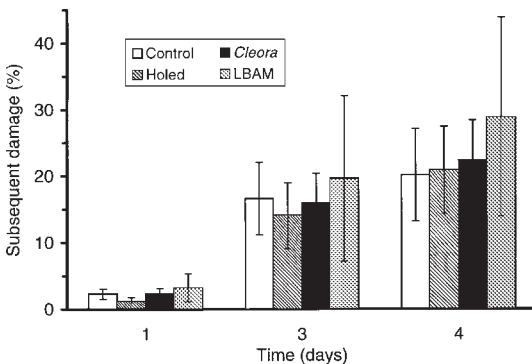


Figure 7: The effect of herbivore and mechanical leaf damage on the amount of leaf subsequently consumed (proportion of leaf area eaten; mean ± s.e.) by *C. scriptaria* larvae in the laboratory.

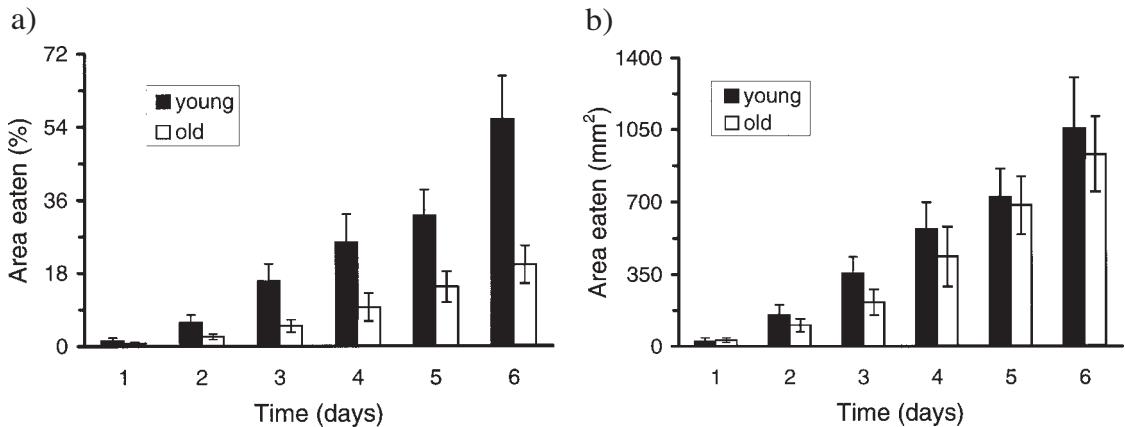


Figure 8: The effect of leaf age on the amount of leaf subsequently consumed (mean \pm s.e.) by a single *C. scriptaria* larva in the laboratory; (a) proportion of leaf eaten (b) actual area of leaf eaten.

Discussion

The results obtained from our study generate a far from clear picture regarding the roles of leaf-shedding and the induction of antifeedant compounds as plant defences in this system. Although observational evidence suggested that kawakawa may preferentially shed damaged leaves and that the feeding pattern of *C. scriptaria* could be dictated by induced defences, none of our experimental work supported these hypotheses.

The low leaf survivorship in kawakawa initially appears counter-intuitive as it can be envisaged that plants in shady, sub-canopy locations, would benefit from retaining their leaves. However, this rapid loss of leaves may be a compromise by the plant to restrict the damaging effects of herbivory (Grime, 1979). In some species of plant there is a direct relationship between leaf abscission and leaf damage (Simberloff and Stiling, 1987) but this appeared not to be the case for kawakawa. It is possible that the occurrence of leaf damage is so consistent in kawakawa (only 3% of leaves had no damage) that most leaves which are shed would have suffered herbivory to some extent. Shedding this high proportion of leaves appears not to inhibit the plant and even an 80% loss of foliage does not cause mortality in kawakawa (Baird, 1983). The plant may benefit from this leaf shedding by lowering the incidence of microbial infection via leaf wounds and preventing induced stresses in undamaged tissue (Addicott, 1982).

