Plant and Microbial Sciences, University of Canterbury, Private Bag, Christchurch 1, New Zealand.

DISPERSAL, GERMINATION AND SURVIVAL OF NEW ZEALAND MISTLETOES (LORANTHACEAE): DEPENDENCE ON BIRDS.

Summary: The dispersal, germination and establishment of the New Zealand Loranthaceae (*Alepis flavida*, *Peraxilla colensoi*, *P. tetrapetala*, *Ileostylus micranthus* and *Tupeia antarctica*) were investigated. The most important bird dispersers were tui, bellbirds and silvereyes. These birds appear to provide reasonably good quality dispersal: fruits were swallowed whole and the seeds later defecated in germinable condition; birds tended to visit plants for only 1-2 minutes and eat a few mistletoe fruits each time.

Germinability of seeds ranged between species from moderate to high (17-96%). None of the study species of mistletoe germinated successfully unless the fruit skin (exocarp) was removed, by hand or by passage through a bird gut. While hand removal of the exocarp gave the same or higher percentage germination as bird removal, in the field bird dispersal is the only effective method of exocarp removal and is therefore essential. Dispersal was limiting at one of three sites studied (Craigieburn), suggesting that reductions in bellbird densities by introduced carnivores or competition for honeydew food sources may be indirectly affecting mistletoe reproduction.

Establishment and survival of seedlings on host branches was low (15-28% depending on species to production of first independent leaves, 0-14% after two years). Survival of adults over one year of the study was 80% for *Tupeia* and 91-95% in the other species, showing that frequent establishment of seedlings is necessary for population maintenance.

While disperser limitation does not seem to currently be a major threat to mistletoe survival, it must be considered as a possible factor both historically and in the future.

Keywords: Frugivory; bird dispersal; germination; establishment; disperser limitation; mistletoe; agents of decline.

Introduction

Mistletoes are stem hemiparasites, which grow on the branches of a host tree or shrub and take water, water-conducted nutrients and organic solutes from the host's xylem. There are two major mistletoe families, Loranthaceae and Viscaceae. The Loranthaceae are principally Southern Hemisphere in distribution, with between 50 and 80 genera (Barlow, 1983). New Zealand has six native species in the Loranthaceae. All have declined in abundance since European settlement. The decreases are attributed to habitat loss and introduced herbivores, especially the Australian brushtail possum (*Trichosurus vulpecula* Kerr) (Ogle and Wilson, 1985; Norton, 1991). In this paper we present evidence of the dispersal, germination and establishment of the New Zealand Loranthaceae, and evaluate to what extent their decline may be a secondary effect of reductions in numbers of their principal bird disperser species. In terms of Caughley (1994), we present data on the natural history of the species to determine which agents of decline may be most important.

Almost all Loranthaceae species have fleshy animal-dispersed single-seeded fruits (morphologically pseudocarps). Mistletoes worldwide are well known for their close relationships with birds, both for pollination and for dispersal (e.g., Kuijt, 1969; Barlow, 1983; Ladley and Kelly, 1995a). Dispersal is particularly important (and difficult) for mistletoes because the safe site for a ripe seed is the branch of another suitable host tree.

As a result, many mistletoes have close relationships with their avian dispersers (e.g., McKey, 1975). Despite the high specificity of some mistletoe dispersal systems, there are no recorded examples of obligate interdependence between a mistletoe species and a bird species throughout the geographical ranges of both mutualists (Reid, 1987a, 1991; Wheelwright 1988).

There have been suggestions that the germination of bird-dispersed seeds might be enhanced by passage through the gut of a bird (e.g., Temple, 1977), but evidence for this is generally lacking (Witmer and Cheke, 1991; Clout and Tilley, 1992). Quantitative studies on the germination and establishment of mistletoe species are rare worldwide and there has been almost no work on the New Zealand species.

There are five extant native Loranthaceae in New Zealand: *Alepis flavida*[1], *Peraxilla colensoi*, *P. tetrapetala*, *Ileostylus micranthus*, and *Tupeia antarctica*. A sixth species, *Trilepidea adamsii*, is thought to have become extinct in the last 50 years (Norton, 1991). All of the species are endemic, except *Ileostylus* which is also found on Norfolk Island (Barlow, 1966). Four of the species (*Alepis*, *P. colensoi*, *P. tetrapetala* and *Trilepidea*) are bird pollinated, with quite complex explosive flower mechanisms in *Peraxilla* and *Trilepidea* (Ladley and Kelly, 1995a, b). The only published works on the reproduction of these species examined seedling development and haustoria of *Ileostylus* (Menzies, 1954) and summarized the life history of *Tupeia* (Smart, 1952).

