

Effects of forest edges on herbivory in a New Zealand mistletoe, *Alepis flavida*

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Abstract: This study examined how forest edges influenced leaf and floral herbivory, as well as seed predation, in a native New Zealand mistletoe species, *Alepis flavida*. Plants growing on forest edges and in forest interior were compared, and effects of plant size and the neighbouring conspecific plant community were also examined. Leaf herbivory by possums was significantly greater on forest edges than in forest interior in a year of high possum damage, but not in a year with low damage levels. Insect leaf herbivory did not differ between forest edges and interior. Although equal numbers of plants on edges v. interior experienced some floral damage by a specialist caterpillar, there were significantly higher levels of damage on plants growing in the forest interior than on forest edges. Plants with floral damage were larger than plants without damage, and distance to neighbouring mistletoe plants was positively correlated with amount of floral damage, but only for plants in the interior. Significantly greater numbers of plants on edges than in the interior exhibited seed predation by the same specialist caterpillar that caused floral damage, suggesting greater fruit abortion rates in the interior. Amounts of seed damage were inversely correlated with plant size. Forest edges had much stronger effects on leaf herbivory by possums, as well as floral herbivory and seed predation, than did plant size or the neighbouring plant community.

Keywords: *Alepis flavida*; edge effect; floral herbivory; forest fragmentation; leaf herbivory; mistletoe; possum; seed predation; *Trichosurus vulpecula*.

Introduction

Habitat fragmentation is one of the most pressing conservation problems today, and recent studies have shown "edge effects" for a variety of animal (Carvalho and Vasconcelos, 1999; Kremsater and Bunnell, 1999; Davies *et al.*, 2000; Vallan, 2000) and plant species (Laurance *et al.*, 1998; Gehlhausen *et al.*, 2000). Forest edge and forest interior differ in microclimate and in the availability of resources, both of which influence plant reproduction (Laurance *et al.*, 1998; Sizer and Tanner, 1999). Forest edges can also alter important animal-plant interactions, which have the potential to strongly influence plant fitness. These interactions include mutualistic ones with animal pollinators (Aizen and Feinsinger, 1994; Jules and Rathcke, 1999; Kelly *et al.*, 2000; Kremen and Ricketts, 2000) or seed dispersers (Restrepo *et al.*, 1999; Dale *et al.*, 2000), as well as negative interactions with herbivores. Few studies have examined whether rates of herbivory vary in forest edges and interior, although insect seed predators have been shown to respond to habitat fragmentation (Burkey, 1994; Cunningham, 2000).

Edge effects can potentially influence herbivory via a number of different mechanisms. Population densities of herbivores could differ on edge v. interior habitats. Edges could also influence herbivory indirectly by altering other parameters that affect herbivory, such as host-plant size or the neighbouring plant community. Larger host plants often suffer higher rates of herbivory (Masumoto *et al.*, 2000; Bach, 2001), but it is not clear whether effects of plant size vary consistently between habitat edges and habitat interiors. Neighbouring plants can dramatically influence rates of herbivory, in terms of the density of conspecific neighbours as well as host plant patch size, both for folivores (Masumoto *et al.*, 2000; Frid and Turkington, 2001) and seed predators (Jennersten and Nilsson, 1993; Bigger, 1999). These effects of the neighbouring plant community could vary on forest edges v. interior.

One might also expect very different edge effects as a function of the type of herbivore and type of plant part being consumed. Insect and mammalian herbivores often show different effects on plants (Gibson *et al.*, 1987; Palmisano and Fox, 1997; Sessions and Kelly, 2001), although some studies report consistent effects

of insect and mammalian herbivores (Schierenbeck *et al.*, 1994). Most studies of herbivory tend to focus on one type of herbivory: leaf herbivory, floral herbivory, or seed predation. In the few studies that have examined several types of herbivory, leaf herbivory is not always correlated with floral herbivory (Mothershead and Marquis, 2000), or with seed predation (Howe and Brown, 1999).

The purpose of this study was to investigate how forest edges influence patterns of herbivory in the native New Zealand mistletoe, *Alepis flavida*. Populations of the seven native species of mistletoes are declining (de Lange and Norton, 1997). Six of the species, including *A. flavida*, are officially categorized as "threatened" (Norton and Reid, 1997). Few studies have investigated how mistletoes are influenced by edge effects, but Bach and Kelly (2004) found that rates of seed dispersal of *A. flavida* did not differ on forest edge and in forest interior. In studies of forest fragment size, Kelly *et al.* (2000) and Montgomery *et al.* (2003) found that smaller forest fragments had improved reproduction in the New Zealand mistletoe, *Peraxilla tetrapetala*, because flower predation decreased and pollination success increased in more fragmented habitats and/or on forest edges.

This study addressed three specific questions: (1) How do amounts of herbivory on *Alepis flavida* vary on forest edges and in forest interior?, (2) How do plant neighbours of *A. flavida* and/or plant size influence amounts of herbivory?, and more importantly, (3) Do effects of neighbours and/or plant size vary on forest edges and in forest interior (i.e. are there interactive effects?). Three aspects of herbivory were investigated: leaf herbivory (by insects and mammals), floral herbivory, and seed predation.