Although we found no relationship between leaf damage and leaf loss at a tree level, the pattern of leaf-shedding appeared not to be completely random

in older leaves. The average damage per leaf stabilised and then fell as the leaves aged, even though the laboratory assay indicated that slightly older leaves were as palatable as young leaves. It would appear that, at least in older leaves, the tree sheds those leaves with the highest damage so that the average level of damage on the surviving leaves decreases.

There are at least two alternative mechanisms by which these remaining older leaves had lower than expected levels of damage for their age. Firstly, if the movement of *C. scriptaria* larvae between leaves is random, some leaves would be missed simply by chance. The second alternative is that some leaves are innately less susceptible to herbivory than others (see also Schultz *et al.*, 1982). Certain leaves may have higher levels of constitutive defence compounds (Levin, 1976) or they may have stronger induced defences (Wagner, 1988). Also, the architecture of the tree may influence the foraging patterns of larvae to an extent that some leaves are missed (Lawton, 1983). Although these persistent old leaves make up only a small proportion of the foliage of the tree, abscission of leaves in kawakawa needs further study; the fate of individually-marked leaves needs to be examined, as do the mechanisms governing why some leaves are less prone to herbivory than others.

Wound-induced defences in kawakawa remain undemonstrated. The regular distribution of damage within and between leaves suggests that the larvae feed for short periods and then move, as shown by Barker *et al.*, (1995) to be the case for insect herbivores of tomatoes. However, assays in the field and the laboratory suggest that kawakawa leaf tissue was not rendered less acceptable by previous

herbivore feeding or artificial damage. The patchy feeding pattern of *C. scriptaria* in the field may result from processes other than induced defences (see Fowler and Lawton, 1985; Slansky, 1993). Feeding bouts may be interrupted because of a need to digest plant material (Reynolds, 1990) or in order for the caterpillar to detoxify (or sequester) toxic substances (Slansky, 1992). Avoiding predators (e.g., birds) which use irregular leaf damage as prey location cues may involve frequent movement between leaves (e.g., Hassell and Southwood, 1978; Heinrich and Collins, 1983). However, this does not take into account caterpillars moving to already-damaged leaves, a process which undoubtedly occurs as damage levels accumulate. Overdispersion of larvae could arise because females distribute their eggs uniformly between leaves to avoid subsequent inhibitory effects between sibling conspecifics (Fowler and Lawton, 1985). This is probably not the case for *C. scriptaria* as females lay their eggs in clusters of 3 - 12 (Hudson, 1928). Alternatively, the feeding behaviour of *C. scriptaria* may be a legacy from having evolved to cope with the defences of an earlier host species. Determining which of these mechanisms actually contribute to the production of the spatial feeding pattern of *C. scriptaria* requires further work.

Induced defences in plants are common but are by no means universal (Chapin *et al.*, 1985; Fowler and Lawton, 1985; Wagner, 1988 and references therein) and it is possible that kawakawa lacks such a system. Most examples of induced defences in insect-plant interactions involve polyphagous herbivores, whereas *C. scriptaria* is virtually monophagous on kawakawa. There is also a possibility that the local ('within leaf') induction examined in our experiments has been over-riden by regional induction of defences over the whole plant. In our experiments, all the leaves for the field and laboratory feeding assays were taken from trees which had suffered some feeding damage. It has been assumed that no induction occurred between leaves and between stems but if these induction processes did occur (as in birch, *Betula* spp. see Wratten *et al.*, 1984) then there were no true 'undamaged' controls (Fowler and Lawton, 1985; Neuvonen and Haukioja, 1985). A further problem is that our laboratory assays did not give the larvae a feeding choice. So although the leaves remained equally acceptable after damage the assays gave no indication of whether the palatability or 'taste' of the leaves had been altered and whether the larvae would have moved on to another leaf given the freedom to do so (Russell and Lane, 1993). Work is planned which takes into account local as well as regional induction of plant defences and will examine movement of the larvae between leaves and

between plants. If induced chemical changes in kawakawa foliage do occur, their effects on *C. scriptaria* may be limited to a behavioural response in the larvae rather than profound consequences on its population dynamics (Fowler and Lawton, 1985).

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