The aims of this study were to:
(1) determine the bird species involved in fruit dispersal of *Alepis flavida*, *Peraxilla colensoi*, *P. tetrapetala*, *Ileostylus micranthus*, and *Tupeia antarctica*, and the extent and quality of dispersal;
(2) determine germination percentages for seeds of each species, including the effect of seed treatment such as passage through a bird;
(3) determine survival and establishment in the field of germinated seedlings and adult plants;
(4) evaluate the importance of dispersers to reproduction and population maintenance in New Zealand mistletoes.

Methods

Study species and sites

The study was carried out between November 1992 and May 1995 at four sites.
1. Craigieburn (NZMS 260 K34 050831): *Alepis*, *P. tetrapetala*. The study site was in Craigieburn State Forest Park, inland Canterbury, at an altitude of 940 m a.s.l. The area is mountainous with a mean annual rainfall of 2000 mm. The climate, landform and vegetation of the area are described in Shanks *et al.* (1990). The vegetation of the area is predominantly *Nothofagus solandri* var *cliffortioides* forest. Two mistletoe species, *Alepis* and *P. tetrapetala* occurred at the site, both parasitising *N. solandri* var *cliffortioides*.
2. Wainui (NZMS 260 N37 021091): *Tupeia*. Wainui is situated in the Banks Peninsula Ecological District. The site has an altitude of 10 m with a mean annual rainfall of 700 mm; Wilson (1992) gives a detailed account of landform, vegetation and climate of the area. The vegetation of the area is heavily modified with little of the pre-human vegetative cover remaining. A large population of *Tupeia* grew on the introduced shrub *Chamaecytisus palmensis* along a 500 m strip of roadside.
3. Wakefield (NZMS 260 N27 121802): *P. colensoi*, *Ileostylus*. *Ileostylus* and *P. colensoi* were studied in Pigeon Valley, Wakefield, 35 km south of Nelson. Elevation of the study sites varied from 60 m to 120 m. The rainfall for the area averaged between 1000 mm and 1150 mm (Kelly, 1982). The area is predominantly pastoral farmland and exotic plantations. However, pockets of remnant native vegetation are scattered through the area. These pockets of native vegetation consist of tall podocarp forest, on the alluvial flats and valley floors, and *Nothofagus* (predominantly *N. menziesii*) stands in other parts of the area. The *Ileostylus* study population grew on scattered remnant *Podocarpus totara*. *P. colensoi* mistletoes occurred along the entire length of the valley in isolated stands of *N. menziesii*.
4. Kerr's Bay, Lake Rotoiti (NZMS 260 N29 972334): *Alepis*, *P. colensoi* and *P. tetrapetala*. Adults of all three beech mistletoes were mapped around Kerr's Bay (altitude 615 m) where they occurred in mixed *Nothofagus* forest. Survival of these adults was monitored over one year.

Fruit dispersal

Observations were made on the fate of flowers followed until fruit set or abortion. Tagged flowers and fruits were checked at least every four weeks, starting from petal abscission and continuing through the fruiting season until all had gone. The fate of each flower was recorded either as aborted, fruit ripened and dispersed, or fruit over-matured and not dispersed.

Observations of fruit dispersal began within a week of the first ripe fruits being noticed at each site

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[1] Plant nomenclature follows Allan, 1961; Connor and Edgar, 1987; and Webb, Sykes and Garnock-Jones, 1988

(April 1993 to June 1993), but did not include *P. tetrapetala* as fruits did not ripen normally (see below). For each foraging visit by an avian disperser to an individual mistletoe, the following was noted: species of bird, behaviour of bird including how it ingested fruits, length of visit, and number of fruits taken.

The importance of bird dispersers for seed germination was tested by experiments measuring whether germination occured when access by birds was prevented. Cloth mesh bags, 200 mm by 450 mm, were placed on up to 5 individual branches for each species, except *Alepis*. Because of the different *Alepis* inflorescence structure, 60 x 50 mm bags were used to cover individual inflorescences. Bags were secured over the branches as the fruit began to ripen and remained covering the fruits for the duration of the dispersal season.

Any fresh bird droppings noticed on plants or the ground at the study sites in the course of field work were examined for mistletoe material, and if present the contents were identified. Generally, the bird species producing the dropping could not be determined.

Fruit size (maximum diameter on shorter axis) was measured for 35 randomly selected fruits of each species. The wet weights of the fruits and seeds were measured.

