

Forest edges benefit adults, but not seedlings, of the mistletoe *Alepis flavida* (Loranthaceae)

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Summary

1 We tested the hypothesis that different life-history stages of the same plant species show different responses to forest edge and interior environments. We investigated the effects of forest edges on growth, survival and density of seedlings, juveniles and adults of an endemic New Zealand mistletoe, *Alepis flavida*, over a 5-year period.

2 Rates of establishment and growth were significantly higher for seedlings in forest interior than on forest edges but both juveniles and adults grew significantly faster on forest edges.

3 Mortality rates were greater for juveniles than for adults, but there was no significant difference between forest edge and interior.

4 Densities of seedlings and the larger size class of juvenile plants were significantly greater in the forest interior than on forest edges, whereas densities of the larger size class of adults were significantly greater on edges.

5 Changes in densities over 5 years showed that larger juveniles increased in density only in the forest interior, whereas larger adults increased in density only on forest edges.

6 Thus, seedlings of *A. flavida* have strong advantages in the forest interior, whereas juveniles and adults grow faster on forest edges.

7 This study emphasizes the need to examine multiple life-history stages in studies of edge effects.

Key-words: edge effect, forest edge, forest interior, habitat fragmentation, life-history stage, mistletoe, plant density, plant growth, seedling recruitment

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Introduction

Habitat fragmentation is considered to be one of the most pressing conservation problems and, of all its components, edge effects have probably been examined to the greatest extent. Many studies have now demonstrated differences in some measure of success (growth, survival or reproduction) in edge environments compared with interior environments, both for animals (Kremsater & Bunnell 1999; Davies *et al.* 2000) and plants (Laurance *et al.* 1998; Gehlhausen *et al.* 2000). Habitat edges have been shown to affect plants by altering the availability of resources and the microclimate (Laurance *et al.* 1998; Sizer & Tanner 1999; Gehlhausen *et al.* 2000), as well as interactions with animals, including herbivory (Cunningham 2000), pollination (Jules

& Rathcke 1999), seed dispersal (Restrepo *et al.* 1999) and seed predation (Restrepo & Vargas 1999).

Despite the large number of studies reporting such edge effects, surprisingly few have compared plant population dynamics in edge vs. interior habitats. Differences in population densities on forest edges and in forest interior have been demonstrated for two species of *Trillium* (Jules 1998; Tomimatsu & Ohara 2004). In addition, Kelly *et al.* (2000) found greater densities of the mistletoe *Peraxilla tetrapetala* in smaller sized forest fragments with a higher edge : interior ratio. One would expect populations of species requiring high light conditions to increase in more fragmented habitats, whereas populations of shade-tolerant species should decline with increased fragmentation.

Different life stages of the same plant species can differ in their resource allocation patterns (Gleeson & Tilman 1994), their response to herbivores (Warner & Cushman 2002), and their response to abiotic factors.

For example, Higgins *et al.* (2000) found that seedling recruitment for savanna trees is limited by rainfall, whereas recruitment into adult size classes is limited by fire. Thus, it may be critical to examine different life-history stages in any study of response to edges. Very few studies have examined effects of forest edges on different life-history stages of the same plant species. In a study of the mechanisms underlying edge effects in *Trillium ovatum*, Jules & Rathcke (1999) found that seed production and seed predation were both significant factors, whereas there was no effect of edges on seed germination, seed dispersal or survival of established plants. Tomimatsu & Ohara (2004) recently reported edge effects for three different life-history stages of *Trillium camschatcense*, with strongest effects on seedling recruitment.

