

Where are New Zealand mistletoe found?

The distribution of New Zealand's Loranthaceous mistletoes varies throughout the country. "Beech mistletoes" show a high degree of host specificity which relates to their distribution patterns. Different species of mistletoe also have specific vertical distributions on host trees. These patterns reflect mistletoe dependence both on suitable host trees for establishment and animals for dispersal.

The "beech mistletoes"

A. flavida is sparsely distributed in the North Island, although in the South Island, it is sometimes common throughout the Alps, northwest Nelson and Southland. These areas contain black and mountain beech, on which *A. flavida* seems to be most often found.⁵

P. colensoi is most common at lower altitudes (0 to 500 m.a.s.l.) and is strongly correlated with the distribution of silver beech. Populations are greatest in the South Island where it can be found most often in the Nelson and Lewis Pass regions, near Haast, and scattered around Dunedin.⁵

The least host specific and widely distributed beech mistletoe is *P. tetrapetala*. It is most abundant in the South Island while in the North Island it is less abundant but still more common than the other two beech species. Populations are primarily found in the higher altitude, black and mountain beech forests of the Alps, (especially in the Craigieburn and Lake Ohau areas), north Westland and northwest Nelson.⁵

Distribution within and amongst host trees

David Norton, Hamish Owen, Graham Powell and Jenny Ladley have been studying areas on host plants where

Box 1. How old are individual mistletoe plants?

It is possible to decipher the age of most woody plants by counting their annual growth rings. However, this technique is not generally used with mistletoes because it is destructive and could further threaten these species. Instead, David Norton, Jenny Ladley and Ashley Sparrow came up with a non-destructive method for ageing *A. flavida*, *I. micranthus*, and *T. antarctica*.¹⁶ Because most mistletoe seedlings establish on young host branches¹⁷, the diameter of the host stem directly below the point of attachment is proportional to the age of an individual mistletoe.¹⁶ Thus, this technique uses the host branch diameter, or HBD, to come up with an age for the mistletoe. Another non-harmful way to determine mistletoe age is to measure its volume. Different size classes can be used to indicate plants of various ages. For example, some *A. flavida* plants in the Craigieburn Ranges were aged in this manner.¹⁴ Correlating mistletoe volume with age is not as direct as measuring the HBD, but volume could be used if the HBD is uncertain. For instance, some mistletoes may be too high in a tree to properly measure the host branch. Also, *Peraxilla* mistletoes have specialised growth forms which makes it impractical to use the HBD.¹⁶ Thus, only for particular species, hosts and sites should the HBD relationship be used.¹⁶

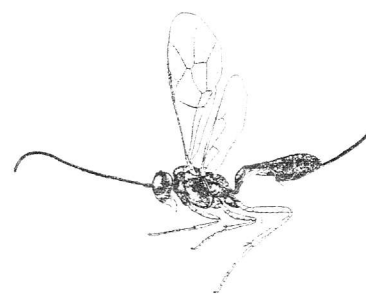
mistletoes grow. They have shown that the distribution of mistletoes follows a consistent pattern. *A. flavida* almost always parasitises the outer branches of its host (93-95% occurrence), while *P. tetrapetala* grows on the inner branches and trunk (79-82% occurrence).^{13,14}

Additionally, the vertical arrangement of mistletoes on host trees is not random. *A. flavida* is more often found in the lower section of the host, while *P. tetrapetala* grows in the middle, and *P. colensoi* lives in the upper part of the tree. Therefore, *A. flavida* and *P. tetrapetala* have evolved to use different habits which can permit them to live together on the same beech without competing for space.

The size of host trees also affect the distribution of beech mistletoes. For instance, as well as being able accommodate a greater volume of mistletoes. This relationship occurs because larger trees are probably older which allows more time for mistletoes to establish, contain better perches for birds, and provide a more regular supply of water, especially in times of

water limitation. The diameter of a host tree branch where the mistletoe is attached may also indicate the age of the mistletoe.¹⁴ (See Box 1).

Forest type can also influence mistletoe distributions. Forests that are structurally or compositionally diverse contain higher light levels which is important to mistletoe establishment. For example, part of a study in South Westland showed that *P. colensoi* was most common in structurally diverse silver beech forest.¹⁵ These forests also provide varying habitats for mistletoe dispersing birds.



An underscribed parasitoid that attacks the caterpillars of the lepidopteran *Zelleria* (see page 4).

Drawing by Tim Galloway

Possum herbivory: how detrimental is it to New Zealand mistletoes?

Previously, the decline of New Zealand mistletoes was attributed to their predation by the introduced Australian brushtail possum (Figure 2). For example, the reduction in plant size of *P. colensoi* and *P. tetrapetala* has been linked to possum browse on Mt. Misery, Nelson Lakes National Park.¹² However, recent information has challenged claims that mistletoes are consistently vulnerable to possum browsing, because both mistletoes and possums coexist at high densities in some areas. Insects may remove as much leaf area on mistletoes as possums.