Germination and establishment

Two types of germination study were conducted: field observations of bird-disseminated seeds, and growth cabinet work. All naturally-disseminated mistletoe seeds located at the field study sites were tagged with jewellers tags and the following details recorded: host species, diameter of the host branch, health of the seed and host. The tagged seeds were revisited at least every four weeks until germination had occurred (i.e., the radicle tip became visible) and continued until the hypocotyl had touched the host branch. A generalised additive model, with logistic link function and binomial error distribution was used to test for the effect of branch diameter on the probabilities of seed germination and seedling establishment. The analysis was carried out using Genstat Software (Genstat 5 Committee, 1987).

The effects of exocarp removal and passage through a bird gut on germination of *Ileostylus*, *Alepis*, *Tupeia* and *P. colensoi* seeds were studied in a Contherm growth cabinet. *P. tetrapetala* seeds did not ripen normally in 1993 so this species was not included. The cabinet was maintained on a 12 hour photoperiod at 15° C alternating with dark at 7° C. Three treatments were compared in the growth cabinet: bird-cleaned seeds, hand-cleaned seeds and whole fruits. The bird-cleaned seeds had passed through a bird and were collected (usually off of the ground) from the study sites. For hand-cleaned seeds, ripe fruit were picked and the seeds were manually squeezed out of the fruit skin. For both bird-cleaned and hand-cleaned seeds the exocarp and fruit pulp was removed but a viscin layer remained on the outside of the seed. Finally, whole ripe fruits were picked and placed in the cabinet. All the treatment seeds and fruits were placed on damp filter paper in petri dishes. Progress of the seeds and fruits in the dishes was checked weekly for about 10 months, by which time the ungerminated seeds were dead. *P. tetrapetala* seeds from the 1995 season were treated as above, except that no bird treatment seeds were collected, and germination was carried out at room temperature (15 - 20° C).

The probability of germination in different treatments (excluding *P. tetrapetala*) was analysed using a Generalised Logistic Model, incorporating a logistic link function and binomial error distribution, using Genstat. The GLM tested for between-species differences across all treatments and between-treatment differences across all species. To compare bird-cleaned and hand-cleaned germination within each species, a 2 X 2 chi-square analysis was performed for each species. To keep the experiment-wise chance of a type 1 error constant, the critical level for the chi-square tests was set to 0.0125 (0.05/ 4 species tested).

Observations on the establishment of *Alepis*, *Ileostylus*, and *P. colensoi* seedlings were made by revisiting the tagged disseminated seeds, at least every four weeks until January 1994, and then six monthly until May 1995 (30 months after germination). On each visit, the health and condition of the seedlings and host plants were recorded. Establishment of *Alepis* and *P. colensoi* seedlings was defined by the production of the first pair of leaves. As germinating seeds of *Ileostylus* can produce their first set of leaves prior to making haustorial contact with the host (Smart, 1952), establishment of *Ileostylus* seedlings was defined by the appearance of the second pair of leaves.

Adult survival

Adult mistletoes of all available species were mapped over summer 1992/93 during field work at Craigieburn, Wakefield, Wainui and Kerr's Bay. These sites were revisited 12 months later and mortality among the mapped plants was recorded. All data for each species were amalgamated as there were insufficient data to analyse for between-site differences. Differences between species were tested with chi-squared analyses.

Results

Fruit dispersal

The percentage of flowers that matured into fruits varied from 26.9% for *P. tetrapetala* to 82.1% for *Alepis* (Table 1). In all five species 18 - 73% of the flowers abscised without ripening fruit. Large numbers of over-mature (non-dispersed) fruit were recorded only for *Alepis* and *P. tetrapetala*, both at the Craigieburn site (Table 1). It should be noted that the results for *P. tetrapetala* may have been abnormal, as the 1992/93 flowering season was later than usual and the young fruit abortion rate was high (73.1%).

Ripe fruits were most abundant at the study sites from April to June (late autumn to winter), but some were present until spring (October), as shown in Table 2. The fruits of *P. tetrapetala* at Craigieburn remained green when ripe, developing a dark green ring at the distal end, rather than turning yellow as indicated by Poole and Adams (1986).

The fruits of all species were bird dispersed, with tui, bellbirds and silvereyes observed taking fruits. Other authors have recorded four additional bird species (Table 2). For all species, fruits were taken in the same manner. Birds grasped the ripe fruit in their beak and twisted, detaching the fruit from its stalk. The bird swallowed the fruit and the seed was later defecated. Birds were not seen regurgitating seeds.