Methods

The system

The mistletoe, *Alepis flavida* (Loranthaceae), has been reported on nine indigenous host species in New Zealand. However, *A. flavida* is the most host-specific of all the New Zealand mistletoes, with over 80% of host records from *Nothofagus solandri* (Norton, 1997). *Alepis flavida* has a variety of leaf herbivores, including lepidopterans, scale insects, thrips, mealybugs, stick insects and weevils (de Lange, 1997). A closely-related mistletoe species, *Peraxilla tetrapetala*, has a specialist leaf miner, *Zelleria maculata* (Patrick and Dugdale, 1997), that also appears to feed on *Alepis flavida*. The introduced Australian brushtail possum, *Trichosurus vulpecula*, is an important herbivore of some New Zealand mistletoes, and potentially one of the causes of mistletoe decline (de Lange and Norton, 1997). Possums prefer *A. flavida* to other mistletoe

species (Sessions and Kelly, 2001), and possum control benefits several species of mistletoes, including *A. flavida* (Sessions *et al.*, 2001).

Flowering in *A. flavida* occurs from January to February, and a lepidopteran causes significant damage to flower buds. In the closely-related mistletoe species, *Peraxilla tetrapetala*, the same specialist caterpillar that mines leaves in early instars (*Z. maculata*), eats the reproductive parts of the flowers in later instars (Patrick and Dugdale, 1997), and our collections of caterpillars from *A. flavida* flowers indicate that this same insect is the species causing the floral herbivory in *A. flavida*. In the past, two species of *Zelleria* have been reported on New Zealand mistletoes, *Z. maculata* and *Z. sphenota* (Patrick and Dugdale, 1997). However, current research now suggests that there may be a single taxon of *Zelleria* in New Zealand, which should now be referred to as *Zelleria* spp. *sphenota* group (Dugdale, *pers. comm.*); thus, throughout this paper, the floral herbivore will be referred to as *Zelleria*. In *Peraxilla tetrapetala*, flower predation by *Zelleria* damaged up to 48% of the flowers on a plant (Kelly *et al.*, 2000). Although birds are essential pollinators of flowers of related mistletoes in New Zealand (Robertson *et al.*, 1999), *Alepis flavida* can autonomously self-pollinate, and thus does not require birds for pollination (Ladley *et al.*, 1997). Although *A. flavida* has not been found to be pollen-limited (Ladley *et al.*, 1997), no information is available on possible inbreeding depression.

Fruiting in *Alepis flavida* occurs from March to May (Kelly *et al.*, 2004). Fruits are fleshy with single seeds and are dispersed by several native New Zealand honeyeaters (Aves: Meliphagidae). Seedling recruitment is absolutely dependent on bird dispersal, because birds must remove the fruit flesh during gut passage for seed germination to occur (Ladley and Kelly, 1996). *Alepis flavida* also exhibits seed damage, and it is likely this damage to seeds is caused by the same insect that is responsible for flower predation, *Zelleria* (Dugdale, *pers. comm.*). *Zelleria sphenota* has been reported to feed on immature fruits of a closely related mistletoe species, *Ileostylus micranthus* (Sullivan *et al.*, 1995). No other insect has ever been reported to cause seed damage to any of the New Zealand mistletoes (Dugdale, *pers. comm.*).

Amounts of herbivory

To examine the patterns by which forest edges influence herbivory, a field experiment was conducted at Jacks Pass (43° 09'S, 171° 43'E, elevation 940 m) in Craigieburn Forest Park, South Island, New Zealand. This site has been used for previous studies on mistletoes (Ladley and Kelly, 1996; Ladley *et al.*, 1997; Robertson *et al.*, 1999; Kelly *et al.*, 2004). At this site, the only host for *Alepis flavida* is *Nothofagus solandri* var. *cliffortioides*. To obtain an approximately equal number

of plants occurring on forest edges and in forest interior, we located six sites: three sites with plants occurring next to roads (henceforth designated as forest edge), and three sites with plants occurring in forest interior, which was defined as occurring at least 10 m (but in practice usually >50 m) from a road or opening (henceforth designated as forest interior). Thus, the six edge and interior sites were interspersed throughout the study site, which is completely forested except for the roads. At each site, we chose 9 or 10 study plants that could be reached without a ladder. The study included a total of 30 "edge" plants and 28 "interior" plants varying in neighbouring plant densities, from fairly isolated individuals to plants with a number of close neighbours of *A. flavida*. Because the sites were interspersed, some plants were closer to plants at other sites than to plants at their own site, so we did not include site as a block effect in the analyses.

