

Explosive flowering, nectar production, breeding systems, and pollinators of New Zealand mistletoes (Loranthaceae)

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Abstract The six New Zealand loranthaceous mistletoes fall into two groups based on pollination biology. Four (*Alepis flavida*, *Peraxilla colensoi*, *P. tetrapetala*, and *Trilepidea adamsii*) are bird pollinated with hermaphrodite flowers while the other two (*Ileostylus micranthus* and *Tupeia antarctica*) are dioecious or sub-dioecious and insect pollinated. We provide data on the pollination biology of the five extant species (*Trilepidea* is extinct).

The two *Peraxilla* species and *Trilepidea* have recently been shown to have explosive flowers. Here we show that *Alepis* has weakly facultatively explosive flowers. The world distribution of explosive mistletoe flowers suggests that the syndrome has arisen a number of times independently within the family, and is found in about half the putatively ancestral genera.

The principal avian visitors to the bird-pollinated species were tui and bellbirds; introduced species are numerically unimportant as pollinators. The nectar production schedules of *Alepis* and *Peraxilla* encourage single-visit pollination as little nectar is produced after the flowers open. However, when bird densities are high, buds of *Peraxilla* may be forced open prematurely, encouraging multiple visits.

Alepis is highly self-compatible and its flowers achieve good seed set in the field even when all pollinators are excluded by mesh bags, partly because pollen contacts the already-receptive stigma before the bud opens. Unvisited *Peraxilla* buds do not open, but their morphology allows a low level (11–22%) of self-pollination in the bud.

The sex ratio of *Tupeia* at Wainui (Banks Peninsula) was 3:1 female:male, while *Ileostylus* at Wakefield (Nelson) was subdioecious with a 2.5:1:1 female:male:hermaphrodite ratio. Hermaphrodite *Ileostylus* plants set seed even when pollinators are excluded, so self-pollination is possible in this species.

Results suggest different species vary in their susceptibility to pollen limitation affecting reproduction. The insect-pollinated species have unspecialised pollination syndromes and are probably adequately pollinated by native and/or introduced insects; *Ileostylus* is also self-compatible. The bird-pollinated species are more susceptible with specialised pollination systems depending principally on endemic birds, but the effect is reduced in *Alepis* as its flowers can open themselves and it achieves good seed set even when pollinators are excluded. *Peraxilla* spp. seem most at risk with obligately-explosive flowers and only low seed set without pollinators. Historical declines in the North Island have been greatest in the species with the most exacting pollination requirements. Long-term conservation of these mistletoes will require conservation of tui and/or bellbirds.

Keywords Loranthaceae; *Peraxilla*; *Alepis*; *Tupeia*; *Ileostylus*; *Trilepidea*; bird pollination; self-compatibility; dioecy; breeding systems; explosive flowering; nectar production

INTRODUCTION

New Zealand has six species of native loranthaceous mistletoe, and there is concern that all have declined in abundance (de Lange et al. 1997). Originally this

was attributed to habitat clearance, overcollecting by botanists, and introduced brushtail possums (*Trichosurus vulpecula*), which all may increase mortality in adult mistletoes (Norton 1991). Recently Ladley & Kelly (1995a, 1995b, 1996) suggested that reproductive difficulties in pollination and dispersal could have affected recruitment and been partially responsible for the declines. In this paper we provide data on pollination of extant native Loranthaceae and evaluate whether they are at risk from pollination failure.

Within the 78 genera of Loranthaceae worldwide (Barlow et al. 1989), most species have large bird-pollinated hermaphroditic flowers, in one of two basic forms: those that open suddenly when visited by a pollinator, known as explosive flowers; and those that open normally over a longer period and are then visited by birds. Explosive flowers may be obligate, where the flower cannot open itself unless visited by a bird, for example as in most Loranthaceae (Docters van Leeuwen 1954; Feehan 1985; Polhill 1989; Ladley & Kelly 1995a); or facultative, where a flower has a period when it is ready to be sprung but will eventually open even if not visited, for example as in the mangrove *Brugiera hainesii* (Noske 1993). Explosive flowering was first described by Evans (1895) for two African mistletoes, *Tapinanthus kraussianus* and *Erianthemum dregrei*. In such flowers, anthers characteristically dehisce in the mature bud, and mature buds usually contain large amounts of nectar (Docters van Leeuwen 1954).

Explosive mistletoe flower mechanisms are either two-stage (flower opening and pollination take place in separate movements) or the more specialised one-stage (a single movement achieves both; Pohill 1989). In both cases some degree of behavioural specialisation by the pollinator is required. If only certain birds know how to, or are large enough to, open flowers then the range of potential pollinators for the plants is reduced. For example, in Indonesia, explosive *Macrosolen* flowers offered to four species of nectarivorous birds which had no previous experience with the plant were not opened (Docters van Leeuwen 1954, p. 139). Moreover, if the plant species becomes uncommon, previously capable pollinating bird species may forget how to open the flowers (Ladley & Kelly 1995a).

The composition of the pollinator assemblage among birds which visit explosive mistletoe flowers is also affected by dominance relationships between the birds, which in turn is modified by the exact timing of nectar production. In most species,

the buds already contain nectar so that they provide a tamper-proof container with an assured reward (Ladley & Kelly 1995a). Therefore, foraging on ripe unopened buds is likely to be energetically more rewarding than revisiting already-opened flowers. In Africa, Gill & Wolf (1975) showed that larger sunbirds tend to feed principally on unopened buds, excluding the smaller bird species which therefore have to concentrate on already-opened flowers.

Although most Loranthaceae are bird-pollinated, some species have insect-pollinated flowers and are dioecious (having separate male and female plants); the flowers of these species are usually small and not brightly coloured (Kuijt 1969). New Zealand has six native Loranthaceae. Four, *Alepis flavida**, *Peraxilla colensoi*, *P. tetrapetala*, and *Trilepidea adamsii* are bird-pollinated with hermaphroditic flowers. The remaining two species, *Ileostylus micranthus* and *Tupeia antarctica*, are thought to be insect-pollinated (Barlow 1966) and are dioecious or sub-dioecious. All species are endemic, except for *Ileostylus* which also occurs on Norfolk Island. *Trilepidea* has become extinct this century (Norton 1991) but the other species are still extant.

Recent research into the floral biology of the New Zealand Loranthaceae has documented explosive flower opening in *Peraxilla* and *Trilepidea* (Ladley & Kelly 1995a, 1995b; Kelly et al. 1996). Explosive flowers in Loranthaceae are well known from Africa and to a lesser extent India and Indonesia, but were previously unreported from Australasia. Therefore, the pollination systems of *Peraxilla* and *Trilepidea* are most similar to those of the African mistletoes. However, other data suggest that the two groups are not closely allied within the family. All of the New Zealand Loranthaceae are thought to be ancestral relict genera, based on chromosome numbers and the presence of ancestral characteristics, including secondary runners (Kuijt 1969; Barlow 1983; Martin 1983). Therefore, either explosive flowers have arisen independently several times, or the current view of New Zealand Loranthaceae as ancestral must be revised.