Below the exocarpic skin of Loranthaceae fruit is a layer of glue-like viscin, which sticks the seed to the substrate once dispersed. When first defecated, seeds of the study species were whitish in colour and the viscin around the seed was wet and sticky. The viscin on the seeds of *Alepis*, *P. colensoi* and *P. tetrapetala* formed a ring around the base of the seed, whereas in *Ileostylus* and *Tupeia* the viscin layer completely covered the seed. Within hours of defecation the viscin dried and became clear, but remained somewhat sticky.

The number of fruits removed per visit and duration of visits varied between bird species (Table 3). For *Alepis*, *P. colensoi* and *Ileostylus*, birds took fruits before they were fully ripe, suggesting fruits were a preferred food item. The alternative foods being used while fruit were ripening was also of

Table 1: *Fate of flowers (%) of each mistletoe species in the 1992/93 season.*

	Alepis flavida	*Ileostylus micranthus*	*Peraxilla colensoi*	*Peraxilla tetrapetala*	*Tupeia antarctica*
Aborted before ripening	17.9	42.2	60.5	73.1	39.0
Fruits ripened and dispersed	64.5	57.8	39.4	0	61.0
Fruits over-matured and fell off	17.6	0	0.1	26.9	0
Total number of flowers	609	1143	3337	1046	755

Table 2: *Bird dispersers seen taking fruits of New Zealand mistletoes (arranged in decreasing order of size), and summary of fruit characteristics.*

Bird species	*Peraxilla colensoi*	*Alepis flavida*	*Ileostylus micranthus*	*P. tetrapetala*	*Tupeia antarctica*	Gape size[a] (mm)
NZ pigeon	4				4	14
Tui	1, 2		1	5		9
Blackbird	5			5		9
Bellbird	1, 5	1	1	5	1	6
Silvereye	3, 5	1	1	5		5
Yellowhead				2		>5
Fruit dia (mm)[b]	6.88 ± 0.01	6.09 ± 0.15	4.27 ± 0.08	4.15 ± 0.29	4.05 ± 0.08	
Fruit ripening (1993)	Apr-May(-Sep)	(Apr-)May-Jun	(Apr-)May-Jun	[Jun-Nov][c]	May-Sep	
Fruit colour	yellow	yellow (or red)	yellow	green	white, purple flecks	
Fruit weight[b] (g)	0.275 ± 0.009	0.151 ± 0.01	0.057± 0.003	0.064 ± 0.008	0.057 ± 0.02	
Seed weight[b] (g)	0.090 ± 0.004	0.024 ± 0.001	0.042 ± 0.003	0.030 ± 0.003	0.035 ± 0.002	

Sources: 1 this study, 2 C. O'Donnell *pers. comm.*, 3 S. Barnett *pers. comm.*, 4 P. Wilson *pers. comm.*, 5 O'Donnell and Dilks (1994), who also record kaka feeding on fruits of "*Peraxilla* spp".
Notes: [a] from Clout and Hay (1989). [b] mean ± 95% C.I. of 35 fruits; weights are fresh weights. [c] unusual season, ripening Apr-Oct in 1995, see text.

Table 3: *Bird visitors to fruiting mistletoes. Data are means ± 95% C.I., with sample sizes in parentheses.*

	Alepis flavida	*Ileostylus micranthus*	*Peraxilla colensoi*	*Tupeia antarctica*
(a) Number of fruits taken per visit				
Tui	-	12.8±14.7 (6)	2.0±2.1 (6)	-
Bellbirds	1.2±0.9 (5)	2.5±19.1 (2)	2.7±0.6 (27)	5.1±3.7 (13)
Silvereye	1 (1)	nd	0	-
(b) Duration of bird visits, in seconds.				
Tui	-	150±55 (31)	200±34 (51)	-
Bellbird	37.5±24 (4)	30 ± 0(3)	57±16 (27)	40±27 (9)
Silvereye	nd	60 ± 0(4)	0	-
Total hours of observations	25	13	19	11

- bird species absent.
0: bird species present but ignoring the fruit.
nd: bird present and visiting mistletoe, but no data collected.

interest. During the *Alepis* dispersal period, bellbirds spent most of their time harvesting honeydew from *Nothofagus* trunks. When ripe fruits of *Ileostylus* were being harvested, the same birds were also eating the fruits of *P. totara*, its host tree. At Wainui, bellbirds harvesting *Tupeia* fruits were also collecting nectar from flowers of the host *Chamaecytisus palmensis*.

