

Establishment and early growth of *Alepis flavida* in relation to *Nothofagus solandri* branch size

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Abstract Hand planted seeds of the mistletoe *Alepis flavida* establish much better on small *Nothofagus solandri* branches (<5 mm diameter: 48.4% establishment after one year) than on large branches (20–30 mm: 6.1%), whereas intermediate sized branches have intermediate establishment rates (10 mm: 21.6%). Wild 1–4-year-old *Alepis flavida* seedlings occurred on branches 0.5–6 mm diameter (mean = 1.9 mm). There was no significant difference in original branch size between tagged mistletoe seedlings that died and those that lived, but *Alepis flavida* shoot extension was positively correlated with host branch diameter increment. These data suggest the early establishment and survival of *Alepis flavida* seedlings is strongly dependent on the size and vigour of the branch on which the seed has been deposited.

Keywords *Alepis flavida*; establishment; Loranthaceae; mistletoe seedlings

INTRODUCTION

Recruitment of mistletoes is dependent on successful dispersal of seed from the parent plant and establishment of the seedling on a suitable host plant (Reid et al. 1995; Norton & Reid 1997). Dispersal is dependent on bird behaviour, particularly feeding

patterns and method of voiding the seed, while establishment is dependent on the disperser voiding the seed onto a compatible host species and on an appropriately sized branch of that tree.

Recent research on New Zealand mistletoes has confirmed the importance of birds for mistletoe dispersal (Ladley & Kelly 1996) and has highlighted the dependence of individual mistletoe species on particular hosts (de Lange et al. 1997). In the only published study of mistletoe establishment on different sized branches in New Zealand, Ladley & Kelly (1996) found no significant difference in establishment for *Alepis flavida*, *Ileostylus micranthus*, and *Peraxilla colensoi*. Branch size has, however, been suggested as an important determinant of mistletoe establishment success in Australia (Reid 1987; Yan & Reid 1995) and Costa Rica (Sargent 1995) with best establishment on small branches (typically <20 mm diameter). Better establishment on these branches might either be because of thinner bark providing less resistance to haustorium penetration (Reid 1987; Sargent 1995) or because these are the branch sizes on which mistletoe dispersing birds most frequently perch (Reid 1989; Yan & Reid 1995).

As a contribution towards a better understanding of establishment in New Zealand loranthaceous mistletoes, this paper documents the establishment success of *Alepis flavida* seedlings on different sized *Nothofagus solandri* branches.

METHODS

The study was undertaken on the lower slopes of the Craigieburn Range, eastern South Island, New Zealand (43°09'S, 171°43'E; Craigieburn Ecological District) in monodominant *Nothofagus solandri* forest. Two mistletoes, *Alepis flavida* and *Peraxilla tetrapetala*, are present in these forests, both parasitising *Nothofagus solandri* (Norton et al. 1997).

On each of five mature healthy *Nothofagus solandri* trees located 2–4 m apart in open canopied

forest, we selected and tagged five branches. Each branch was then divided into three sections based on branch diameter: < 5 mm, c. 10 mm, and 20–30 mm diameter. Ten *Alepis flavida* seeds were planted on each branch section. Planting involved the harvesting of 750 ripe *Alepis flavida* fruits from mistletoe plants within a 1 km radius of the tagged trees over a two day period in April 1996 when the mistletoe was fruiting. Over the same two days, seeds were carefully squeezed out of the fruit skins and placed on the tagged branch sections. Care was taken to ensure that the seeds' viscin was wiped on to the host branch to ensure good adhesion (see Ladley et al. 1997 for more details on planting methods).

After planting, seeds were monitored monthly until May 1997 (13 months after trial establishment). At each visit, the state of each *Alepis flavida* seed was recorded based on whether the seed had germinated (when the hypocotyl had emerged), established (when the first set of small leaves appeared), or died. A Generalised Linear Model run in the S-Plus statistical analysis package (MathSoft Inc. 1995) was used to test for the effect of host branch size, as well as tree and branch, on mistletoe establishment.

We also surveyed an area of forest to determine the branch size that young *Alepis flavida* seedlings were establishing on naturally. This involved traversing a number of tracks through the forest and recording all *Alepis flavida* seedlings encountered. For each seedling, we estimated its age based on the number of bud-scars present, assuming annual bud-scar formation (Powell & Norton 1994), and adding an additional year for initial establishment. Only mistletoe seedlings with three or fewer bud-scars were sampled. The diameter of the host branch immediately below the obvious swelling associated with the haustorial attachment was measured using callipers.

These mistletoes were tagged and remeasured one year later in order to assess growth and mortality patterns.