Previous research on the floral biology and pollination of the New Zealand mistletoes is limited. Smart (1952) showed that *Tupeia antarctica* is dioecious. The four-petalled green-yellow flowers of

*Plant nomenclature follows Allan 1961, Connor & Edgar 1987, and Webb et al. 1988.

both sexes are very small and apparently pollinated by insects, such as small flies, which are attracted by the honey disc in the centre of the flower. *Ileostylus micranthus* is thought to have a subdioecious breeding system (i.e., there are some hermaphrodite individuals), and the flowers are insect-pollinated (Menzies 1947). *Ileostylus micranthus* is apparently the only subdioecious species in the Loranthaceae. More recently Ladley & Kelly (1995a, 1995b) and Kelly et al. (1996) described explosive pollination in *Peraxilla* and *Trilepidea*, and reported that *Peraxilla* spp. are self-compatible. In *Peraxilla*, self-pollination was presumed to occur when the petals abscise, lifting the attached anthers over the stigma which remains attached to the ovary (Ladley & Kelly 1995a). Although *Peraxilla* flowers are principally adapted for bird pollination, the flowers of *P. tetrapetala* are also sometimes opened by native *Hylaeus* bees (Kelly et al. 1996). There is no other published work on New Zealand mistletoe floral biology. Outbreeding is thought to be the norm within the family generally, although self compatibility may be common (Bernhardt & Calder 1981; Barlow 1983). Standard throughout the Loranthaceae is the production of only one seed per fruit in a pseudoberry (Kuijt 1969).

The general aim of this study was to provide a more complete understanding of the floral biology of the surviving New Zealand Loranthaceae. In particular, six areas were addressed where information in the literature is inadequate. For bird-pollinated species (*Alepis flavida*, *Peraxilla colensoi*, and *P. tetrapetala*): (1) what are the main avian pollinator species, and how is pollination effected? (2) When is nectar produced, and how does this affect visitation? (3) Is *Alepis* self-compatible? For insect-pollinated species (*Ileostylus micranthus* and *Tupeia antarctica*): (4) what are the sex ratios of these dioecious species in the field? (5) Is *Ileostylus* self-compatible? And for all species: (6) are pollination difficulties likely to be limiting reproduction in any of the New Zealand Loranthaceae?

METHODS AND MATERIALS

Study sites and species

All five extant Loranthaceae of New Zealand were included in the study. *P. colensoi* was studied at Wakefield (grid reference NZMS 260 N27 121802, 41°23'S 173°02'E), at the boundary of Motueka and Moutere Ecological Districts, 30 km south-west of Nelson. The average annual rainfall in the area is

approximately 1100 mm. *P. colensoi* plants were situated in isolated *Nothofagus menziesii* stands surrounded by pasture along the length of Pigeon Valley (60 to 120 m a.s.l.). *I. micranthus* was studied at Wakefield growing in a large stand of *Podocarpus totara* (60 m a.s.l.), and at Otanerito (N37 145074, 43°51'S 173°04'E), Akaroa Ecological District, Banks Peninsula, growing on shrubs of *Coprosma rotundifolia* and *Melicope simplex* in open kanuka (*Kunzea ericoides*) forest at an altitude of 50 m. *T. antarctica* was studied at Wainui (N37 024089, 43°50'S 172°55'E), also in the Akaroa Ecological District. The site is 10 m a.s.l. and it has an average annual rainfall of 700 mm. A large population of *Tupeia* grows on the introduced shrub *Chamaecytisus palmensis* along a 500 m strip of roadside. Two species (*A. flavida* and *P. tetrapetala*) were studied growing on *Nothofagus solandri* var. *cliffortioides* hosts at Craigieburn (K34 050831, 43°09'S 171°43'E), Craigieburn Ecological District, Canterbury. The site is in intact native forest dominated by *N. solandri* var. *cliffortioides* at Jacks Pass at 940 m altitude in the Craigieburn Range and has an average annual rainfall of 2000 mm. For more information on the sites see Ladley & Kelly (1996).

Pollination observations of *P. tetrapetala* were made at four additional locations: Belgrove (N28 061724, 41°28'S 172°57'E), 10 km south-west of Wakefield; Lake Ohau (H38 557619, 44°12'S 169°49'E); Waiouru (T20 559908, 39°27'S 175°52'E); and Little Barrier Island (S08 972536, 36°12'S 175°02'E). At Belgrove, Lake Ohau, and Waiouru the mistletoes were growing on *N. solandri* trees surrounded by open grassland. On Little Barrier the *P. tetrapetala* was growing near the top of the island (700 m a.s.l.) on *Quintinia serrata*.

Bird-pollinated species

Observations on flower visitors and pollinators were carried out for *A. flavida*, *P. colensoi*, and *P. tetrapetala*. In 1992/93, observations were made in the field of birds visiting flowers; in later years, videotapes were made of flowering plants and visits per hour were noted from the tapes. Native bees also open flowers of *P. tetrapetala*, and visit flowers of *P. colensoi*, but produce lower fruit set rates (Kelly et al. 1996); the effectiveness of insects as pollinators on the bird-adapted mistletoes will be considered further elsewhere.

Nectar production was measured in summer 1992/93 (*Alepis*, *P. colensoi*, and *P. tetrapetala*) and 1993/94 (*P. colensoi* only) by enclosing buds in fine-mesh cotton bags to prevent nectar being harvested.

From the day that flowers self-opened (in *Alepis*) or ripened enough to be opened by hand (in *Peraxilla*), the nectar production per flower was measured daily using micropipettes (5 μ l to 100 μ l) and then the bags were replaced on the flowers. The sugar content of the nectar was measured in brix (% w/w: weight of sugar per weight of solution) with a hand-held Atago refractometer, and the results converted to % w/vol solution (so that sucrose equivalents per flower could be evaluated; Kearns & Inouye 1993). In 1995/96, we measured *Peraxilla* nectar production again, this time taking careful note of the degree of flower ripeness. Measurements were made of: (1) *premature* buds that were not quite ripe but were able to be forced open using more pressure than normally required for 'ripe' flowers; (2) *ripe* buds – showing coloration of ripe buds and easily opened by hand; and (3) *overripe* buds that were older and had begun to show signs of aging such as small splits in the corolla. Once again, the volume was measured with capillary tubes and the sugar content with a refractometer.

Pollination experiments to test for self-compatibility, cross-pollination, and autogamy were carried out on randomly selected reproductive *A. flavida* plants at Craigieburn (seven in 1992/93 and five in 1996/97). In 1992/93, inflorescences on each of these plants were tagged and randomly allocated to one of four experimental treatments: bagged and self-pollinated by hand; bagged and cross-pollinated by hand using pollen from several nearby plants; bagged and not hand-pollinated; and unbagged control. The bags used were made of fine cotton mesh buttercloth. The same procedure was used in 1996/97 except that the hand-self-pollination treatment was replaced with enclosing buds in a wire mesh cage which excluded birds but not insects. Fruit set on the individual flowers on each inflorescence was monitored every 2–3 weeks until fruit ripened. The data were analysed in S-plus statistical software using a generalised linear model with binomial error distribution and logit link function. Self-compatibility has already been documented in both *Peraxilla* species (Ladley & Kelly 1995a; Kelly et al. 1996).

Self-compatibility was also assessed in *Alepis* by examining harvested styles from buds and open flowers for pollen tube growth. The styles were preserved in formalin acetic acid fixative (FAA) and then cleared in 4N NaOH for at least an hour at 60°C, rinsed in distilled water for > 2 hours, and then placed in decolourised aniline blue stain mixture (K₂PO₄ with 0.0015% aniline blue) for at least 20 hours. The styles were then mounted in a drop of

aniline blue mixture and viewed under a UV fluorescence microscope (Snow & Spira 1991).