All *A. flavida* plants were tagged on 10 January 1998. Flowers and fruits were counted over a 5-month period between 17 January and 9 June, as part of a study of seed dispersal rates (Bach and Kelly, 2004). Floral herbivory was assessed on 23 January and 1 February, by recording the number of undamaged and damaged flowers. Damaged flowers had brown spots, showed evidence of caterpillar feeding damage (holes), and often had silk present. Seed predation was assessed on five dates (8, 15, and 30 April, and 12 and 31 May) by recording the number of undamaged and damaged fruits. For young fruits, seed predation could be easily distinguished by the presence of a large number of characteristic brown spots on fruits. Older fruits with seed predation were often oblong in shape (rather than round as for normal fruits), shrivelled, and possessed a sticky substance and/or frass on the outside of the fruit.

To confirm that the designation of seed predator fruit, based on outward fruit appearance, is an accurate predictor of actual seed damage, collections of fruits were made on 8 April 1998. Both ripe and unripe fruits in each of four categories were collected: (1) perfect fruits ($n = 23$ ripe and 5 unripe), (2) fruits with one small brown spot ($n = 32$ ripe and 8 unripe), (3) fruits with one large brown spot ($n = 45$ ripe), and (4) fruits categorized as having seed predator damage (i.e. with a large number of characteristic brown spots and/or shriveled; $n = 24$ ripe and 9 unripe). The single seed present in each fruit was extracted and scored into one of three damage categories: (1) seed with no damage, (2) seed with feeding damage present, and (3) seed completely consumed. All perfect fruits and all fruits with a small brown spot contained only seeds with no visible feeding damage. Of the ripe fruits with a large brown spot, 44 out of 45 seeds had no damage and one seed had a small amount of damage. In contrast, 21 out

of 24 seeds in ripe fruits categorized as having seed predation were damaged ($n = 13$ seeds with feeding damage; $n = 8$ completely destroyed seeds), and all of the seeds in the 9 unripe "seed predator" fruits had feeding damage. Thus, these observations confirm that the external signs of seed predation used here are associated with actual damage to the seeds.

Estimates of amounts of leaf damage were taken from 23–25 March, using the following damage scale for each leaf: 0 = 0% leaf area removed, 1 = <5%, 2 = 5–24%, 3 = 25–49%, 4 = 50–74%, 5 = 75–99%, and 6 = 100% leaf area removed. Because *A. flavida* grows very slowly (Ladley and Kelly, 1996), this one-time measure of herbivory presumably provides a record of past herbivory over several years. In addition, qualitative estimates of the presence/absence of damage from brushtail possums (*Trichosurus vulpecula*) were made on 31 March. Possum damage was characterized both by observations of branches with all of their leaves missing (only the stem remaining) and large chew marks, which could not have been made by insects (Sessions and Kelly, 2001).

Amounts of possum damage were also assessed on 25 January 2003 using the same plants and the same methods as in 1998, for two reasons: (1) because amounts of possum damage were so low in 1998 (only 14% of plants had possum damage), and (2) a recent study has shown that the appearance of possum damage is only a short-term record because leaves with extensive possum damage abscise quickly (Sessions and Kelly, 2001).

Plant size and neighbour sampling

To determine whether herbivores might be responding to plant size, the total number of leaves was used as an index of plant size. This number was determined from the leaf herbivory estimates described above.

The methodology for sampling neighbouring plants involved locating the four closest plants of *Alepis flavida* to each study plant, constrained by a maximum search distance of 5 m (including vertically). For each of the neighbours that did not have fruits, we recorded data for the next closest neighbour of that species with fruits (always within 5 m of the study plant), yielding information on up to four additional neighbours for each individual. All plants with multiple stems were sampled, which excluded data on small, single-stemmed seedlings. For each neighbouring plant, the following information was recorded: (1) distance from study plant, (2) length, width, and height of each plant (to allow a calculation of volume, assuming that the shape of each plant was approximated by an ellipsoid, as in Norton *et al.*, 1997), and (3) presence or absence of fruits.

To determine whether herbivores and seed predators might be responding to size of neighbours

and/or proximity of neighbours, neighbour size (volume) and neighbour proximity (distance) were analyzed separately. Because the scale of neighbour effects can not be known beforehand, neighbour variables were analyzed at two different scales: the nearest neighbour (volume and distance), and the neighbouring community, which included the four closest neighbours within the 5 m sampling area (total volume and mean distance). Because these variables could only be analyzed in a valid statistical manner if all plants had four neighbours, the missing neighbours for each plant with less than four neighbours within 5 m were coded as having a volume of 0 and a distance of 5.1 m. Obviously, this distance is an underestimate, because the next closest neighbours may in fact have been much farther away. Throughout the paper, only analyses using the four nearest neighbours are presented, because the analyses using just the nearest neighbour showed exactly the same patterns.

These neighbour variables were calculated separately for: (1) analyses of herbivory, for which the four closest neighbours to each plant were used, and (2) analyses of floral herbivory and seed predation, for which the four flowering and fruiting closest neighbours to each plant were used. This distinction was made because if floral herbivores and seed predators were responding to the neighbouring plant community, they presumably would be responding only to neighbours that provided the resources they use (i.e. flowers and fruits).