The extinction of *T. adamsii*

T. adamsii was first described by Cheeseman in 1880, and had conspicuous, large flowers similar to those of *Peraxilla*. It was found in the northern North Island until it was last seen in 1954.³ Some blamed possums for the extinction. However, the direct responsibility of possums for the decline and eventual extinction of *T. adamsii* has been seriously questioned.³

Evidence suggests that possum numbers were low to zero in the former ranges of *T. adamsii*. For instance, it had disappeared from the Coromandel before possums spread into the area during the 1950's. *T. adamsii* also became extinct on Great Barrier and Waiheke Islands which were possum-free. In addition, investigations have discovered that browse shown on herbarium samples of *T. adamsii* were caused by insects rather than possums. Therefore, possums could not have been the only factor leading to the decline. Factors such as forest clearance, over-collecting or perhaps reproductive failure (see next section) are also thought to have contributed to the disappearance of *T. adamsii*.^{3,5}

Influence of plant "architecture" on browsing

Powell and Norton also suggest that the respective "plant architecture" (growth forms) of *A. flavida* and *Peraxilla* spp. influences the amount of predation a plant receives and how possum browse affects each species.¹³

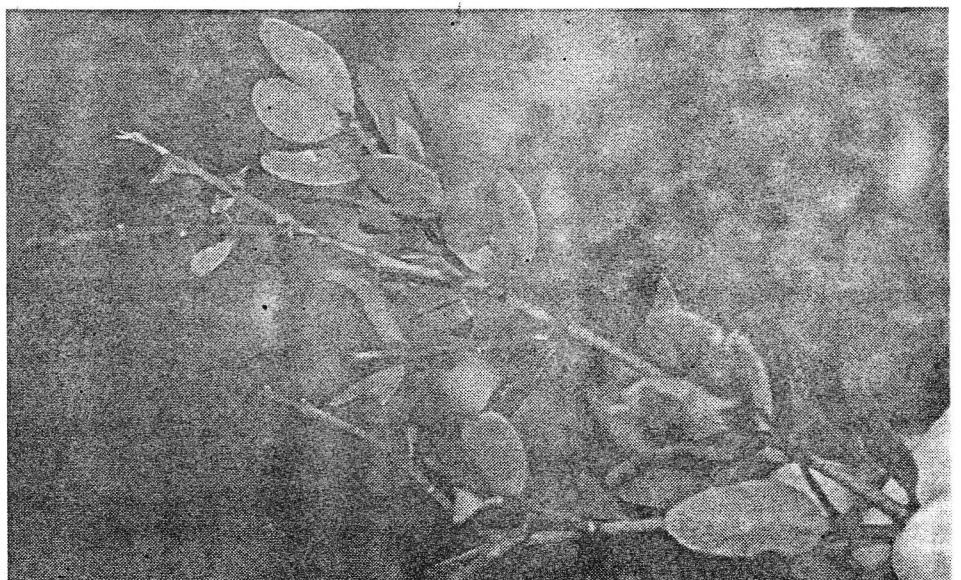
Following germination, *A. flavida* produces runners but remains on the outer branches of the host tree, while *Peraxilla* uses its runners to gradually shift to the tree's inner branches and trunk. *A. flavida* becomes long and loosely clumped in places where possums would have difficulty perching; hence, it may be less often browsed. Conversely, *Peraxilla* forms large clumps located in areas susceptible to possum destruction. However, this species can form new branches from either new buds or old sprouts that are contained within the bark of its host. Therefore, *Peraxilla* may be able to quickly recover if eaten by possums. Studies are currently underway at Craigieburn which test whether these ideas predict how mistletoes respond to simulated possum browse.

Possum impacts: an example in south Westland

Possums were liberated into the Makarora catchment (east of Haast Pass) in 1914 and reached Pleasant Flat by 1950.¹⁸ Possums continue to invade this area of south Westland silver beech forest, and it has been assumed that *P. colensoi* has been declining as a result.

David Norton and Hamish Owen have shown that only a small portion of *P. colensoi* in this area have been affected by possums, although browsing can be severe on some plants. This can lead to a decline in photosynthetic rates due to a reduction in annual leaf budgets, and may eventually result in the plant's death.¹⁸ However, it was also found that browsing is strongly influenced by the availability of other foods within a particular forest. *P. colensoi* was not a favoured food at Pleasant Flat and was not common in those possum diets. Instead, depending upon the season, wineberry (*Aristotelia fruticosa*) and pohuehue (*Muehlenbeckia complexa*) were the preferred foods.

Figure 2. Possum browse on *P. tetrapetala* leaves



Possum versus insect browse

Possum density and browsing on beech mistletoes has been intensively studied during 1997 and 1998 at four sites in the South Island by Laura Sessions, a Fulbright student doing an MSc at Canterbury University.