The morphology of buds of *A. flavida*, *P. colensoi*, and *P. tetrapetala* was described in the lab using FAA-preserved material. The relative positions of the stigma and anthers inside a number of mature buds and flowers were noted to investigate the possibility of self-pollination prior to the bud opening (autogamy). For both *Peraxilla* species, we measured on fresh material the area of the stigma that appeared to be receptive using the simple presence-of-bubbles version of the peroxidase test (Zeisler 1938). The position and the proportion of the area that was receptive was scored, after 60 seconds in 3% hydrogen peroxidase, for five buds of each of the three bud stages recognised above (premature, ripe, over-ripe) from four trees for both species. For analysis, the proportions were arcsine-square-root transformed; analysis of variance was carried out using type III sums of squares treating plants and treatments as fixed effects; comparison of means performed using Tukeys HSD difference tests ($P < 0.05$); and the means back-transformed for presentation.

Insect-pollinated species

Sex ratios for the *I. micranthus* and *T. antarctica* populations were measured by a census of tagged reproductive plants at Wakefield and Wainui, respectively, during the flowering season. Plants of *T. antarctica* were classified as either male or female and *I. micranthus* plants as either male, female, or hermaphrodite, based on their flower morphology.

The possibility of self-pollination within a subdioecious population of *I. micranthus* was investigated by tagging five pairs of branches on five plants (four hermaphrodite and a female) at Otanerito in October 1995. Within each pair of branches, one branch was bagged in fine nylon mesh to exclude potential insect pollinators. The other branch was left open as a control. The number of flower buds was counted just before flowering commenced. The bags were removed once all anthers had been shed, and the number of ripening fruits was counted in January 1996.

RESULTS

The overall timing of flowering and flower characteristics of the New Zealand Lorantheae are given in Table 1. The bird-pollinated species flowered in

mid summer, while the insect-pollinated species flowered in spring.

Visitors to bird-pollinated species

Observation on bird species visiting *Peraxilla* flowers showed that tui (*Prosthemadera novaeseelandiae*) and bellbirds (*Anthornis melanura*) were by far the most numerous avian flower visitors (Table 2). A few individuals of other bird species were seen in mistletoes but some may have been searching for invertebrates. Only at one site have we seen birds other than tui and bellbirds definitely opening *Peraxilla* buds: at Lake Ohau in 1996/97 silvereyes (*Zosterops lateralis*) and chaffinches (*Fringilla coelebs*) opened *P. tetrapetala* buds.

Bellbirds were present at all sites, whereas tui

were absent from Craigieburn and Lake Ohau. At Craigieburn all *P. tetrapetala* bird-pollination was attributed to bellbirds. When both were present, tui were more common than bellbirds on both *Peraxilla* species in Nelson, but bellbirds were more common at Waiouru and Little Barrier. At Wakefield and Belgrove, tui were dominant and aggressive (to other tui, to bellbirds, and to any other species which visited the flowering *Peraxilla* plants) chasing away even nesting house sparrows (*Passer domesticus*). Presumably the relative abundance of the various honeyeaters is determined by their local densities, the attractiveness of alternative food sources at each site, and competitive relationships between the bird species.

Alepis were observed only at Craigieburn (where tui are absent). Flowers were visited by bellbirds and,

Table 1 Flower characteristics of the extant New Zealand Loranthaceae. All data are from the sites and years covered in this paper except where noted. Means are \pm 95% C.I.

Species	Flowering season	Flower colour	Petal length (mm)	Pollinator	Flower morphology
<i>Peraxilla colensoi</i>	Mid Dec–Jan	Red	42.2 \pm 0.7	bird	hermaphrodite
<i>P. tetrapetala</i>	Dec or Jan	Red ^a	26.6 \pm 1.0	bird	hermaphrodite
<i>Alepis flavida</i>	Mid Jan–Feb	Yellow	16.2 \pm 0.8	bird	hermaphrodite
<i>Ileostylus micranthus</i>	Mid Oct–Nov	Greenish-yellow	2.5 ^b	insect	sub-dioecious
<i>Tupeia antarctica</i>	Mid Aug–Oct	Green	1–2 ^c	insect	dioecious

a, yellow on Little Barrier Island; b, Menzies (1947); c, Smart (1952).

Table 2 Bird species observed visiting flowering *Peraxilla* and *Alepis* plants. Bellbirds were present at all sites but tui only at some, as indicated.

Mistletoe species	Site	Tui present?	Year	Total hours of observation	Bird species (total number of visits)
<i>P. colensoi</i>	Wakefield	yes	1994/95	32.9	Tui (39), bellbird (1)
<i>P. colensoi</i>	Wakefield	yes	1995/96	28.2	Tui (4), bellbird (2), silvereye* (2)
<i>P. colensoi</i>	Wakefield	yes	1996/97	9.2	Tui (6)
Total				70.3	Tui 49, bellbird 3, silvereye* 2
<i>P. tetrapetala</i>	Belgrove	yes	1993/94	2.8	Tui (17)
<i>P. tetrapetala</i>	Belgrove	yes	1995/96	2.0	Tui (3), house sparrow* (1)
<i>P. tetrapetala</i>	Little Barrier Island	yes	1995/96	9.2	Bellbird (5), tui (1)
<i>P. tetrapetala</i>	Waiouru	yes	1994/95	2.4	Bellbird (2)
<i>P. tetrapetala</i>	Craigieburn	no	1994/95	24.2	Bellbird (17)
<i>P. tetrapetala</i>	Craigieburn	no	1995/96	33.7	Bellbird (14)
<i>P. tetrapetala</i>	Craigieburn	no	1996/97	12.2	Bellbird (4)
<i>P. tetrapetala</i>	Lake Ohau	no	1996/97	35.4	Bellbird (5), chaffinch (5), silvereye (0†),
Total				121.9	Tui 21, bellbird 47, chaffinch 5, silvereye 0†, house sparrow* 1
<i>A. flavida</i>	Craigieburn	no	1996/97	14.4	Bellbird (1), silvereye (1)

* These birds were not confirmed to be pollinating flowers and may have been foraging for insects or not feeding.

† Silvereyes were seen opening *P. tetrapetala* flowers at Lake Ohau but did not appear on the 29 hrs of videotape.