Analysis of leaf herbivory

Effects of forest edges on possum herbivory were analyzed with χ^2 tests (for both 1998 and 2003). Effects of plant size and neighbour variables on possum herbivory were also analyzed for 2003 because of the higher amounts of possum damage (see Results). Mann-Whitney *U* tests were used to compare the plants with possum damage ($n = 20$) to the plants without possum damage ($n = 25$).

In order to remove potential confounding effects of possum herbivory, data on leaf herbivory by insects (1998) were analyzed only for the 50 plants without possum herbivory. Mean percentage leaf damage for each plant was calculated by multiplying the number of leaves with each of the 6 damage scores by the midpoint of the percent damage for that score, summing the values, and dividing by the number of leaves. These percentages were then converted to proportions, and arcsine transformed prior to analyses. For comparisons of edge and interior plants, Mann-Whitney *U* tests were used. Multiple, linear regressions were used to examine relationships between amount of leaf damage and plant size (number of leaves), neighbour distance, and neighbour size; these regressions were carried out separately for edge and interior plants. For

all analyses using plant size, one outlier data point was excluded; this plant was three times larger than all other plants, and its inclusion in the analyses would have invalidated the regressions.

Analysis of floral herbivory

Amounts of floral herbivory (number of damaged flowers/total number of flowers) were calculated for all plants for the two dates during which floral damage was assessed (23 Jan and 1 Feb 1998), and then averaged for analyses. Amounts were calculated based on the total number of flowers at the beginning of the flowering season on 17 January, rather than the number of flowers open on each date, because this date is the best estimate of flower availability during the time of *Zelleria* oviposition. To distinguish whether potential differences between habitats were caused by differences in the number of plants experiencing floral damage and/or the amount of damage on plants experiencing damage, two types of analyses were conducted to answer the following questions: (1) what factors influence which plants incur floral damage? and (2) on those plants with floral damage, what factors influence how much damage plants incur? To analyze the first question, plants were placed into two categories, depending on whether they experienced floral damage over the course of the study. The potential factors explaining which plants incurred floral herbivory were then examined using χ^2 tests to test for forest edge effects and Mann-Whitney *U* tests for plant size and neighbour variables. To analyze the second question, amounts of floral herbivory were analyzed for the subset of plants experiencing floral damage. The effect of forest edges on the amount of floral herbivory on those plants with floral damage was examined with a Mann-Whitney *U* test. Because edge and interior plants differed significantly in the amount of floral damage (see Results), separate multiple linear regressions for edge plants and interior plants were carried out to examine the effects of plant size and neighbour variables. It is important to note here that edge and interior plants did not significantly differ in plant size, neighbour distance, or neighbour size ($P > 0.05$ for all). All proportions were arcsine transformed prior to analysis.

Analysis of seed predation

Data on seed predation (number of fruits with seed predation/total number of fruits) were analyzed in a similar manner to those on floral herbivory. Plants were again categorized as to whether they ever incurred seed damage over the study. As with floral herbivory, amounts of seed predation were calculated out of the total number of fruits at the beginning of the fruiting season (1 March), rather than the number of fruits on each date, because fruits were continually being

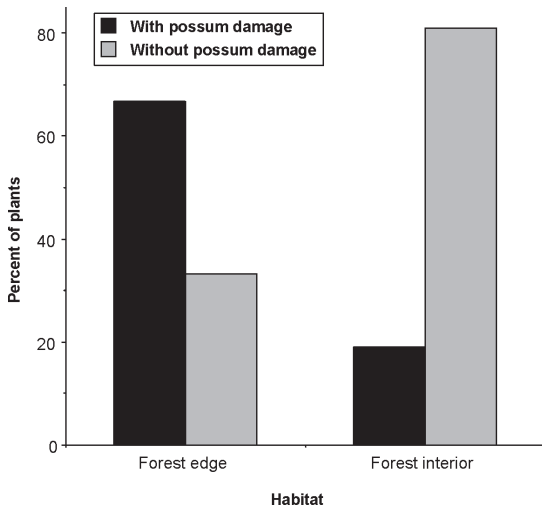


Figure 1. Percent of *Alepis flavida* plants with and without possum leaf damage in 2003 on forest edges ($n = 30$) and in forest interior ($n = 28$).

dispersed, which would result in over-estimates of amounts of seed predation. It is important to note, however, that these estimates of seed predation are underestimates if any fruit abortion is occurring. As for floral herbivory, factors influencing which plants incurred seed predation were analyzed first. Then, factors examining the amount of seed predation on those plants with seed damage were analyzed; mean amounts of seed damage were averaged for the two dates with the highest amounts of seed damage (8 and 15 April 1998).

Throughout the Results, means are presented with the standard error of the mean.