The purpose of this study was to investigate the effects of forest edges on growth, survival and densities of different life-history stages of the New Zealand mistletoe, *Alepis flavida*. Populations of *A. flavida* are declining, and one of the suggested explanations involves habitat fragmentation (de Lange & Norton 1997). *Alepis flavida* is a hemiparasite, obtaining water and nutrients from host xylem, thus emphasizing that mistletoes are not only directly affected by environmental conditions, but that they can be indirectly affected through changes in host tree physiology. Mistletoes are generally considered to be edge plants with high light requirements (Norton & Reid 1997), although studies documenting greater success on edges are lacking. Seedlings of mistletoes are especially vulnerable to desiccation before they make initial contact with host xylem (Yan & Reid 1995), and Norton & Ladley (1998) suggest that seedling establishment is best on branches with the highest water potentials. Thus, different resources may be important at different life stages, leading to the prediction that there should be different effects of forest edge environments (with their higher light levels, higher temperatures and greater potential for desiccation) on seedlings and adult plants.

This study addressed three questions. Do forest edges influence growth and survival of *Alepis flavida*? If so, do effects of forest edges differ between life-history stages? Finally, do differences in growth and survival translate into differences in densities of different life-history stages on forest edges and in the forest interior? To investigate growth and survival as a function of life-history stage, we investigated patterns of seedling growth, as well as mortality and growth of juveniles and adults, on edges and in the interior of forests.

Methods

THE SYSTEM

The mistletoe *Alepis flavida* (Hook. F) Tiegh. (Loranthaceae) is the most host-specific of all the New Zealand mistletoes, with the vast majority of host records from *Nothofagus solandri* (Norton 1997). Flowering

occurs from January to February, and fruiting occurs from March to May. Fruits are dispersed by several native New Zealand honeyeaters (Aves: Meliphagidae). Seedling recruitment is absolutely dependent on bird dispersal; seeds must pass through a bird's digestive tract to germinate and seedlings can only establish if seeds are deposited on a host branch (Ladley & Kelly 1996). *Alepis flavida* has a fruit-colour polymorphism, in which some plants have orange fruits whereas in others orange fruits ripen to red, and fruit removal rates are significantly higher for the red-fruited morph (Bach & Kelly 2004).

STUDY SITE

The study was conducted at Jacks Pass (43°09' S, 171°43' E, elevation 940 m) in Craigieburn Forest Park, South Island, New Zealand, from 1998 to 2003. The only host for *Alepis flavida* at this site, which has been used for previous studies on mistletoes (Powell & Norton 1994; Ladley & Kelly 1996; Ladley *et al.* 1997; Robertson *et al.* 1999; Bach & Kelly 2004), is *Nothofagus solandri* var. *cliffortioides*, which forms a monospecific stand with a canopy at 15–20 m height.

The study included 58 focal adult mistletoe plants, which were initially measured in 1998, when all were flowering. To compare effects of forest edges without the potentially confounding factor of height in the canopy, all plants sampled occurred at a height of 1–2.5 m. Although *A. flavida* occurs at all heights throughout the forest, 62–71% of plants occurred in the lowest one-third of the tree in a 3-ha survey of this forest (Norton *et al.* 1997a). The plants in this study therefore occurred in the most common location for this species.

Nine or 10 plants were chosen at each of three sites occurring next to roads (henceforth designated as forest edge), and at each of three sites in the forest interior (defined as occurring at least 10 m, but in practice usually > 50 m, from a road or opening). The six sites were spread across the study site, which is completely forested except for the roads. The total of 30 edge plants and 28 interior plants differed in neighbouring plant densities, from fairly isolated individuals to plants with a number of close neighbours of *A. flavida*. As individual sites covered quite large areas, some plants were closer to plants at other sites than to plants at their own site, and we did not therefore include site as a block effect in the analyses.

SEEDLING GROWTH

The relationship between age and size was assessed for seedlings in both edge and interior habitats in 2003. Past research has shown that branching in *Alepis flavida* is slow and can vary with plant age, but the primary axis of seedlings tends to remain unbranched until at least year 5 (Powell & Norton 1994). Single-branched plants were therefore randomly chosen from road edges and from forest interior (> 10 m from a road edge) on

11 March ($n = 32$ edge; $n = 32$ interior) and 10 April ($n = 67$ edge; $n = 101$ interior). For each seedling, age was determined by counting the number of annual resting bud scars between the haustorium and the branch tip, as in Norton *et al.* (1997b). The number of annual resting bud scars correlates very strongly with age ($r^2 = 0.72$, $n = 26$, $P < 0.0001$; Norton *et al.* 1997b). Plant size was measured as the number of leaves and the length of stem with leaves. On 10 April, the total length of seedling (from haustorium to tip) was also recorded.