Interspecific competition between birds was observed at the Wakefield study sites on *P. colensoi* (between tui and bellbirds) and on *Ileostylus* (between tui, bellbirds and silvereyes). Tui dominated bellbirds and silvereyes, and bellbirds dominated silvereyes. This affected the visitation rate and length of visit made by the different birds (Table 3). The smaller birds made shorter visits than tui. Only a few fruits were generally removed per visit (Table 3).

Bird droppings contained only a few seeds each (Table 4). The contents of droppings gave an indication of where else the birds were visiting (potential dispersal sites). Droppings which

contained *Ileostylus* seeds also contained *P. totara* seeds, as expected, since the birds were seen feeding on both plants (see above).

For all species the effect of bagging ripening fruits was the same. All the bagged fruits over-ripened, fell off the fruit stalk and rotted. The seeds of *Ileostylus*, *Alepis* and *P. colensoi* within these fruits showed no sign of germinating. Several of the seeds within the overripe *Tupeia* and *P. tetrapetala* fruits began to germinate, but the hypocotyl did not emerge through the fruit skin.

Germination

The process of germination of *Alepis*, *P. colensoi* and *Tupeia* seeds was similar. The radicle tip germinated from the distal end of the seed. As the green hypocotyl grew from the seed, a disc of pale yellow tissue (the developing holdfast) formed at the tip of the radicle with a small brown spot at its centre (Smart, 1952). The hypocotyl continued to grow until the radicle tip contacted the substrate

Table 4: *Contents of bird droppings containing mistletoe material (mean ± 95%C.I.).*

	Number of seeds per dropping	Number of fruit skins per dropping	Other identifiable contents of droppings	Total number of droppings
Alepis flavida	5.06±1.17	3.31±1.24	2 wasp abdomens.	30
Ileostylus micranthus	6.98±1.68	1.06±0.59	20 *Podocarpus totara* seeds 1 *Peraxilla colensoi* seed	48*
Peraxilla colensoi	1.77±0.61	0.77±0.72	4 *P. totara* seeds 1 *Dacrycarpus dacrydioides* seed 12 *I. micranthus* seeds	26*
Tupeia antarctica	2.73±1.77	1.82±1.05	2 *Coprosma* spp. seeds	12

* one dropping, containing both *P. colensoi* and *I. micranthus* seeds, is counted in both rows.

usually within 8 weeks of the seed germinating. However, if the radicle did not make contact with the substrate, the hypocotyl continued to extend out of the endosperm until the cotyledons had nearly left the endosperm. Once contact with the host branch had occurred a period of inactivity ensued apart from a clear cement being secreted from the endosperm of the seed and from the holdfast. Eventually, if the seedling did not die, the hypocotyl would straighten, pulling the two cotyledons out of endosperm usually at about 24 weeks after germination. The tiny green cotyledons function as leaves, with the first pair of true leaves usually appearing about 4 weeks later.

In contrast, in *Ileostylus* the emerging radicle did not break through the coat of viscin. Rather, the green hypocotyl curved towards the substrate while still under the clear viscin layer. As with the other mistletoe species a whitish ball of tissue formed at the end of the hypocotyl. Germination also differed in that the cotyledons were retained within the

endosperm. The first set of leaves appeared about 3 weeks after germination; these leaves were about 7 mm long.

All species had high germination percentages in the field (Table 5a). Germination percentage was not significantly affected by the diameter of the host branch in *Alepis* ($F_{1, 64} = 1.01$, NS), *Ileostylus* ($F_{1, 34} = 1.39$, NS) or *P. colensoi* ($F_{1, 57} = 0.19$, NS). Successful germination of bird-disseminated seeds was also observed in the field on rocks, concrete, and fenceposts.

In the growth cabinet, seed treatment had a large effect on germination levels (Table 5b). None of the seeds left in whole fruits successfully completed germination. Some *Tupeia* and *P. tetrapetala* seeds began germination inside fruits, but the hypocotyl did not emerge through the fruit skin and eventually the seeds died. Analysis of the germination data (excluding *P. tetrapetala*) found significant differences between species (mean deviance ratio $D_{3, 32}$ =

Table 5: *Germination and establishment percentages of mistletoe seeds (means $\pm$ 95%C.I, with sample sizes in parentheses).*

(a) Field germination and establishment of bird-dispersed seeds at the study sites.

	Germination of seeds (%)	Establishment of germinated seeds (%)
Alepis flavida	82 $\pm$ 18 (66)	28 $\pm$ 6 (49)
Ileostylus micranthus	69 $\pm$ 8 (36)	16 $\pm$ 6 (25)
Peraxilla colensoi	82 $\pm$ 4 (59)	15 $\pm$ 40 (41)

(b) Germination of seeds (%) in growth cabinet. Seeds collected in 1993 except for *P. tetrapetala* = 1995.