RESULTS

No *Nothofagus solandri* branches died during the study, but all *Alepis flavida* seeds were lost from two host branch sections and these data were not used in the analyses. Of the remaining 730 mistletoe seeds placed on host branches, 16.8% disappeared from branches, either through predation by insects or birds or by simply falling off, and 1.2% remained on the branches but did not germinate. The remaining 82% of seeds germinated successfully. We found a significant difference in germination between trees ($P < 0.001$) and between branches ($P < 0.001$), but no significant difference between different sized branches ($P = 0.225$, Table 1).

Of the 82% of seeds that germinated, we found a significant difference in establishment between trees ($P = 0.039$), between branches ($P < 0.001$), and between different sized branches ($P < 0.001$, Table 1), with the most variance explained by differences in branch size. Mean establishment on branches < 5 mm was 48.4%, on 10 mm diameter branches was 21.6%, and on 20–30 mm diameter branches was 6.1%, with all means being significantly different ($P < 0.05$) from each other (Table 2).

The 99 wild *Alepis flavida* seedlings encountered had a mean length of 23.7 mm (s.e. 1.51, range 5–64) and were located on branches with a mean diameter of 1.9 mm (s.e. 0.09, range 0.5–6). Of these 99 seedlings, 72 were relocated in 1997; 54 were still alive and 18 had died. There was no statistically significant difference ($F = 0.684$, $P = 0.411$) between

Table 1 Analysis of deviance table for mistletoe germination and mistletoe establishment of different sized branches using a binomial GLM model with terms added sequentially.

Term	df	deviance	df	resid. dev.	Pr(Chi)
Germination					
null			72	208.3	
tree	4	32.7	68	175.6	<0.00001
branch	20	56.9	48	118.8	0.00002
branch size	2	2.99	46	115.8	0.22457
Establishment					
null			72	297.5	
tree	4	10.1	68	287.4	0.03886
branch	20	61.7	48	225.7	<0.00001
branch size	2	129.5	46	96.2	<0.00001

the 1996 branch diameter and 1997 dead and alive mistletoes, although the 1996 diameter tended to be smaller for those that died than for those that lived (1.7 mm cf. 1.9 mm). For those mistletoes alive in 1997, there was no correlation between mistletoe growth (measured as increase in mistletoe length between 1996 and 1997) and 1996 host branch diameter, but there was a correlation when mistletoe growth and change in host branch diameter between 1996 and 1997 were compared ($R = 0.473$, $n = 54$, $P < 0.001$, Fig. 1).

DISCUSSION

The significant difference in germination between trees and branches (Table 1) is mainly attributable to differences in pre-germination seed loss and could reflect differences in animal removal of seeds from our study branches and trees. Little information is available on mistletoe seed predation in New Zealand, although birds have been documented taking mistletoe seed in Australia (Yan & Reid 1995) and it is likely that similar predation occurs in New Zealand.

The very high variation in *Alepis flavida* establishment between branches independent of branch size (Table 1), with establishment varying from 3.3–56.7%, was an unexpected result of this study. Reasons for variation in establishment could be attributable to differences in branch vigour or microclimate. Differential disperser behaviour is not relevant in this experiment as seeds were hand dispersed. The importance of branch vigour has already been demonstrated in the analysis of wild *Alepis flavida* seedlings (Fig. 1) and could also have been important in the seed planting experiment although we did not measure it. Light intensity can also influence mistletoe distribution (Hawksworth 1961), and *Alepis flavida* establishment in *Nothofagus*

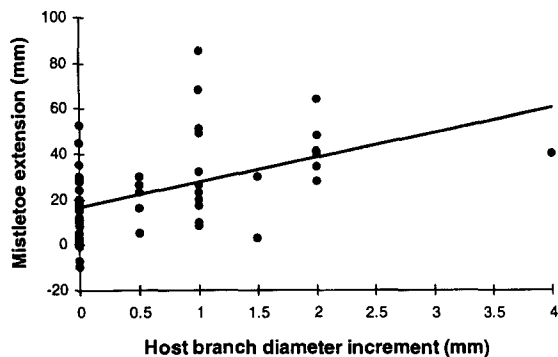


Fig. 1 Relationship between mistletoe growth (shoot extension) and host branch growth (diameter increment) between 1996 and 1997. The fitted regression line has the equation $y = 10.998x + 16.4$ ($R = 0.473$).

solandri forests may be better on branches experiencing higher light levels. This result suggests that more attention needs to be given to within-tree establishment patterns in future studies of mistletoe establishment.