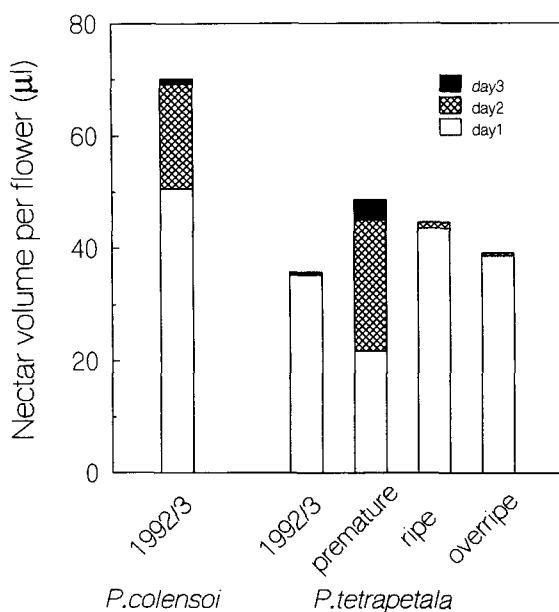


Fig. 1 Nectar production (μl) in *Peraxilla* spp. flowers with increasing age after opening. Data are for 1995/96 except where noted. In 1992/93, *Peraxilla* flowers were opened by hand when the buds ripened, and bagged between measurements to prevent nectar harvesting. In 1995/96, flowers were classified into three stages of ripeness (see text for details) prior to sampling. For sample sizes see Table 3.

less frequently, by silvereyes; the low visitation rates per hour in Table 2 are an artifact of the small size of the videotaped *Alepis* plants. All of the observed foraging visits were to newly opened flowers. The flowers of *Alepis* were classified as non-explosive by Ladley & Kelly (1995a) since bagged flowers do open unaided (i.e., are not obligately explosive, in contrast to *Peraxilla*). However, Godley (1979, p. 445) saw native bees (*Hylaeus agilis*: Hymenoptera, Colletidae) successfully opening buds, and Ladley & Kelly (1995a) reported seeing a bellbird trying unsuccessfully to twist open unripe buds. We have not observed any *Alepis* buds being opened by birds or bees despite careful searching, including at sites where *Hylaeus agilis* was opening flowers of *P. tetrapetala* (Kelly et al. 1996). Therefore, *Alepis* flowers seem to be weakly facultatively explosive, and are sometimes opened by native bees and perhaps also by bellbirds, but this is far less common than for *Peraxilla*.

For the two *Peraxilla* species virtually all the foraging bouts were on mature unopened buds. Later in the season when most *Peraxilla* flowers were already opened, it was difficult to see whether a bird was probing an open flower or twisting a ripe bud. Some flowers were probably revisited after being opened, but overall there was a clear emphasis on visiting buds rather than open flowers in *Peraxilla*. After flowers are opened, there are colour changes over the next 24–36 hours in both *Peraxilla* (from yellowish-red to dark red) and in *Alepis* (from yellow to orange) which would allow birds to distinguish newly-opened from older flowers.

Table 3 Nectar energy production of *Peraxilla* species measured as sucrose equivalents (mg/flr). In 1992/93, flowers were opened by hand when the buds ripened, and bagged between measurements to prevent nectar harvesting. In 1995/96, flowers were also classified into three stages of ripeness (see text for details) prior to opening. The subsequent production of *P. tetrapetala* flowers was followed for a further 48 hours. Buds cease to produce nectar about the time they become ripe (i.e., ready to be opened without excessive force).

	Year	Stage at opening	n	Day 1	Day 2	Day 3	Total (\pm se)
<i>P. colensoi</i>	1992/3	mostly ripe	128	9.62	—	—	—
	1995/96	premature	20	2.47	—	—	—
	1995/96	ripe	89	5.15	—	—	—
	1995/96	overripe	21	5.80	—	—	5.80* \pm 0.73
<i>P. tetrapetala</i>	1992/93	mostly ripe	48	4.52	—	—	—
	1995/96	premature	20	2.47	2.28	0.22	4.98 \pm 0.34
	1995/96	ripe	36	4.58	0.06	0.00	4.64 \pm 0.27
	1995/96	overripe	12	4.01	0.02	0.00	4.02 \pm 0.34

*Assuming negligible production of nectar in overripe flowers after they are opened.

Nectar production in bird-pollinated species

In total, all three bird-pollinated species produced large quantities of nectar and sugar (Tables 3 and 4), especially the two *Peraxilla* species. In other Loranthaceae worldwide only the Australian *Muellerina eucalyptoides* had greater energy production per flower (Table 4).

For the New Zealand species there was usually very little nectar produced after the flower opened itself (*Alepis*) or ripened enough to be opened by an animal (*Peraxilla*). Indeed, for *A. flavida* in 1992/93 there was zero nectar production after the first day in all of the 15 flowers measured. In 1992/93, *P. tetrapetala* flowers also produced negligible nectar volume after opening (Fig. 1), with only 1.5% of the total produced after day 1. For *P. colensoi* in 1993/94, 72.1% of all nectar volume was presented when the flowers were first opened, and some (26.6%) was produced during the following day. The production after opening could be because either some of the flowers genuinely continued producing nectar after ripening (18% had their peak nectar production a day after opening) or they had been forced open prematurely by hand a day before they were really ripe. A very small amount of nectar (1.3% of the total) was produced on days 3 and 4. Converting these volumes to sucrose equivalents showed that in the summer of

1992/1993, *P. colensoi* flowers produced twice as much sugar (9.62 mg) as *P. tetrapetala* (Table 3).

In the summer of 1995/96, we further tested the possibility of anticipating peak production by prematurely opening flowers of *Peraxilla*. Flowers that were not quite ripe (premature) contained only half as much nectar volume (Fig. 1) and sugar (Table 3) as fully ripe flowers. In *P. tetrapetala*, these prematurely opened flowers went on to produce more nectar over the next 48 hours so that in the end they had produced about the same total as the flowers that were opened when ripe (Fig. 1). Ripe and overripe *P. tetrapetala* flowers essentially contained all their nectar when opened and produced very little subsequently. The further production of nectar in opened flowers was not studied in *P. colensoi* in that summer, but premature buds also contained only half the nectar seen in ripe buds. If we assume that over-ripe flowers contain all the nectar that is likely to be produced by a flower, the sugar content was down in this species compared with 1992/93 (Table 3).

Bud structure, self-pollination, and self-compatibility in bird-pollinated species

Mature buds of *A. flavida* and the two *Peraxilla* species form fenestrae (splits between the petals) as seen in African explosive-opening mistletoes. In all

Table 4 Nectar quantities per flower for Loranthaceae. Where a range is given, the values are the highest and lowest means from different datasets.

Species	Nectar in closed bud			Nectar in open flower			References
	Quantity µl	Sugar % (w/w)	Sucrose equivalents (mg/bud)	Quantity µl	Sugar % (w/w)	Sucrose equivalents (mg/flower)	
<i>Muellerina eucalyptoides</i>						6.34	6
<i>Peraxilla colensoi</i>	50.6	14.3 ± 0.7	5.15–9.62	69.1 ± 2.6*		5.80*	this paper
<i>Peraxilla tetrapetala</i>	35.2–43.5	12.2 ± 1.6	4.01–4.58	35.7 ± 2.9*		4.02–4.98*	this paper
<i>Phragmanthera dshallensis</i>	20	17.5	3.85	3.5	17.5	0.67	3
<i>Amyema miquelii</i>				5.1	36.5	1.98–2.15	1, 6
<i>Lysiana exocarpi</i>						0.93–1.71	4, 6
<i>Amyema pendula</i>				3.7	21.4	0.85–1.26	2, 6
<i>Amyema quandang</i>				4.7	24.3	1.07–1.08	2, 6
<i>Alepis flavida</i>				2.4 ± 1.6*			this paper
<i>Amyema miraculosa</i>				1.3	33.8	0.50	1
<i>Tapinanthus bangwensis</i>	4.7	8.3	0.39	0.75	9.0	0.07	5
<i>Globimetula braunii</i>	3.0	10.4	0.31	0.65	11.2	0.07	5
<i>Gaidendron poasense</i>					16.0		7

* Total production (± standard error) over life of flower (2–4 days).