Growth rates of seedlings were analysed by examining the relationship between seedling size and age. A two-way ANOVA was used to test for effects of seedling age (ages from 3 to 6 years had sufficient sample sizes), forest edge and their interaction on number of leaves, total stem length, and stem length with leaves.

MORTALITY AND GROWTH OF JUVENILES AND ADULTS

Growth was assessed over a 5-year period. All 58 focal adults were surveyed for number of leaves, as well as length, width and height of each plant (longest axis and two perpendicular axes) in 1998. Size measurements, which did not include dead branches were used to calculate plant volume, assuming that the shape of each plant was approximated by an ellipsoid (Norton *et al.* 1997b). Although neither juvenile nor adult plants can be aged accurately, Norton *et al.* (1997b) found that volume is very well correlated with age for *Alepis flavida* ($r^2 = 0.80$, $n = 26$, $P < 0.0001$). The size measurements also enabled a comparison of the relationship between number of leaves and volume in the two habitats.

We also sampled neighbours of the focal plants. In 1998, the four *Alepis flavida* closest to each focal plant were located, constrained by a maximum search distance of 5 m (including vertically). If a fifth or sixth neighbour occurred within 10% of the distance containing four neighbours, then these plants were also sampled, to ensure greater accuracy in the follow-up data in 2003. All plants with multiple stems were sampled (i.e. both adults and juveniles were included), whereas small, single-stemmed seedlings were excluded. For each neighbouring plant, we recorded distance from the focal plant, plus length, width and height (again allowing a calculation of volume).

In 2003, 52 of the focal plants were relocated and the 45 that were still alive were re-measured. For all neighbours that could be relocated, the distance and size (length, width and height) were recorded. To be absolutely sure of the identity of neighbours over the 5-year period, a conservative 10% rule was used. Neighbour presence in 2003 was confirmed if a neighbour occurred within $\pm 10\%$ of the original search distance and no other neighbours were present within that distance ($n = 87$). Mortality was considered to have occurred if there were no neighbours in 2003 within $\pm 10\%$ of the original search distance ($n = 44$).

Growth and mortality for juvenile and mature plants were analysed using combined data from focal plants and neighbours ($n = 132$ for growth; $n = 189$ for mortality). Plants less than $12\,000\text{ cm}^3$ in volume in 1998 were classified as juveniles and larger plants as adults, based on information from Powell & Norton (1994) that the youngest age of flowering in *A. flavida* is 8 years and that the dimensions of plants up to 10 years old are rarely $> 40 \times 30 \times 20\text{ cm}$. Growth rates were calculated as $\ln(\text{volume in 2003}/\text{volume in 1998})$.

DENSITIES OF THE LIFE-HISTORY STAGES OF *ALEPIS FLAVIDA*

Effects of forest edges on *A. flavida* densities in 2003, as well as changes in densities from 1998 to 2003, were examined for four size classes. Juvenile and adult plant neighbours were each divided into equal samples, yielding two size categories of juveniles ($< 1600\text{ cm}^3$ and $1600\text{--}12\,000\text{ cm}^3$) and two size categories of adults ($12\,000\text{--}73\,000\text{ cm}^3$ and $> 73\,000\text{ cm}^3$). Densities of *A. flavida* were calculated from the measurements of the distances to the four nearest neighbours around each of the 58 focal plants in 1998 and the 52 focal plants that were located in 2003 (see above). Density (plants 1000 m^{-3}) was calculated by dividing the number of plants by the volume searched. Densities included all neighbours, but did not include the focal plant. An initial volume calculation for the area searched was made for each plant by using the formula for a sphere, with a radius of the distance searched. This spherical volume had to be corrected for the height of the plant above the ground and the presence of roads (for edge plants only). The height above ground was measured for each plant, and the formula for a spherical cap was used to correct the spherical volume. For plants on roads, the distance to the road was measured, again enabling a correction using the formula for a spherical cap. Changes in density were then calculated for the 5-year period for each of the two size categories of both juvenile and mature plants. There was no difference between forest edges and interior in either the distances ($t = 0.28$, d.f. = 50, $P = 0.78$) or volumes searched for neighbours ($t = 1.1$, d.f. = 50, $P = 0.28$).