Results

Leaf herbivory by possums

Amounts of damage by possums did not differ between forest edge (4 out of 30 plants) and interior (4 out of 28 plants) for 1998 when only 14% of the plants were damaged by possums ($\chi^2 = 0.011$, d.f. = 1, $P = 0.92$). However, there was a highly significant effect of forest edges on possum damage in 2003 ($\chi^2 = 10.8$, d.f. = 1, $P = 0.001$), when amounts of possum damage were much higher (44%). Two-thirds of edge plants were damaged by possums, whereas less than 1/5 of interior plants had possum damage (Fig. 1). There was no difference in the sizes of plants damaged by possums v. undamaged ($U = 264.0$, $P = 0.41$). Plants with and

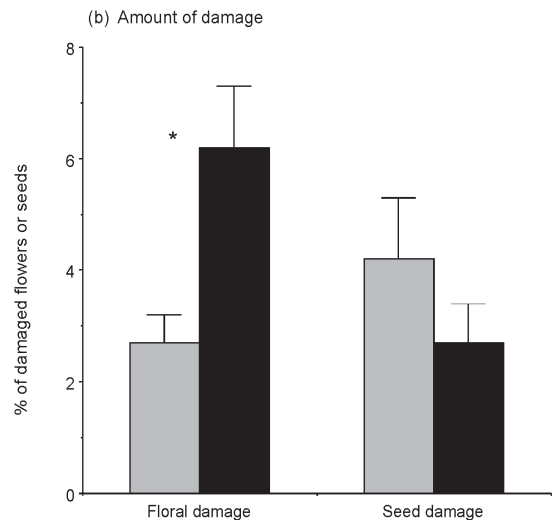
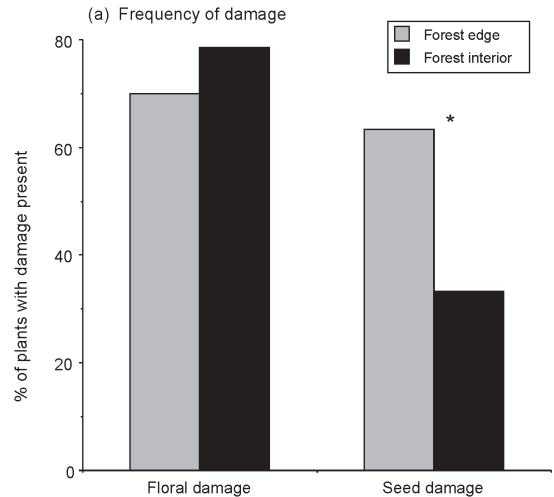


Figure 2. (a) Percent of plants with some floral damage or seed damage for *Alepis flavida* growing on forest edges and forest interior. Stars indicate a significant difference from a χ^2 test. (b) Percent of flowers or seeds damaged for *Alepis flavida* growing on forest edges and forest interior. Means and standard errors are presented for all plants with floral damage or seed damage. Stars indicate a significant difference from a Mann-Whitney U test.

without possum damage also did not differ in total neighbour size ($U = 244.0$, $P = 0.92$) or mean distance to the four closest neighbours ($U = 310.5$, $P = 0.097$).

Leaf herbivory by insects

Mean amounts of leaf damage by insects (proportion leaf area removed) did not differ between edge plants (mean = $5.2 \pm 0.7\%$ leaf area removed) and forest interior plants (mean = $4.7 \pm 0.6\%$ leaf area removed; $U = 342.0$, $P = 0.56$). There was no significant effect of plant size, neighbour size, or mean neighbour distance on mean damage levels, either for edge plants or interior plants ($P > 0.05$ for all factors in stepwise regressions).

Floral herbivory

Similar percentages of edge and interior plants exhibited some floral damage (Fig. 2a; $\chi^2 = 0.56$, d.f. = 1, $P = 0.46$). However, there was a very strong difference in the amount of floral herbivory that plants experienced on forest edges and in forest interior. For those plants with floral damage, interior plants had significantly higher amounts of damage than edge plants ($U =$

136.0, $P = 0.021$). Interior plants had more than twice as high a percentage of damaged flowers as did edge plants (Fig. 2b).

Plant size had a significant effect on which plants were chosen by floral herbivores ($U = 460.0$, $P = 0.009$). Plants that incurred floral damage averaged 58% more leaves (mean = 460.8 ± 33.4) than did plants without any floral damage (mean = 292.3 ± 36.8). The neighbouring plant community had no effect on which plants incurred floral damage, either in terms of total neighbour size ($U = 310.0$, $P = 0.82$) or mean neighbour distance ($U = 342.0$, $P = 0.73$).

Of the three potential factors influencing amounts of floral herbivory for those plants with damage, only the mean distance to the four closest neighbours explained a significant amount of variation, and this relationship was significant only for interior plants ($r^2 = 0.25$, $P = 0.017$). The farther away the neighbouring plants were in the interior, the greater the percentage of damaged flowers (Fig. 3). For edge plants, there was no relationship between neighbour distance and amount of floral damage ($r^2 = 0.00$, $P = 0.93$; Fig. 3). Neither plant size nor neighbour size were significant factors in explaining amounts of floral damage ($P > 0.05$ in stepwise regressions).