References: 1: Bernhardt (1984); 2: Bernhardt & Calder (1981); 3: Gill & Wolf (1979); 4: Ford (1979); 5: Kirkup (1984); 6: Reid (1986); 7: Wolf et al. (1976).

Table 5 Stigma receptivity in *Peraxilla* species. (a) The proportion of the stigma that is receptive in buds of three ages, measured as the area of the stigma that produced bubbles after one minute of submergence in 3% hydrogen peroxide. Within each column, means (back-transformed from the arcsine-square-root transformed data) with the same superscript are not significantly different (Tukeys HSD test, $P < 0.05$). (b) Analyses of variance on the proportions using type III sums of squares treating plants and treatments as fixed effects.

(a)		Proportion of stigma receptive			
		<i>P. tetrapetala</i>	<i>P. colensoi</i>		
Stage					
Premature		0.18 ^a	0.21 ^a		
Ripe		0.36 ^b	0.58 ^b		
Over-ripe		0.65 ^c	0.71 ^b		
(b)					
Species	Source	df	MS	F	P
<i>P. tetrapetala</i>	stage	2	0.865	19.06	<0.0001
	plant	3	0.071	1.56	0.2103
	stage*plant	6	0.130	2.86	0.0183
	error	59	0.045		
<i>P. colensoi</i>	stage	2	0.793	14.91	<0.0001
	plant	3	0.119	2.24	0.0962
	stage*plant	6	0.162	3.04	0.0134
	error	59	0.053		

three species, the anthers dehisce and pollen is released prior to the bud opening, and observations of sectioned buds showed that the stigma and anthers are in close proximity at the tip of the bud. The stigmatic surface is firmly pressed up against the trichome cap, formed by the underside of the tips of the petals, and the anthers are packed tightly around the style, just below the stigma.

In mature *A. flavida* buds, the lower half of the stigma is in direct contact with the dehisced anthers. Fluorescence microscopy showed pollen tube growth in styles from both open flowers (7.45 ± 2.36 tubes per style, mean \pm 95% CI) and from buds (5.19 ± 1.34 tubes), showing that pollen does get onto the stigma and germinate before the flowers open. Therefore, the stigma must be receptive before the bud opens, i.e., there is no dichogamy.

In both *Peraxilla* species, the first part of the stigma to ripen is the distal part (furthest from the anthers) and receptivity spreads towards the base of the stigma as it ripens (Table 5a). Hence self-pollen is only likely to contact a receptive surface in over-ripe buds, even though the anthers dehisce well before the flower is ready to be opened. This is confirmed by the finding that in *Peraxilla* buds, pollen tubes are found in the styles of only very old, over-ripe buds (Robertson, Kelly, and Ladley

Table 6 Effect of different pollination treatments on *Alepis flavida* plants at Craigieburn. (a) Mean fruit set (% with number of flowers in parentheses). (b) Overall significance tests for analysis of effect of pollination treatments on fruit set, by means of generalised linear models with binomial errors and logit link functions. Plants were inserted into the model first as a block effect and treatments tested next. In both cases there was a significant plant (block) effect; treatments differed significantly only in 1996/97.

(a)		Fruit set 1992/93		Fruit set 1996/97		
Treatment						
Open controls (bird pollinated)		82.5 (610)		71.3 (754)		
Cross-pollinated by hand		58.3 (108)		83.2 (68)		
Self-pollinated by hand		48.3 (85)		—		
Bagged, pollinators excluded		64.7 (258)		90.2 (151)		
Caged (birds excluded, insects not)		—		89.6 (262)		
Number of plants		7		5		
(b)		Residual		Residual		
Year	Model	df	Deviance	df	deviance	Pr (Chi)
1992/93	Null			33	99.96	
	plants	6	64.8	27	35.11	<0.001
1996/97	treatments	4	6.87	23	28.24	0.14
	Null			23	176.5	
1996/97	plants	4	84.1	19	92.45	<0.001
	treatments	4	55.8	15	36.61	<0.001

unpubl. data). The only differences between the species in stigma receptivity are that ripe *P. colensoi* buds have a bigger proportion of the stigma receptive than in *P. tetrapetala*, and there is no significant subsequent increase in receptive area for *P. colensoi* (Table 5). There is a significant plant-stage interaction suggesting that some plants' stigmas ripen at different rates which could affect selfing rates.

A high percentage of flowers set fruit in *Alepis* under all pollination treatments, including bagged flowers from which all pollinators were excluded (Table 6). Statistical analysis showed that there was a significant plant effect in both years ($P < 0.001$) but a significant difference among treatments only in 1996/97. However, in both years there was very good fruit set under all treatments. This confirms the pollen tube and structural information suggesting that self-pollination occurs readily, and also shows no significant difference between flowers hand-pollinated with self- or cross-pollen.

Insect-pollinated species

Surveys of the sex ratios of populations of *I. micranthus* and *T. antarctica* revealed that for *I. micranthus* at Wakefield there was a ratio of 2.5:1:1 (female:male:hermaphroditic plants), while *T. antarctica* had a ratio of 3:1 (female:male plants).

Results from the experiment on self-compatibility of *I. micranthus* showed that there was considerable variation between plants (Table 7). Some leaves and flowers were damaged by caterpillar predation in both bagged and control branches, especially on plants 3 and 5. One plant was structurally female with only rudimentary anthers and this plant set no seed inside the bag, showing that the bag did prevent movement of pollen. While the other plants were all structurally hermaphrodite, one (plant 3) set no ripe fruits in either treatment. The remaining three

hermaphrodites all set some seed when pollinators were excluded.

DISCUSSION

Distribution of explosive flowering

Explosive flowers have been reported in at least 17 genera of Loranthaceae worldwide (Table 8). Barlow (1983) reviewed the evolutionary relationships of the Loranthaceae as a whole and described four major groups, based on chromosome numbers and presumed-ancestral characters (such as root parasitism and epicortical runners). The first group contains relict genera found in Australia, New Zealand, and South America (Gondwana is the putative centre of origin of the family) with a variety of ancestral characteristics, all with $x = 12$ chromosomes. The second group are also $x = 12$ but include recently diversified groups in south-east Asia and India. The final two groups are large, recently diversified collections of species in the New World ($x = 8$) and the Old World especially Africa ($x = 9$). These last two groups are each more closely related to the ancestral groups than to each other (Barlow 1983).

It is in the Old World group, centred on *Tapinanthus* in Africa, that explosive flowers are best known. Polhill (1989) recorded that most of the 25 African genera have some explosive-flowered species. *Tapinanthus* alone consists of some 200 species, and many of these have explosive flowers. However, from Table 8 it is apparent that explosive flowers are found in all four of Barlow's major groups. While the more advanced $x = 12$ group and the New World $x = 8$ group have only one recorded genus each with explosive flowers, it is striking how many of the putative ancestral relict genera are now proven or suspected to have explosive flowers. In this group, four genera have explosive flowers, four

Table 7 Fruit set in bagged (pollinator-exclusion) and unbagged *Ileostylus micranthus* flowers, Otanerito, 1995.