Seedling density was assessed in 2003 by recording every single-branched plant occurring within the search distance (established in 1998) around each focal plant.

Results

SEEDLING GROWTH

Seedlings on forest edges were significantly older (mean = 4.2 years) than seedlings in forest interior (mean = 3.8 years; $t = 2.6$, d.f. = 230, $P = 0.01$), as well as significantly smaller for all three measures of growth (number of leaves, total stem length and length of stem with leaves, Table 1). Seedling age also significantly influenced all three measures of plant size, but there were

Table 1 Results from two-way ANOVAs on seedling size (number of leaves, total stem length, and stem length with leaves), testing for effects of forest edge, age, and an interaction between forest edge and age

	Effect	F	d.f.	P
Number of leaves	Forest edge	6.03	1,208	0.015
	Age	16.0	3,208	< 0.001
	Edge × age	0.64	3,208	0.59
Stem length	Forest edge	15.5	1,152	< 0.001
	Age	33.1	3,152	< 0.001
	Edge × age	0.23	3,152	0.88
Stem length with leaves	Forest edge	10.8	1,208	0.001
	Age	14.0	3,208	< 0.001
	Edge × age	1.05	3,208	0.37

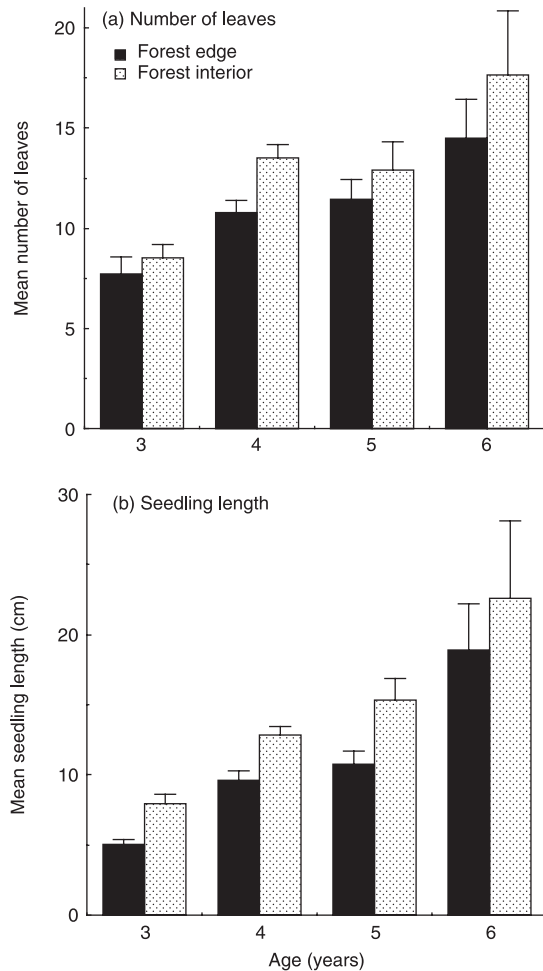


Fig. 1 Size of *Alepis flavida* seedlings as a function of age for (a) number of leaves and (b) stem length. Means and standard errors are plotted for seedlings with ages from 3 to 6 years. Sample sizes are: number of leaves ($n = 99$ edge; $n = 133$ interior); stem length ($n = 67$ edge; $n = 101$ interior).

no significant interactions between age and forest edge (Table 1). Thus, for all seedling ages, those growing in the interior had more leaves and longer stems than those on the forest edge (Fig. 1). Interior plants added more leaves (an average of 3.0 vs. 2.5 year⁻¹; $t = -2.97$, d.f. = 230, $P = 0.003$) and grew faster (3.0 cm vs.