Seed predation

Patterns of seed predation on forest edges and interior were opposite to the patterns observed for floral herbivory. Almost twice as many edge plants experienced seed damage as did plants growing in forest interior ($\chi^2 = 5.20$, d.f. = 1, $P = 0.023$; Fig. 2a). In contrast, there was no difference in the amount of seed damage on plants with damage growing on the edge v. in the interior (Fig. 2b; $U = 88.0$, $P = 0.90$).

The greater percentage of edge plants than interior plants with seed damage is especially interesting, given that there was no difference in the proportion of edge v. interior plants that incurred floral damage. It appears that edge plants and interior plants are responding differently to the presence of floral herbivory, in terms of their tendency to abort fruits arising from damaged flowers. Of the edge plants with floral damage, over 80% also exhibited seed damage, whereas of the interior plants with floral damage, only 38% exhibited seed damage (Fig. 4), and this difference was significant ($\chi^2 = 8.3$, d.f. = 1, $P = 0.004$). There was no difference in the sizes of plants with floral damage that exhibited seed damage v. those that did not, either for edge plants ($U = 28.0$, $P = 0.59$) or for interior plants ($U = 71.0$, $P = 0.17$). However, of the interior plants with floral damage, plants that exhibited seed damage had significantly lower amounts of floral herbivory (mean = $3.1 \pm 0.6\%$ damaged flowers) than did plants that did not exhibit seed damage (mean = $8.5 \pm 1.5\%$ damaged flowers; $U = 19.0$, $P = 0.017$). It

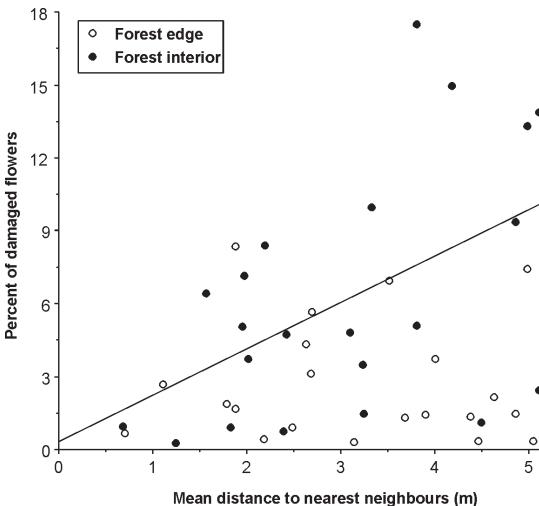


Figure 3. Relationship between percent of damaged flowers and mean distance to the four nearest neighbours (cm) for all *Alepis flavida* with floral damage. Data are presented separately for plants growing on forest edges (open circles) and forest interior (closed circles). The regression was not significant for plants growing on forest edges ($r^2 = 0.00$, $n = 21$, $P = 0.93$). The regression line for plants growing in the interior is: $y = 0.019x + 0.33$, $n = 22$ ($r^2 = 0.25$, $P = 0.017$).



Figure 4. Percent of *Alepis flavida* plants with floral damage that did and did not exhibit seed damage. Percents are presented separately for plants growing on forest edges ($n = 21$) and forest interior ($n = 21$).

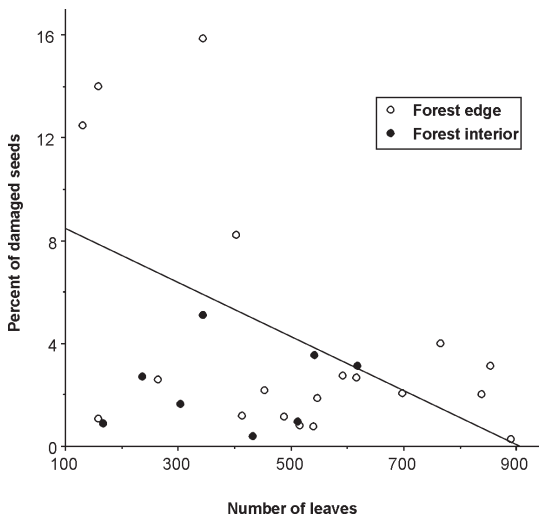


Figure 5. Relationship between percent of damaged seeds and number of leaves for all individuals of *Alepis flavida* with seed damage. Data are presented separately for plants growing on forest edges (open circles) and forest interior (closed circles). The regression was not significant for plants growing in forest interior ($r^2 = 0.03$, $n = 8$, $P = 0.68$). The regression line for plants growing on the edge is: $y = -0.011x + 9.5$, $n = 19$ ($r^2 = 0.27$, $P = 0.023$).

appears that plants with the highest amounts of damage had a greater tendency to abort fruits, at least in the forest interior. Thus, at least part of the explanation for the apparent greater fruit abortion in interior plants appears to result from the greater amounts of floral herbivory on interior plants.

Again, as for flower damage, plant size was a significant factor in explaining which plants incurred seed damage. Plants with seed damage had significantly greater numbers of leaves than did plants with no seed damage ($U = 512.0$, $P = 0.048$). As was found for flower damage, neither neighbour size ($U = 419.0$, $P = 0.84$) nor neighbour distance ($U = 320.5$, $P = 0.17$) influenced which plants had seed damage.