Plant	Host	Sex	% Fruit set (<i>n</i>)	
			Control branch	Bagged branch
1	<i>Melicope simplex</i>	female	40.4 (57)	0 (48)
2	<i>Coprosma crassifolia</i>	hermaphrodite	40.8 (125)	6.4 (78)
3	<i>Melicope simplex</i>	hermaphrodite	0 (31)	0 (38)
4	<i>Coprosma crassifolia</i>	hermaphrodite	no data	28.8 (80)
5	<i>Coprosma crassifolia</i>	hermaphrodite	0 (31)	12.5 (24)

Table 8 Worldwide distribution of explosive flowers in Loranthaceae. Groups and plant names follow Barlow (1983) and Barlow et al. (1989), respectively.

Group and Mistletoe species	Region	Pollinating birds ^a	Flower type ^b	Floral Characteristics	Reference ^c
Ancestral, x = 12					
<i>Peraxilla colensoi</i>	New Zealand	honeyeaters	2	Flowers do not open unaided. Bagged flowers set some seed.	14
<i>Peraxilla tetrapetala</i>	New Zealand	honeyeaters	2	Flowers do not open unaided. Bagged flowers set some seed.	14
<i>Alepis flavida</i>	New Zealand	honeyeaters	2	Flowers open unaided; bagged flowers set seed.	9, 14
<i>Trilepidea adamsii</i>	New Zealand		1	Extinct. Explosive opening inferred from structure of open flowers.	14
<i>Tristerix tetrandus</i>	South America		2	Buds have fenestrae but explosive opening not confirmed.	10
<i>Tristerix aphyllus</i>	South America		2	Buds have fenestrae but explosive opening not confirmed.	10
More advanced, x = 12					
<i>Macrosolen parasiticus</i>	India, Sri Lanka	sunbirds	2	Bagged buds may (ref. 13) or may not (ref. 14) open and self-pollinate.	4, 11
<i>Macrosolen cochinchinensis</i>	Java	flowerpeckers	2	Flowers symmetrical, bagged buds do not open but do set seed.	5
Advanced New World, x = 8					
<i>Psittacanthus</i> spp.	S/Cent. America	hummingbirds	2	Orange-red flowers unzipped upwards by short-tongued hummingbirds.	13
Advanced Old World, x = 9					
<i>Tapinanthus</i> spp.	Africa	sunbirds, chats	1 or 2	Two groups of species: 1. Buds with fenestrae, flowers asymmetrical, one-stage pollination. 2. Buds without fenestrae, flowers symmetrical, two-stage pollination. Some spp. have extended nectar production.	5, 6, 7, 12, 15
<i>Erianthemum</i> spp.	Africa	sunbirds	1	Symmetrical orange flowers, fenestrae present in the buds, lots of nectar.	6, 7, 15
<i>Phragmanthera</i> spp.	Africa	sunbirds	1	Some species asymmetrical, short nectar production, others long nectar production.	7, 8, 15
<i>Agelanthus</i> spp.	Africa		1	Similar pollination method to <i>Phragmanthera</i> .	15
<i>Globimetula</i> spp.	Africa	sunbirds	2	No fenestrae, flowers asymmetrical. Some spp. have extended nectar production.	7, 12, 15
<i>Moquiniella</i> spp.	Africa		2	Similar pollination method to <i>Globimetula</i> .	15
<i>Englerina</i> spp.	Africa	sunbirds	1	Flowers asymmetrical, petals don't split completely.	5, 7
<i>Taxillus cuneatus</i>	India, Sri Lanka	flowerpeckers, sunbirds	2	Flowers green-yellow; nectar renewed after visit; one fenestra in corolla tube.	2, 3, 4, 11
<i>Taxillus tomentosus</i>	Sri Lanka	sunbirds		Flowers asymmetrical when open.	11
<i>Taxillus recurvus</i>	India			Nectar not renewed after first visit.	4
<i>Dendrophthoe falcata</i>	India	flowerpeckers	2	Red flowers; no self pollination in unopened buds; nectar fills corolla tube.	1, 2, 4, 5, 11
<i>Dendrophthoe neelgherrensis</i>	India, Sri Lanka	sunbirds	2	Flowers slightly asymmetrical, nectar not renewed after opening, able to self-seed.	2, 3, 4, 5, 11
<i>Dendrophthoe suborbicularis</i>	Sri Lanka	sunbirds		Exploding flowers can be heard some metres away.	11
<i>Dendrophthoe pentandra</i>	Java	sunbirds	2	Flowers symmetrical, last 24 hrs, lots of nectar. Bagged buds don't set seed.	5
<i>Dendrophthoe nova-guineae</i>	New Guinea		2	Has fenestrae in mature buds.	5

a As listed in source. Bird families mentioned: sunbirds = Nectariniidae, flowerpeckers = Dicaeidae, honeyeaters = Meliphagidae; hummingbirds = Trochilidae; chats = *Anthreptes* spp.

b Types of explosive flower opening: 1 = One stage opening, 2 = Two stage opening.

c References: 1 Ali (1931), 2 Ali (1932), 3 Davidar (1983), 4 Davidar (1984), 5 Docters van Leeuwen (1954), 6 Evans (1895), 7 Feehan (1985), 8 Gill & Wolf (1975), 9 Godley (1979), 10 Johow (1900), 11 Keeble (1896), 12 Kirkup (1984), 13 Kuijt (1969), 14 Ladley & Kelly (1995a, 1995b), 15 Polhill (1989).

apparently do not (*Nuytsia*, *Atkinsonia*, *Gaiadendron*, and *Notanthera*), and one (*Tupeia*) is insect-pollinated.

Interestingly there has been no demonstrated explosive flower opening in any Australian Loranthaceae (Calder et al. 1979). Armstrong (1979) stated that birds have been observed visiting unopened mature buds of *Amyema* and forcing the buds open. However, he then goes on to say that the flowers of *Amyema* are not dependent on explosive opening (i.e., are not obligately explosive). In *A. pendula*, Bernhardt & Calder (1981) considered whether the species is explosive but did not come to a clear conclusion. They showed that buds will separate “with gentle probing for nectar with a capillary tube”, and they reported that a large number of buds wither with the corolla still fused at the top. On the other hand, Bernhardt (1983, p. 89) states “no *Amyema* species had ever been described displaying the ‘exploding flower’ mechanism common to so many Paleotropical genera”. However, the evidence hints that some *Amyema* spp. may be at least facultatively explosive, as we suggest for *Alepis*. Explosive flowering may be surprisingly cryptic, especially if facultative, as recent New Zealand discoveries have shown. The dividing line between facultatively explosive flowers, and normal flowers which may be occasionally forced open prematurely by birds, is not sharp; however, facultatively explosive flowers should open very suddenly when probed and have pollen released in the bud.

The large number of ancestral genera with explosive flowers leads to the question of whether explosive flowers are ancestral (shared) or have arisen independently four or more different times. Since a majority of Loranthaceae do not have explosive flowers, independent origin may be more likely. Loranthaceae have close relationships with birds, both for pollination and for dispersal (Reid 1991; Ladley & Kelly 1996), and the flower structure may be such that explosive flowers are readily selected for. The *Alepis* – *Peraxilla* group suggests how this may develop. If loranth flowers, like *Alepis*, generally have most or all of their nectar present in the bud (see Table 4, and also Davidar (1983) and Feehan (1985)), then when there is competition among pollinators (i.e., when pollinators are abundant) there will be pressure for birds to get first access to the nectar by opening buds prematurely. The presence of fenestrae between the petals assists premature opening since it allows access to the interior of the flower. If pollen is released in the bud this premature opening could be classified as

facultatively explosive. Once some birds open flowers by twisting buds or unzipping fenestrae, there can be selection for flowers whose petals adhere together tightly for longer, to protect the nectar from rain or to exclude nectar thieves (Ali 1931), i.e., become obligately explosive. This process could have occurred independently a number of times.