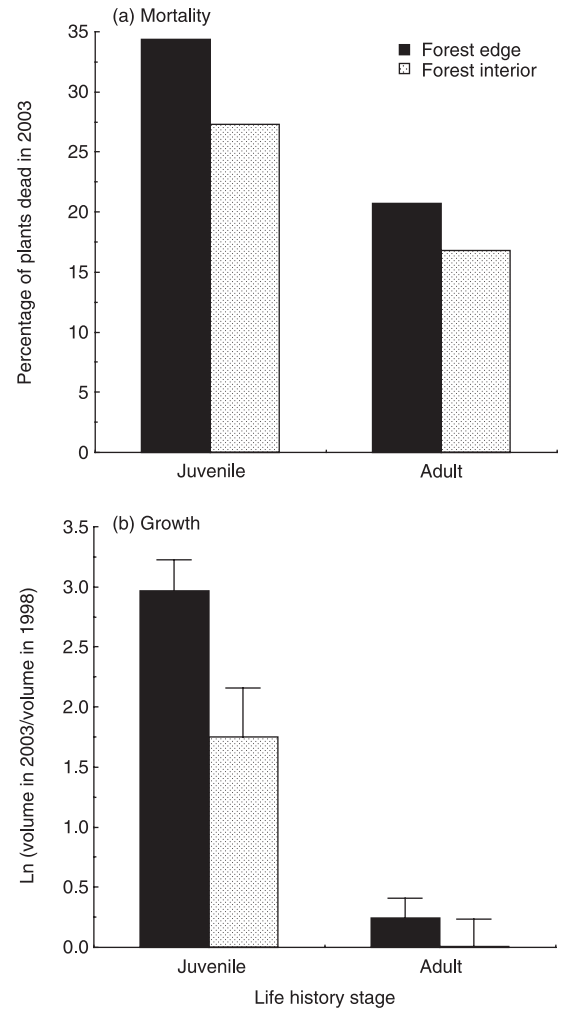


Fig. 2 Mortality and growth for juvenile and adult individuals of *Alepis flavida* on forest edges and in forest interior: (a) mortality (percentage of plants alive in 1998 that were dead in 2003); (b) mean growth rates, measured as \ln (volume in 2003/volume in 1998). Bars indicate standard error of the mean.

2.3 cm year⁻¹ for edge plants; $t = -4.1$, d.f. = 166, $P < 0.001$).

MORTALITY AND GROWTH OF JUVENILES AND ADULTS

Overall, 23.6% of edge plants died over the 5-year period, in comparison to 19.4% for plants growing in the forest interior. There was a significant effect of volume in 1998 on mortality (logistic regression, $P = 0.014$), with greater mortality for smaller plants than larger plants. In fact, mean mortality for juveniles was almost twice as high as for adults (Fig. 2a). However, there was no effect of forest edge (logistic regression, $P = 0.40$), or an interaction between edge and volume (logistic regression, $P = 0.63$) on mortality.

Growth rates, measured as \ln (volume in 2003/volume in 1998), were significantly greater for juveniles than for adults (two-way ANOVA; $F_{1,126} = 60.5$, $P < 0.001$), and significantly greater on forest edges than in the forest interior (two-way ANOVA; $F_{1,126} = 6.4$, $P = 0.013$; Fig. 2b).