	Whole fruits	Bird-cleaned seeds	Hand-cleaned seeds	χ2 (bird vs hand)[b]
Alepis flavida	0$\pm$0 (95)	26$\pm$2 (223)	17$\pm$2 (199)	4.40 NS
Ileostylus micranthus	0$\pm$0 (40)	53$\pm$4 (142)	46$\pm$4 (146)	1.12 NS
Peraxilla colensoi	0$\pm$0 (21)	41$\pm$4 (169)	83$\pm$2 (157)	58.6 ***
Peraxilla tetrapetala	0$\pm$0 [5$\pm$15[a]] (80)	no data	96$\pm$6 (152)	no data
Tupeia antarctica	0$\pm$0 [26$\pm$4[a]] (120)	50$\pm$8 (133)	83$\pm$2 (120)	29.1 ***

[a] seeds germinated inside fruit skins, but did not emerge outside it. [b] Chi-squared test statistic for bird-cleaned vs hand-cleaned fraction germinating (NS not significant, *** $P < 0.001$); see text.

Table 6: *Survival of mistletoe seedlings germinating in autumn 1993, and adult plants from 1992/93 season.*

	Number of germinated seeds	% seedlings alive after 6 months	% seedlings established*	% seedlings alive after 1 year	% seedlings alive after 2 years	Initial number of adult plants	% of adult plants surviving 1 year
A. flavida	49	69	28.6	28.6	14.3	81	91.4
I. micranthus	25	44	16	12	4	76	94.7
P. colensoi	41	37	15	2.4	0	24	91.6
P. tetrapetala	-	-	-	-	-	36	94.4
T. antarctica	-	-	-	-	-	50	80.0

* Defined by appearance of the first pair of leaves (after the cotyledons); for *I. micranthus,* defined by appearance of the second set of leaves. - no data

5.62, $P < 0.01$) and between treatments ($D_{2, 32} = 8.01$, $P < 0.01$) but no significant interaction effect. In no species was there a significantly higher germination percentage for bird-cleaned seeds than hand-cleaned seeds, but in *Tupeia* and *P. colensoi* bird-cleaned seeds had significantly lower germination (Table 5).

Few germinated seeds successfully established (Tables 5 and 6). *Alepis* had the highest establishment percentage. The probability of a seed establishing (Table 5a) was not affected by the diameter of the host branch in *Alepis* ($F_{1, 52} = 0.06$, NS), *Ileostylus* ($F_{1, 23} = 0.02$, NS) or *P. colensoi* ($F_{1, 39} = 0.01$, NS) although sample sizes were small. Approximately 12 months after germination *Alepis* and *P. colensoi* seedlings usually consisted of a single main shoot about 10 mm long (the straightened hypocotyl) terminating in the green cotyledons and several small leaves. The *Ileostylus* seedlings had about 6 small leaves which emerged directly from the seed endosperm. After 24 months, *Alepis* and *P. colensoi* seedlings (the latter sown in 1994) had grown to an average of 15 mm and consisted of up to 7 small leaves. Some of the *Alepis* seedlings also had started growing a short secondary runner. By 24 months, only one *Ileostylus* seedling remained alive: it had a 25 mm long stem with 6 leaves, and a 45 mm long secondary runner. Survival to 24 months was highest (14%) in *Alepis*, and lowest (0%) in *P. colensoi*.

Survival

Deaths of adult mistletoes were due to various causes, including the host branch breaking off or dying, or the host tree dying. Survival of adult plants between 1992/93 and 1993/94 was 91-95% in each species, except for *Tupeia* with 80% survival (Table 6). The differences among species were significant ($\chi^2 = 9.91$, d.f. = 4, $P = 0.042$) which was due to *Tupeia* being lower than the rest combined ($\chi^2 = 7.54$, d.f. = 1, $P = 0.006$). With such a high rate of turnover of adults, frequent establishment of seedlings is necessary for the population to maintain itself.

Discussion

Dispersal quantity

Fruits of all the native mistletoes were dispersed by birds, principally the native tui and bellbird, and to a lesser extent the self-introduced silvereye. All mistletoe species have small enough fruits to be taken by a range of bird species, although silvereyes can apparently take *P. colensoi* fruits which are

larger than their gape width (Table 2). In South Westland, silvereyes were seen bashing *P. colensoi* fruits in their beaks against branches in order to ram the fruit down their throats (S. Barnett, *pers. comm.*). All the fruit-frugivore relationships shown here are unspecialised (the birds are all generalist feeders with fruit being a small part of the diet: O'Donnell and Dilks, 1994). Nevertheless, very few introduced birds have been recorded feeding on mistletoe fruits, even where the plants occur in mixed native and exotic vegetation with abundant introduced birds, such as at Wakefield and Wainui.