Finally, consider the distribution of one-stage versus two-stage explosive flower mechanisms (Polhill 1989). In two-stage opening, the foraging bird first grasps the bud in its bill and gently squeezes or twists. This causes the petals to explode open into a symmetrical flower. The bird then inserts its beak into the open flower and takes the nectar (as illustrated by Ladley & Kelly 1995a). In one-stage opening, the foraging bird inserts its bill into one of the fenestrae (the splits between the petals) in the corolla of a mature bud. This causes the petals to unzip and the flower explodes open zygomorphically. The stigma and anthers often swing out towards the bird, enhancing the effectiveness of pollination. Two genera (*Globimetula* and *Moquiniella*) show an intermediate two-stage mechanism where the second movement produces a zygomorphic flower oriented towards the pollinator (Polhill 1989). One-stage flower opening is apparently more advanced, and in several African genera flowers have extensive specialisations for this mode of opening (Feehan 1985; Polhill 1989) such as in *Erianthemum dregei* in which the anthers are thrown out of the flower by the explosion (Evans 1895). One-stage flower opening is more common in Africa than two-stage opening (Feehan 1985). The only species reported with one-stage explosive flowers outside the African group with $x = 9$ chromosomes is the extinct *Trilepidea adamsii* in New Zealand (Ladley & Kelly 1995a). The existence of one-stage explosive flowers in this ancestral species is remarkable (although as *Trilepidea* is extinct, its pollination mechanism can only be inferred from structural cues). Since explosive opening was only recently discovered in *Trilepidea*, there may be other one-stage explosive flowers in the Loranthaceae which have not yet been described.

Flower visitation and nectar production schedules

All three bird-pollinated New Zealand species produced large quantities of nectar, especially the *Peraxilla* spp. Most overseas Loranthaceae produce much smaller amounts and present smaller rewards (Table 4), although *Muellerina eucalyptoides* has a large reward. The abundant nectar in *Peraxilla*

flowers may be due to the relatively large size of the New Zealand pollinators compared with the birds which pollinate overseas mistletoes. Male tui weigh 121 g and male bellbirds weigh 30.7 g (Craig et al. 1981), compared with average weights of 5–10 g for four common mistletoe pollinators (two sunbirds, a flowerpecker, and a white-eye) in southern India (Davidar 1984). Therefore, the New Zealand birds have higher energetic needs and are likely to forage preferentially on plants which produce abundant nectar. The same arguments may apply to *M. eucalyptoides*, which is visited by five birds (Reid 1986), the largest of which is the little wattlebird at 65 g (Paton & Ford 1977).

The timing of nectar production can affect the visitation schedules of pollinators (Paton 1982). In *Alepis* and *Peraxilla*, unless flowers are forced open prematurely, little nectar is produced after the bud is opened. This would encourage single-visit pollination systems where the birds concentrate on opening ripe buds, where the nectar has demonstrably not already been harvested by another bird. Field observations on *Peraxilla* show that this is largely what tui and bellbirds do. However, when ripe buds are rare (late in the flowering season, or if pollinators are abundant) the search time to find ripe buds increases and it may be more profitable to glean small amounts of nectar from open flowers. If birds are abundant a fraction of flowers may also have been opened prematurely and these will continue to secrete nectar after opening. Both *Peraxilla* and *Alepis* flowers change colour with age after flowers have been opened, so birds could identify recently-opened flowers. At some sites, *P. tetrapetala* flowers may be opened by pollen-harvesting bees (Kelly et al. 1996), in which case open flowers with abundant nectar would be present which would also encourage birds to forage on open flowers. Therefore, we would expect both *Peraxilla* and *Alepis* to have low but non-zero levels of revisitation of open flowers by birds.

Dominance relationships between bird species are also important. Gill & Wolf (1975) found that in *Phragmanthera dshallensis* larger sunbirds were mainly opening ripe buds to get nectar, whereas the smaller species of sunbird were more often mopping up already-open flowers. In Australia, the smaller honeyeater species visit *Amyema* flowers early and late in the flowering season, while the larger, dominant honeyeaters concentrate on the middle of the flowering season when the number of open flowers is highest (Bernhardt & Calder 1981). In this study we found that tui excluded other bird species,

including bellbirds, from both *P. colensoi* and *P. tetrapetala* at the Nelson sites, but not at Waiouru or on Little Barrier Island. Presumably tui defend the most valuable resource at any given time, which was *Peraxilla* at Nelson (in a mixed grassland/*Nothofagus* forest area) but something else on Little Barrier (in diverse continuous native forest).

Breeding systems

If birds visit solely or mainly buds, the flowers get visited only once or a few times. This limits the options of the plant for separation of male and female function. Lloyd & Webb (1986) hypothesised that herkogamy (separation of male and female function in space) and dichogamy (separation in time) evolved to avoid interference between the two functions of pollen receipt and pollen dispatch. If the flowers are only visited once then dichogamy would not be successful, and the flowers would be expected to show some form of herkogamy. This is the case in *Peraxilla* and *A. flavida*. After opening there is a spatial gap between the stigma and the dehisced anthers, and in all three species if the foraging bird enters the flower from the top it contacts the stigma before touching the anthers. In *Alepis* there is no dichogamy as the anthers dehisce in the bud and the stigma is simultaneously receptive, as shown by pollen tube growth in the bud. *Peraxilla* also shows anther dehiscence in the bud, but in ripe buds, only the distal portion of the stigma is receptive ensuring that a spatial separation of the receptive surface and the exposed pollen is maintained. However, with increasing age the receptive portion spreads over the entire stigma, allowing the possibility of selfing late in the life of unopened buds shortly before buds normally 'bottom-open'. Indeed, examination of the style using aniline blue staining and fluorescence microscopy reveals that pollen tubes are sometimes found in very old unopened buds of both *Peraxilla* species (Robertson, Kelly, and Ladley unpubl. data). These conclusions are consistent with the relatively low fruit set (11–22%) in bagged *Peraxilla* buds (Ladley & Kelly 1995a; Kelly et al. 1996).

If *Peraxilla* flowers are opened prematurely they may not only lack the full complement of nectar but also may not be easily pollinated at that time as only a small portion of the stigma is receptive. Such flowers may need to be double-visited, as noted in the previous section. On the first visit pollen may be removed and exported; fertilisation may take place on the second visit (dichogamy). This system introduces some flexibility in visitation schedule allowing single visit pollination when pollinators are rare

but encouraging multiple visits when pollinators are abundant enough to be prematurely opening flowers.