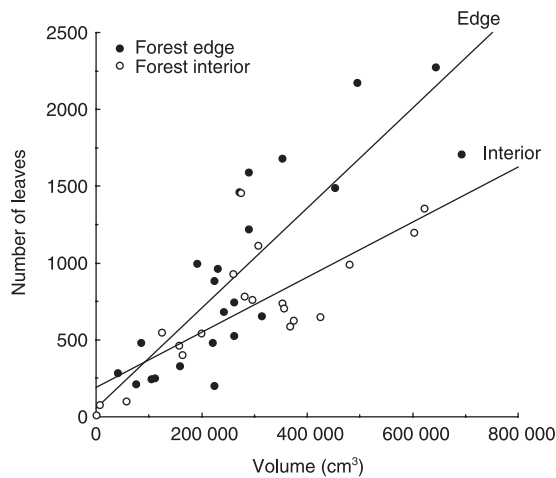


Fig. 3 Relationship between number of leaves and volume for *A. flavida* growing on forest edges and forest interior in 2003. Equations for regression lines are: forest edge ($y = 0.003x + 57.3$, $r^2 = 0.71$, $P < 0.001$); forest interior ($y = 0.002x + 191.9$; $r^2 = 0.61$, $P < 0.001$).

The lack of a significant interaction effect (two-way ANOVA; $F_{1,126} = 2.9$, $P = 0.091$) indicates that the greater growth rates on edges were consistent for juveniles and adults (Fig. 2b). In fact, mature plants on average increased in size over the 5-year period on edges, but did not grow in the forest interior (Fig. 2b).

Patterns of growth also differed between edges and interior in terms of the relationship between number of leaves and volume, with plants with the same volume having significantly more leaves on forest edges (Fig. 3). Although there was no significant main effect of forest edge in a two-way ANOVA on number of leaves ($F_{1,39} = 0.52$, $P = 0.47$), there was a significant interaction between forest edge and volume in influencing number of leaves ($F_{1,39} = 6.5$, $P = 0.015$). Thus, as plants increased in volume, they increased in numbers of leaves faster on edges than in the interior.

DENSITIES OF THE LIFE-HISTORY STAGES OF *ALEPIS FLAVIDA*

Densities of the five size categories in 2003 depended strongly upon habitat (Fig. 4). For seedlings and juveniles, densities were higher in the forest interior than on forest edges (Fig. 4), and these differences were significant for both seedlings and larger juveniles (Table 2). Although there was no difference for smaller adults there were significantly greater densities of the larger adults on edges than in the interior (Table 2, Fig. 4).

Because the analyses of densities in 2003 examine just one point in time, it was essential to also examine the changes in density from 1998 to 2003. The larger juveniles had significantly greater increases in density over the 5-year period in the interior than on the edges where the median change was zero (Table 2, Fig. 5). Larger adults again showed the reverse pattern, with changes in density significantly greater on the edges than in the interior (Table 2). For this largest size class,

Table 2 Results from Mann–Whitney U -tests comparing forest edges and forest interior for densities in 2003 and changes in density from 1998 to 2003

	Density in 2003		Change in density 1998–2003	
	U	P	U	P
Seedlings	168	0.002	*	*
< 1600 cm ³	261	0.16	276	0.26
1600–12 000 cm ³	229	0.044	193.5	0.008
12 000–73 000 cm ³	292	0.40	394	0.54
> 73 000 cm ³	449	0.041	441.5	0.053

*Changes in densities of seedlings could not be analysed because seedlings were not sampled in 1998.

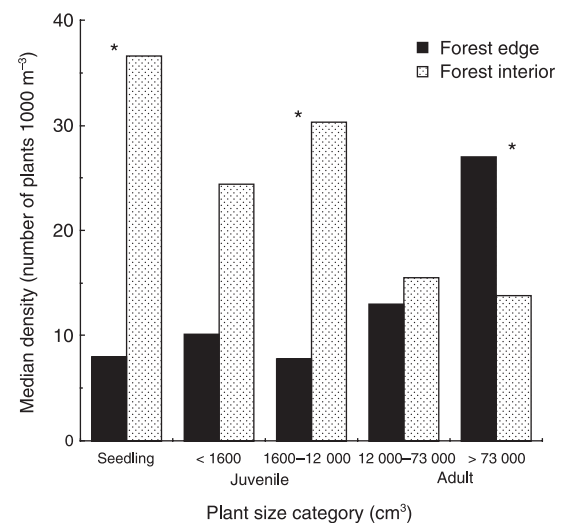


Fig. 4 Median density (number of plants 1000 m⁻³) in 2003 for five size categories of *Alepis flavida*: seedlings, juveniles (< 1600 cm³; 1600–12 000 cm³) and adults (12 000–73 000 cm³; > 73 000 cm³). Stars indicate a significant difference between edge and interior with a Mann–Whitney U -test.