For three mistletoe species (*Ileostylus*, *P. colensoi* and *Tupeia*), essentially all of the fruits were taken by dispersers before they became over-ripe. However, the two species studied at Craigieburn (*Alepis* and *P. tetrapetala*) both had a substantial fraction of their non-aborted fruits not taken by a bird in 1992/93. Even though the *P. tetrapetala* fruit did not appear to ripen normally, these data suggest a shortage of willing dispersers at Craigieburn, and that dispersal was limited by bird availability. The bellbirds in the area at the time were feeding preferentially on honeydew produced by the sooty beech scale (*Ultracoelostoma brittini* Morales). During January to March honeydew availability is very low in the area due to harvesting by wasps (Moller and Tilley, 1989; Markwell, Kelly and Duncan, 1993). It is possible that particularly since the arrival of common wasps (*Vespula vulgaris* L.) in the area 15 years ago, less honeydew is available to bellbirds during summer when wasps and bees are abundant, which may have reduced bellbird populations (Moller and Tilley, 1989). When wasps die off in autumn, the honeydew standing crop increases markedly. This may provide an attractive, abundant food source for the remaining bellbirds just as the mistletoe fruits are ripening, to the detriment of dispersal of the fruits.

Another possible explanation for inadequate dispersal is that bird numbers have been reduced in the areas due to other factors such as habitat loss and predation by stoats, cats and rats (King, 1990). If bird populations have declined, in the peak of the mistletoe fruiting season there may be more fruit than the remaining birds can use. In the literature, there is no mention of the fruit of any overseas mistletoes becoming over-mature on the plant.

Dispersal quality

Dispersal quality is essentially the fraction of dispersed seeds which land in a safe site in germinable condition. In mistletoes this depends on the behaviour of dispersers. The method of handling fruits, size of disperser, and interspecific competition

between fruit-eating birds affect the probability of the mistletoe seed being deposited in a safe site for germination and establishment (i.e., the branch of a suitable host tree).

There are three different methods used by birds to handle fleshy mistletoe fruits: defecation, regurgitation and pecking. Defecation of seeds is the standard method of mistletoe seed dispersal in southeast Asia (Docters van Leeuwen, 1954; Davidar, 1983a), and in Australia, where honeyeaters (Meliphagidae) and the mistletoebird (*Dicaeum hirundinaceum*) are principal dispersers (Calder, 1981; Liddy, 1983; Reid, 1989, 1990). Regurgitation of mistletoe fruits has been reported in Africa (Godschalk, 1985; Polhill, 1989) and South America (Frost, 1980; Parker, 1981; Davidar, 1983b; Monteiro, Martins and Yamamoto, 1992). Pecking (eating fruit pulp without ingesting the whole fruit) is ineffective at mistletoe dispersal and birds which do it are usually of secondary importance as dispersers.

Godschalk (1985) found in Africa that the time from when seeds are swallowed until they are regurgitated is shorter than for those mistletoe seeds that are swallowed and defecated, thus decreasing the possibility that the bird is in a new plant. In this study all seeds were swallowed whole, and defecated later. Reported gut passage times for small frugivorous birds (including silvereyes) are typically 15 - 80 minutes, although in some flowerpeckers and the mistletoe bird it may be as low as 3 minutes (Murphy *et al.*, 1993). Since these gut passage times are long compared to single visits to mistletoe plants (Table 3), most seeds would be defecated away from the parent plant (unless birds return repeatedly to the same plants), enhancing dispersal quality (Howe, 1993). While the smaller birds took fewer seeds per visit to a mistletoe plant, and spent less time per visit, even the largest birds (tui) still made relatively short visits.

While removal of the fruit pulp is necessary for successful germination, seed germination percentages were the same or lower after passage through a bird than when the pulp was removed by hand. The data suggest damage to around half the *Tupeia* and *P. colensoi* seeds passed through bird guts, but caution is required. Hand-cleaned seeds came from ripe fruits collected fresh from the plants, whereas bird-cleaned seeds were collected from droppings whenever they were encountered. The species of bird producing droppings was unknown; for *Tupeia* most were probably bellbirds, but both tui and bellbirds were common around *P. colensoi*. More controlled experiments are required to confirm lower germination due to damage to mistletoe seeds in bellbird and tui guts.