The significant branch size effect on mistletoe establishment observed here agrees with the results of earlier studies in Australia (Reid 1987; Yan & Reid 1995) and Costa Rica (Sargent 1995), but differs from the results of Ladley & Kelly (1996) for three New Zealand mistletoes including *Alepis flavida* where no branch size effect was observed. Ladley & Kelly's (1996) sample sizes were small ($n = 25$ – 49), suggesting caution in interpreting their results. Our data suggest that for *Alepis flavida*, optimum establishment occurs on the smallest branches (<5 mm diameter), with wild seedlings 1–4 years old observed on branches with a mean diameter of 1.9 mm. Powell & Norton (1994) also commented that *Alepis flavida* seedlings usually established on 1–2-year-old host branches. Reid (1987) recorded maximum establishment of *Amyema quandang* on very small diameter *Acacia*

Table 2 Fate of mistletoe seeds (means out of 10) established on different sized host branches (with s.e. in brackets).

Branch size	seed fate			
	fell off	did not germinate	germinated	established
< 5 mm	1.32 (0.275)	0.20 (0.082)	8.48 (0.289)	4.84 (0.515)
c. 10 mm	1.76 (0.371)	0.12 (0.066)	8.12 (0.371)	2.16 (0.519)
20–30 mm	2.00 (0.553)	0.04 (0.042)	7.96 (0.548)	0.61 (0.157)

papyrocarpa branches (1–6 mm), but Sargent (1995) and Yan & Reid (1995) found maximum establishment on larger sized branches for *Phoradendron robustissimum* on *Sapium oligoneuron* (10–14 mm) and *Amyema miquelii* on *Eucalyptus blakelyi* and *E. melliodora* (7–20 mm), respectively. However, all authors concluded that establishment is poorest on the largest sized branches (usually >20 mm diameter).

The most probable reason for enhanced establishment on small branches is that mistletoes are best able to penetrate thin host bark in order to develop haustorial connections with the host xylem (Reid 1987; Sargent 1995). This certainly appears to be the case with *Nothofagus solandri* where older larger branches have thicker bark than younger thinner branches (Wardle 1984; Milne 1996). Reid (1989) and Yan & Reid (1995) suggest that in some cases the optimum branch sizes for establishment are also those preferred by seed dispersing birds as perches, but this is not a factor affecting establishment success in our experiment where bird dispersal was not involved.

Sargent (1995) observed that in *Phoradendron robustissimum* greatest mistletoe mortality occurred on both small and large branches, but that the causes of each were different. On the smallest branches, mortality occurred because the host branch died, while on the largest branches mortality occurred because the mistletoe appeared unable to develop a haustorial connection with the host. Although we observed that naturally established mistletoe seedlings that died between 1996 and 1997 were on smaller diameter branches than those that survived, this mortality was not associated with branch death which suggests that other factors might be involved. One difference between *Alepis* and *Phoradendron* is the presence of runners. *Alepis flavida* seedlings produce runners by about year 3 (Powell & Norton 1994) and we observed runners on 85% of our live mistletoe plants in 1997; *Phoradendron* species do not have runners. Runners enable a mistletoe to spread away from the original establishment site producing multiple haustorial connections along one or more branches, thus enabling them to exploit a greater amount of host resources.

We did observe that the highest mistletoe growth rates (expressed by shoot extension) were correlated with branches that had the greatest diameter growth rates (Fig. 1), suggesting that mistletoes do best when the host branch is most vigorous. Lorantheaceous mistletoes are water and nutrient parasites, and to some extent carbon parasites (Reid

et al. 1995; Norton & Reid 1997), suggesting that mistletoes that are able to maximise solute uptake from the host will have maximum growth rates. Hosts and host branches with the fastest diameter growth rates are likely to be those with the highest water potentials and xylem solute amounts, and hence the greatest resources potentially available to the mistletoe. Furthermore, mistletoe growth is constrained by the area of the xylem-xylem contact and the transfer of water and solutes across this interface; faster growing branches enable mistletoes to develop a greater area of xylem-xylem contact and hence to grow better.

Early establishment and survival of mistletoe seedlings appear to be strongly dependent on the type of branch on which the seed is deposited. Although *Alepis flavida* germination occurs readily on a variety of substrates (Ladley & Kelly 1996), successful establishment and early growth requires deposition of seed onto a small diameter (<6 mm), fast growing branch of *Nothofagus solandri*. These results have implications for conservation of New Zealand mistletoes. It has been suggested that declining abundances of mistletoes are in part a consequence of declining abundances of seed dispersing birds (Ladley & Kelly 1996). While some of the dispersal role of declining indigenous bird species has been taken up by exotic species such as black birds (*Turdus merula*; eg., Williams & Karl 1996), to be effective as mistletoe dispersers (*sensu* Reid 1989) such birds need to deposit seeds on appropriately sized host branches. Thus differences in bird behaviour could potentially alter the dispersal efficiency of *Alepis flavida*, especially if "new" dispersers avoid using small diameter branches as perch and defecation sites.

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