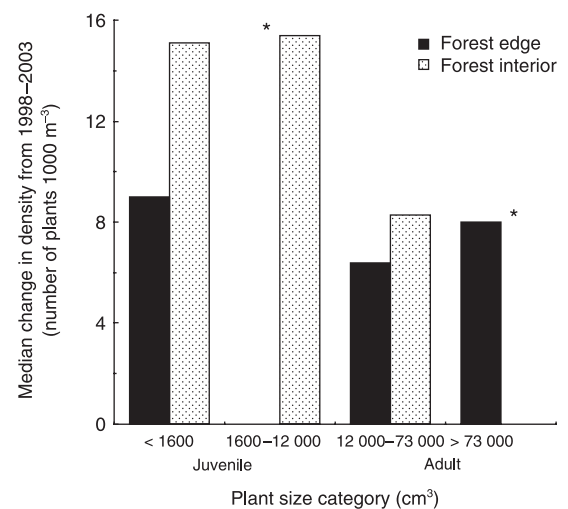


Fig. 5 Median changes in density from 1998 to 2003 (number of plants 1000 m⁻³) for the four size categories of *Alepis flavida*: juveniles (< 1600 cm³; 1600–12 000 cm³) and adults (12 000–73 000 cm³; > 73 000 cm³). Asterisks indicate a significant difference between edge and interior with a Mann–Whitney U -test.

there was a median change in density of zero for the interior (Fig. 5). These results show that the numbers of plants in the smaller size classes are increasing only in the interior, whereas numbers of plants in the largest size category are increasing only on edges.

Discussion

Our results clearly document strong differences in densities of the different life stages of *A. flavida* on forest edges and in the forest interior. Seedlings and juveniles have much higher densities in the forest interior, whereas the larger adults have a much higher density on forest edges. This study is the first to document different responses to forest edges by different life stages of the same plant species, and emphasizes the importance of the forest interior, even for a species that is considered to be an edge specialist with high light requirements (Norton & Reid 1997).

The greater seedling densities in the interior match results for two species of *Trillium* (Jules 1998; Tomimatsu & Ohara 2004), whereas Restrepo & Vargas (1999) found no edge effect on seedling growth for two montane shrubs. The greater seedling densities in the forest interior for *Alepis flavida* appear to result from greater survival and growth of seedlings in the interior. Seed deposition does not appear to contribute to the differences in seedling densities, because preliminary data from six seed traps placed under plants showed that twice as many seeds were deposited per unit area on edges as in the interior (C. E. Bach and D. Kelly, unpublished data). Greater growth rates of interior seedlings are supported by the same age of seedling having more leaves, longer stems and longer lengths of stem with leaves. Norton & Ladley (1998) suggested that seedling establishment is best on branches with the highest water potential, and it therefore seems possible that seedlings in the interior may benefit from better access to this limiting resource.

The faster growth rate of seedlings in the interior has two important consequences. First, seedlings move out of very small size categories more quickly, thus decreasing their vulnerability to mortality. In two different experiments involving planting *A. flavida* seeds on host branches in forest interior, the percentage of seedlings still alive after 2 years was 4% (Norton *et al.* 1997b) and 14% (Ladley & Kelly 1996). Thus, as survival in the first few years is extremely low, small but significant differences in growth rates could be critically important. Secondly, the higher growth rates of seedlings lead to greater densities of juveniles in the forest interior (see Fig. 4). In fact, larger juveniles showed large increases in density in the forest interior, but did not change in density at all on forest edges over the 5-year period (see Fig. 5).