One common behavioural characteristic seen in both tui and bellbird which assists dispersal is perching in high branches; a high perch increases the likelihood of defecated seeds landing on a branch (e.g., Reid, 1989). In three of the four species for which observations were made, dispersers were also visiting uninfested host plants for other food sources (*P. totara* fruits in the case of *Ileostylus*, *C. palmensis* flowers in the case of *Tupeia*, and beech honeydew in the case of *Alepis*). This must assist in concentrating seed deposition in the most suitable microsites for mistletoe establishment, increasing dispersal quality.

Overall, dispersal quality for New Zealand mistletoes is enhanced by short visit durations, but reduced by apparently reduced germinability of seeds in two species and by lack of any behavioural adaptations to place defecated seeds onto branches (*cf.* Reid, 1987a).

Germination

Our data show that for the New Zealand Loranthaceae, germination seemed to be insensitive to substrate, and in three species there was no significant effect of host branch diameter on the probability of a seed germinating or establishing.

In contrast, germination is strongly retarded by presence of the exocarp. The growth cabinet experiments showed that passage through a bird's digestive tract is not necessary for germination, as hand-cleaned seeds germinated as well or better. It would seem that removal of the exocarp is the important prerequisite for germination, as was also found by Lamont and Perry (1977). Yan (1993b) found germination of *Amyema preissii* and *Lysiana exocarpi* was 93-100% for seeds passed by mistletoebirds and 90-97% for seeds passed by spiny-cheeked honeyeaters, and that these percentages were comparable to those of seeds that had the exocarp manually removed. More generally, Burrows (1993) showed that in a number of fleshy-fruited New Zealand woody plants, seed germination is inhibited by the fruit pulp. In these mistletoe species, the seeds die relatively quickly if not removed from the fruit, whereas in the species described by Burrows, germination is merely delayed until the fruit pulp rots.

Therefore, passage through a bird gut is no better, and sometimes worse, than simple removal of the exocarp by hand. However, under natural conditions it is only through birds that the removal of the exocarp can occur. This is highlighted by the fate of the fruits that were bagged for the duration of the fruiting season. If the fruits remained on the plants they became over-mature and rotted, and the embryos died. Similar results were found in bagging

experiments with *Amyema quandang* (Reid, 1987b). Therefore, fruits which are not dispersed by a bird have no chance of successfully germinating and hence establishing a new plant. This makes bird dispersal much more important for mistletoes than for most plants, where non-dispersed seeds may still germinate under the parent. In this light, the disperser limitation shown at Craigieburn could be seriously affecting regeneration.

Establishment and growth

The germination and establishment of New Zealand mistletoes is slow when compared to the early growth of tropical mistletoes. Slow rates of growth were particularly noticeable for *Alepis*, *P. colensoi* and *P. tetrapetala*, with the seedlings consisting of one main stalk and no more than eight leaves after two years of growth. Yan (1993a) found that the initially slow growth of *A. preissii* and *L. exocarpi* seedlings was related to slow development of the haustorial connection to the host xylem. Penetration of host cells by the haustorial cells of *Ileostylus* seedlings occurred 6 to 9 months after dissemination of the seed (Menzies, 1954). Both *Alepis* and *P. tetrapetala* are 6-8 years old before they commence flowering (Powell and Norton, 1994), limiting the ability of these species to respond quickly to demographic pressures such as an increase in herbivory.

Conclusion: agents of decline in New Zealand Loranthaceae

In many parts of New Zealand, native Loranthaceae are less common now than they were last century. The traditional view of this decline is that it is due to habitat clearance (Norton, 1991), and more recently, to possum browsing (Ogle and Wilson, 1985). Our data on fruit dispersal in the New Zealand Loranthaceae show that germination is entirely dependent on bird dispersal, as the only effective means of removing the exocarp. Dispersal is almost wholly by native bird species (and the self-introduced silvereye). Introduced frugivorous birds such as blackbirds and thrushes take few mistletoe fruit, so cannot compensate for the decrease in native bird densities following the introduction of mammalian predators. At one of our three sites, dispersal was partially limited not by fruit production but by bird availability; this may be related to reduced densities of bellbirds at this site, or to competitive interactions with introduced insects for honeydew food supplies.

Therefore, while these dispersal data do not suggest an immediate threat to the continued reproduction of the mistletoe species in question, they do show that population densities may now be limited partially by availability of bird dispersers. Since mistletoes are unable to reproduce without dispersers, this is another factor which must be taken into account in the analysis of agents of decline (Caughley, 1994) of native mistletoes.

Acknowledgements

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