The only variable that explained significant variation in the amount of seed damage on plants with damage was plant size, and this relationship was significant only for edge plants ($r^2 = 0.27$, $P = 0.023$). The greater the number of leaves on a plant, the lower the seed damage (Fig. 5). Plant size was not correlated with amount of seed damage for interior plants ($r^2 = 0.03$, $P = 0.68$), most likely because of the small sample size of only 8 plants with seed damage. For plants with seed damage, neither of the neighbour variables was correlated with amount of seed damage ($P > 0.05$ in stepwise regressions).

Discussion

Results from this study show that forest edges affect patterns of herbivory. Three types of herbivory showed significant differences in their impact on *Alepis flavida* growing on forest edges compared with forest interior: leaf herbivory by possums, floral herbivory, and seed predation. Only insect herbivory on leaves did not differ between edge and interior plants. More importantly, some types of herbivore damage were greater on forest edges (possum herbivory and seed predation), whereas others (floral herbivory) were greater in forest interior. These results agree with those of Davies *et al.* (2000), who found that some animal species showed increased population densities on edges, whereas other animal species showed the opposite pattern.

Leaf herbivory

The most striking difference in amounts of herbivory between edge and interior plants was in the frequency of possum damage. Over 2.5-times as many plants growing on forest edges as in forest interior experienced possum damage in 2003. There is evidence from other systems that possum damage is greater in fragmented habitats. Efford (2000) reported greater possum densities in forest edges bordering on pasture. The greater possum damage on edges in the current study

presumably correlates with greater possum densities on edges, although Sessions *et al.* (2001) found that possum herbivory was not simply related to possum density. Experiments are needed to assess whether there might be differences in palatability of mistletoes growing on edges v. interior. Although other studies have reported greater animal densities in edge habitats than in forest interior (Kremsater and Bunnell, 1999; Davies *et al.*, 2000), few studies have documented actual amounts of mammalian herbivory in edge and forest interior habitats.

Recent evidence suggests that possum damage can be a significant factor influencing mistletoe growth and reproduction. Possums are at least partly responsible for the disappearance of *A. flavida* from many parts of the North Island (de Lange and Norton, 1997). In a study of three loranthaceous mistletoes in New Zealand, including *A. flavida*, Sessions *et al.* (2001) showed that mistletoes declined in size to a much greater extent in areas with possums than in areas with possum control operations. Although the amount of possum damage was not quantified in our study, observations indicated many plants had > 20% of their leaves damaged. These results agree with those of Sessions and Kelly (2001), who found that while possums only damaged a subset of mistletoe plants (32% in their study), the amount of damage per plant could be quite high. The effect of this magnitude of defoliation on growth and reproduction in mistletoes needs to be investigated. It is unfortunate that the study site at Craigieburn, which was one of the South Island sites with the lowest rates of possum damage for loranthaceous mistletoes (e.g. 14% in 1998 in this study, see also Sessions and Kelly, 2001), now has significant damage on almost half of the *A. flavida* plants.

The lack of a significant difference in amounts of insect herbivory on edge and interior plants may have resulted from the low amounts of leaf damage overall. Plants on average experienced less than 5% damage by insects. Sessions and Kelly (2001) also found low rates of insect herbivory on *Alepis flavida*, as well as on two other mistletoes, and that all plants incurred some leaf damage from insects, with relatively low variation in damage levels among plants. An additional explanation for the lack of edge effects in insect herbivory is that herbivory is presumably caused by several species of insects. Weevils, stick insects, and generalist caterpillars have all been reported to feed on *A. flavida* leaves (Patrick and Dugdale, 1997). Thus, if different insects respond differently to forest edges, then overall patterns of leaf damage would be fairly similar on edge and interior plants. The non-significant effects of plant size and the neighbouring plant community disagree with results from other studies reporting strong effects of both plant size (Masumoto *et al.*, 2000; Bach, 2001) and plant neighbours

(Masumoto *et al.*, 2000) on rates of insect herbivory. Perhaps plant size and neighbour effects are operating at a larger spatial scale than was sampled in this study.

Floral herbivory

Plants on the interior suffered significantly greater amounts of floral damage than plants on the edge. Lower amounts of damage on edge plants agrees with results from another study of floral damage by *Zelleria* on a closely-related mistletoe, *Peraxilla tetrapetala* (Kelly *et al.*, 2000). Three possible mechanisms worth further study include greater oviposition preference for shaded habitats, lower predation/parasitism in interior habitats, and differences in chemical or other defenses between plants in edge v. interior habitats. The differences between amounts of floral herbivory on edge and interior plants clearly do not result from differences in plant size and/or neighbour proximity, because there were no differences in the sizes of *A. flavida*, or in neighbour proximity variables between edge and interior.

Larger plants had more chance of experiencing floral damage, probably as a result of the positive correlation between plant size and number of flowers. It would make sense that *Zelleria* would choose plants with greater flower resources. Positive relationships between plant size and many types of herbivory have been well documented. Larger plants incur greater amounts of leaf herbivory (Bach, 2001) and floral herbivory (Cunningham, 1995).