Although this study did not assess seed germination and seedling establishment, it seems very likely that differences in seedling establishment also contribute to the greater seedling densities in the forest interior. Past research has shown that *A. flavida* seeds can germinate

on a number of different surfaces (Ladley & Kelly 1996) and that germination rates are nearly 100% (Norton *et al.* 2002), so it is unlikely that there are differences in germination as a function of forest edge. Given preliminary data that seed deposition per unit area is lower in the interior, seedlings must establish much better to give rise to the much greater densities there. Because small seedlings are especially vulnerable to desiccation until they make contact with host xylem (Yan & Reid 1995), it seems likely that rates of initial establishment after germination are higher in the moister, shaded environment of the forest interior. Yan & Reid (1995) found improved mistletoe recruitment after times of above-average rainfall. Another important cause of death of mistletoe seedlings is death of the host branch (Sargent 1995), and rates of tree-fall and damage are likely to be higher on forest edges because trees in this position are more exposed to high winds.

The switch from greater seedling and juvenile densities in the interior to greater adult densities on forest edges appears to result from the higher growth rates of juveniles and adults on the edges. Light levels are significantly higher on edges than in the interior for this ecosystem (Montgomery *et al.* 2003), as well as other forest ecosystems (Laurance *et al.* 1998; Gehlhausen *et al.* 2000). Because *A. flavida* has high light requirements (Norton & Reid 1997), it is not surprising that it grows faster on edges. However, differences in host tree physiology may also be involved, as fragmentation can result in an increase in water and nutrients for host trees as overall local tree densities decrease. Because of the higher growth rates of both juveniles and adults on edges, individuals there both move into larger size classes more quickly and experience lower mortality (mortality decreases strongly with size, Fig. 2a). The density of the largest size class of plants therefore increased on edges, but remained constant in the interior over the 5-year period (Fig. 5)

Patterns of growth also varied between forest edges and the interior. For a given volume, larger plants on edges had more leaves (Fig. 3), which means that growth rates based on volume underestimate the actual differences between habitats for large plants.

In conclusion, the different life stages of *Alepis flavida* respond very differently to forest edges vs. forest interior, in terms of both growth and resulting density. Seedlings of *Alepis flavida* are clearly at an advantage when in the interior, both in terms of establishment and growth. In contrast, both juvenile and adult plants have much faster growth rates when growing on forest edges, but survival rates do not differ. Past work on *A. flavida* also shows greater rates of flowering on edges (C. E. Bach, unpublished data), and therefore greater rates of fruiting, because *A. flavida* has very high rates of fruit set (Ladley & Kelly 1996). However, pollination rates are very high in all habitats because *A. flavida* can self-pollinate (Ladley & Kelly 1996) and rates of fruit removal by birds do not differ significantly between edges and interior (Bach & Kelly 2004).

The complete shift from greater seedling and juvenile density in the forest interior to greater adult density on edges may result from a shift in the limiting resource. We hypothesize that host water is the most important factor limiting seedling recruitment, whereas a different resource, light level, is likely to limit growth of juveniles and adults. Higgins *et al.* (2000) report a change in which resource is limiting from the seedling stage to the adult stage for savannah trees. The greater success of seedlings in the interior and adults on edges may also result from a decreasing dependence on host tree physiology as mistletoes age. Future research needs to examine whether different life stages of other plant species also show different growth responses to forest edges and whether the growth responses lead to differences in densities as shown here. In the meantime, we should be cautious about generalizations from studies of edge effects that focus on only one life stage.

Overall, our results predict that the highest densities of *A. flavida* would occur in a mosaic of forest patches. As forests become more and more fragmented, adults will grow faster, and flower at higher rates, but seedling establishment will be decreased substantially. In forests with no openings or disturbances, even though seedling establishment will be enhanced, decreased flowering and fruiting may limit seed deposition. In order to draw generalizations about the overall benefits of edges vs. interior, it will be necessary to carry out studies of population dynamics in forests that differ in degrees of fragmentation.

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