In comparison with most Australian *Amyema* spp. which show a trend towards strong dichogamy (Bernhardt & Calder 1981), the New Zealand species show much weaker protandry with the male and female phases overlapping, and both phases starting before buds are fully ripe and ready to be opened. Another Australian mistletoe, *Nuytsia floribunda*, resembles *A. flavida* in having no dichogamy at all (Sargent 1918). However, one *Amyema* species (*A. quandang*) shows some overlap as the stigma appears to be partially receptive in the male phase (Bernhardt et al. 1980) and thus appears to occupy an intermediate position in the continuum from complete dichogamy (most *Amyema* spp.) to very slight (*Peraxilla* spp.) to no dichogamy (*Alepis* and *Nuytsia*). Dichogamous species would be expected to have more extended periods of nectar production (to encourage multiple visits) than species with no temporal separation of male and female function.

Outbreeding is thought to be the norm within the Loranthaceae, although self-compatibility may be common (Barlow 1983); six of eight *Amyema* species tested showed full or partial self-compatibility (Bernhardt & Calder 1981; Bernhardt 1982). Work on the breeding systems of explosive flowering species elsewhere is limited to a few bagged pollinator-exclusion experiments, with varying results (Table 8). Some species (e.g., *Dendrophthoe pentandra*, *Tapinanthus kraussianus*, *Erianthemum dregei*) do not set seed within bags, while others (e.g., *Macrosolen cochinchinensis*, *Dendrophthoe neelgherrensis*) do set seed and hence must be self-compatible (Evans 1895; Docters van Leeuwen 1954). Self-compatibility has been shown in both species of *Peraxilla* (Ladley & Kelly 1995a; Kelly et al. 1996), and in *Alepis* and *Ileostylus*. The floral structure, high levels of investment in nectar production, and in *Peraxilla* dependence on birds for flower opening and low fruit set in bagged flowers, all suggest that outbreeding via birds should be common in the New Zealand species. However, data are not yet available which would allow assessment of the levels of autogamy, geitonogamy, and outcrossing in natural populations.

Insect-pollinated species

Ileostylus micranthus and *T. antarctica* were found to be dioecious or sub-dioecious, confirming earlier work (Menzies 1947; Smart 1952). For both *I. micranthus* and *T. antarctica* the flowers were small,

less than 5 mm in diameter, and were highly scented. These characteristics match those of the other described species of unisexual loranthaceous mistletoes (Kuijt 1969), except that *I. micranthus* seems to be the only member of the family which is subdioecious. The *T. antarctica* population had a female-biased sex ratio, and *I. micranthus* had a higher number of female plants than male or hermaphrodite plants. Sex ratios are commonly skewed in dioecious plant species, but usually towards males (Delph 1997). However, mistletoes tend to show female-biased sex ratios, such as in the loranthaceous *Barathranthus axanthus* (Docters van Leeuwen 1954). Two Viscaceae have been studied: *Phoradendron tomentosum* had a female bias (Nixon & Todzia 1985), while *P. juniperinum* was 1:1 or male-biased (Dawson et al. 1990). Delph (1997) considered that the common male bias may arise from higher female mortality caused by higher reproductive allocations, whereas the female bias in *Phoradendron* may be caused by differences in photosynthetic water use efficiency between the sexes.

Ecological implications

Finally, we address the question of whether any of the New Zealand mistletoes have pollination syndromes which would render them vulnerable to a failure of reproduction consequent on a reduction in their pollinating animal(s). The insect-pollinated species (*T. antarctica*, *I. micranthus*) seem to give least grounds for concern here. While the spectrum of flower visitors has not been fully described (see Smart 1952), there are no evident specialised mechanisms which would prevent introduced invertebrates such as honey bees from effecting pollination even if native invertebrates declined in abundance. Moreover, *I. micranthus* is subdioecious, and the hermaphrodite plants can autonomously set self-pollinated seed. There seem to be few grounds for concern over pollination of these two species.

Alepis flavida is probably the least at risk of the three bird-pollinated species. Although it has explosive flowers, these are facultatively explosive and can self-open, unlike *Peraxilla*. This makes the flowers accessible to opportunist pollinators such as silveryeyes or insects like native bees. Moreover, *Alepis* is highly self-fertile and bagged *Alepis* flowers set as much seed in the absence of pollinators as when hand-pollinated. For *Alepis*, levels of pollinator visitation probably mainly affect levels of outcrossing, rather than levels of seed production.

In contrast, *Peraxilla* flowers are obligately

explosive and hence highly dependent on endemic birds. Tui and bellbirds (both endemic) were responsible for the vast majority of pollinator visits, although native silvereyes visited flowers of both *Peraxilla* species, and introduced chaffinches opened *P. tetrapetala* flowers at one site. O'Donnell & Dilks (1994) also reported seeing silvereyes and the endemic kaka (*Nestor meridionalis*) visiting *Peraxilla* flowers, at sites in Westland. However, our data suggest that non-endemic birds are numerically unimportant for pollination, which is exactly the same situation as for fruit dispersal in New Zealand mistletoes (Ladley & Kelly 1996). Native bees (*Hylaeus agilis*) do open flowers of *P. tetrapetala* (but not *P. colensoi*) at some sites, which increases fruit set above that in unopened buds (Kelly et al. 1996). Despite this, in some areas many flowers of both *Peraxilla* species currently do not get opened by anything before abscission, and unopened flowers have much reduced seed set, which led Ladley & Kelly (1995a, 1995b) to suggest that pollination could be limiting to these species. The data in this paper confirm that view.

Therefore, we would predict that *Tupeia* and *Ileostylus* are least likely, and *Peraxilla* spp. most likely, to suffer from reduced seed set through inadequate pollination. If problems with pollination have been significant over the last 150 years, then we would predict the smallest decreases in the insect-pollinated species and the greatest declines in *Peraxilla*. This is borne out by distribution data (de Lange et al. 1997). *Tupeia* and *Ileostylus* have adapted most readily to human ecosystems and are relatively widespread in lowland New Zealand, but this may be more due to their very wide host ranges including many introduced plants (de Lange et al. 1996) than their pollination systems. *Alepis*, *P. colensoi*, and *P. tetrapetala* are now very uncommon in the North Island, but de Lange et al. (1997) concluded that *Alepis* and *P. colensoi* were never common there, whereas *P. tetrapetala* was previously abundant and widespread. Therefore, it seems that in the North Island the decline of *P. tetrapetala* has been more marked than of *Alepis*, as predicted from its greater vulnerability to pollination failure. The rate of decline of *P. colensoi* is less well known. The extinct *Trilepidea adamsii* also had a highly specialised explosive pollination system, which may have contributed to its rapid decline (Ladley & Kelly 1995a). Other factors such as fruit dispersal (Ladley & Kelly 1996), habitat clearance, and herbivory by possums (Norton 1991) seem certain to also be involved for all native mistletoes. While possum

control has been the main focus in the past, the conservation of the surviving Lorantheaceae will be very difficult unless populations of tui and/or bellbirds can be maintained to provide pollination and dispersal services.

ACKNOWLEDGMENTS

We thank the landowners for allowing us access to their properties, including at Wakefield the Bashford, Gullery, and Jones families, and the Department of Conservation; Donald and Bunty Ladley for accommodation on field work; the Public Good Science Fund for financial support; Ashley Sparrow for help with the analysis; Sandra Anderson for helpful discussions on pollination in New Zealand; and Lynda Delph, Jo Kenrick, David Norton, Nick Reid, and Ashley Sparrow for helpful comments on the manuscript.

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