Forest edges can have important effects on herbivory via influencing the effects of plant neighbours. Neighbour proximity affected amounts of floral damage only in the interior and not on edges. Perhaps insects can locate plants more easily in edge habitats (either because of use of habitat edges as flight paths and/or because of greater ease of transmission of chemical cues used for host location) and thus do not need to use neighbouring plants as a cue. Birds that disperse the seeds of *A. flavida* have also been shown to respond to density of neighbouring plants in forest interior, but not on forest edges (Bach and Kelly, 2004). The pattern of greater floral herbivory on more isolated plants in the interior was unexpected, but agrees with results from two studies of folivorous herbivores (Masumoto *et al.*, 2000; Frid and Turkington, 2001).

Although average amounts of floral herbivory were low, some plants had as many as 15% of their flowers damaged, which could directly affect plant fitness. Even for plants with low amounts of floral damage, indirect effects on fitness could occur. Recent studies have demonstrated that floral herbivory can have important indirect effects on other aspects of plant reproduction, including pollination. Floral herbivory has been shown to decrease visitation rates

by pollinators in a number of plant species, including another hemiparasite, *Castilleja indivisa* (Adler *et al.*, 2001) and *Isomeris arborea* (Capparaceae) (Krupnick *et al.*, 1999). The low amounts of floral herbivory found for *A. flavida* are in striking contrast to those reported for the same insect on the closely related *Peraxilla tetrapetala*, where Kelly *et al.* (2000) found that *Zelleria* destroyed up to 48% of the flowers on a plant.

Seed predation

Overall, amounts of pre-dispersal seed predation were very low, partly because they were calculated out of the total number of fruits at the beginning of the season. Thus, the amounts of seed predation reported in this paper most probably underestimate the actual amounts of seed predation, because it appears that some fruit abortion occurred. Fruit abortion rates of 14.4% have been reported for *A. flavida* at this same site (Ladley and Kelly, 1996). The only other study reporting rates of seed predation in New Zealand mistletoes reports a similar low seed predation rate (6%) for *Ileostylus micranthus* fruits damaged by *Zelleria* (Sullivan *et al.*, 1995).

Plants had a greater chance of experiencing seed predation on forest edges than in forest interior, which at first appears to be the opposite pattern from that for floral herbivory. However, only the chance of having seed predation varied on edges and in interior, not the amount of seed predation on plants with seed damage. Forest edges may influence the tendency of plants to abort fruits resulting from damaged flowers. Until this study, it was thought that flowers damaged by *Zelleria* rarely produce seeds (Kelly *et al.*, 2000). Results from this study suggest that a portion of plants continue to mature fruits with seed damage from the floral herbivore/seed predator, and that this occurs at a higher rate on forest edges. However, these edge plants have no advantage as a result of this, because it is unlikely these damaged seeds can germinate.

Evidence for differential fruit abortion rates on edges and in the interior comes from the striking difference in the percentage of plants exhibiting floral damage that also exhibit seed damage. Less than 40% of interior plants that suffered floral damage exhibited any seed damage, whereas 80% of edge plants that suffered floral damage also exhibited seed damage (Fig. 4). Perhaps plants growing in the interior have a greater tendency to abort fruits from damaged flowers than do plants on edges because of lower light levels in the interior. It also appears that the amount of floral damage plays a role in which plants abort fruits. Plants with the greatest amounts of floral damage tended not to have seed damage, suggesting that plants with high floral damage abort fruits. Niesenbaum (1996) found that defoliation increases fruit abortion rates. In this

system, edge and interior plants had equal chances of experiencing floral damage (Fig. 2a), but the interior plants exhibited greater amounts of damage (Fig. 2b). Those interior plants with the most damage seem to have greater fruit abortion rates, reducing loss to seed predators, which leads to greater numbers of plants on edges with seed damage (Fig. 2a). Because the interior plants with the highest amounts of floral damage presumably had the greatest tendency to abort their damaged fruits, there was no subsequent difference in amounts of seed predation on edges and interior (Fig. 2b). Work on yuccas shows that abortion rates of developing fruits may be affected by complex interactions among levels of predation and other factors, such as pollen quantity and quality (Huth and Pellmyr, 2000).

Conclusion

This study demonstrated significant forest edge effects on leaf herbivory by possums, floral herbivory, and seed predation in *Alepis flavida*. It seems likely that the herbivory by possums would have the greatest negative impact on plant fitness, as the other two sources of damage (floral herbivory and seed predation) were at low levels. Thus, these results suggest that possum control efforts targeted at mistletoe conservation should be concentrated in edge habitats. When considering all three types of herbivory, it appears that plants growing in the forest interior are at an advantage. However, this study emphasizes the need for mechanistic studies focusing on the relative importance of all of the various factors influencing plant fitness (herbivory, seed predation, pollination, seed dispersal) and how they are affected by forest edges.

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