Laura measured the possum numbers and browsing effects over a 12 month period at each site. Possum densities were studied using leg-hold traps and were highest at Craigieburn (20 per 100 trap nights). Despite this, the amount of leaf area lost due to possums was similar to that lost by insect herbivory (Table 1). Importantly, it was discovered that possum browsing varied considerably between branches and between plants. A small number of plants suffered very high rates of browse. In contrast, insects were more consistent feeders causing a uniformly moderate amount of damage to all plants. These differences mean that possums could cause a gradual loss of mistletoe individuals from the population.

Caterpillar predation of *P. tetrapetala* buds

Zelleria spp. (Lepidoptera: Yponomeutidae)²⁰ are moths native to New Zealand and have a patchy distribution throughout the country. The caterpillar stage has been recorded predated internal reproductive structures of *P. tetrapetala* buds (Figure 3), although rates vary throughout New Zealand. Females oviposit eggs into flower buds, and after the caterpillar has eaten its fill, either moves on to another bud or pupates. Predated buds rarely produce fruit and are usually aborted. Also, it is highly likely that neighbouring buds will also be damaged.

Lisa Crowfoot, an Honours student at the University of Canterbury, spent the

Table 1. Annual average leaf loss (%) at Craigieburn

species	leaf abscission	insect browse	possum browse
<i>P. tetrapetala</i>	9.7	0.6	1.2
<i>A. flavida</i>	38.4	0.9	0.9
<i>P. colensoi</i> *	45.5	4.0	2.0

*(Owen 1993-Haast)¹⁹

These data from Laura Session's Craigieburn site show that total leaf loss each year is greater from insect browse than possum browse for both *P. tetrapetala* and *A. flavida* at Craigieburn. Similar results have also been found by Hamish Owen for *P. colensoi* in south Westland.¹⁹ Browsing percentages were also quite small when compared to annual leaf turnover for each species, especially for *A. flavida* and *P. colensoi*.

1997-98 season investigating predation rates of *Zelleria* at several locations throughout New Zealand. She found that rates varied from 13% of buds at Lake Ohau to 44% at Craigieburn. The Boyle area (Lewis Pass) also had high rates of *Zelleria* infestation, with nearly 41% of buds showing predation. Oddly, *P. tetrapetala* buds at both the Kaweka and Tongariro sites in the North Island

contained no signs of predation.

It is important to further investigate the consequences of *Zelleria* distribution and predation, as they can have a significant impact on fruit set when the original number of buds are low.

Figure 3. *Zelleria* Caterpillar inside a *P. colensoi* bud. Note predation of reproductive structures.



Pollination: breakdown of a mutualism

New Zealand mistletoes can be separated into two groups by their mode of pollination. *I. micranthus* and *T. antarctica* are both insect-pollinated, while the beech mistletoes, *A. flavida*, and *Peraxilla* species are bird-pollinated. These bird-pollinated mistletoes are hermaphroditic,² meaning they have both female, (stigmas), and male, (anthers and pollen), reproductive parts contained within an individual flower. They are also morphologically adapted for bird pollination, as their flowers are explosive, large and tubular. For example, *P. colensoi* bud length averages 43mm, and *P. tetrapetala* is 27mm. Beech mistletoes also contain large quantities of nectar. Regional surveys and pollination experiments have been conducted over the last few years to determine if New Zealand mistletoes are pollen-limited.

Tui and bellbirds visit the red-flowered *Peraxilla* mistletoes (Figure 4). While working on her MSc in 1992, Jenny Ladley noticed that the birds tweaked the tops of ripe buds with their beaks. The buds exploded open and showered the bird with pollen, revealing nectar in the tube below. This entire process

occurred in less than one second per flower before a bird moved to the next ripe bud. Flower buds that were enclosed inside a fine mesh bag almost never opened (3 of 394 *P. tetrapetala* and 1 of 82 *P. colensoi* buds). The remaining buds eventually "bottom-opened", (they abscised at their base with their petals still fused at the top).¹¹

Since then, Dave Kelly, Alastair Robertson and Jenny Ladley have discovered that native New Zealand bees also open *P. tetrapetala* buds in some locations.²¹ (See box 2.) Only on a few occasions have introduced birds been seen opening *P. tetrapetala* and are therefore numerically unimportant in their reproduction.²

New Zealand honeyeaters recognise that *Peraxilla* buds are ripe when the tip of the bud turns pink. Tui and bellbirds prefer to visit these buds rather than previously opened flowers because *Peraxilla* species contain up to 70-98% of all the nectar they will ever produce when they are first opened.² Consequently, birds gain large amounts of nectar by arriving at a ripe flower bud first, which also benefits the mistletoe over a period of time due to more

faithful pollinator attention.

"Explosive" flowers

"Explosive" flowering has been known in the Loranthaceae since 1895 when it was first observed in two African mistletoes. Since then, at least seventeen genera of explosive Loranthaceous mistletoes have been noted, including the New Zealand species.²

The discovery of explosive flowering in New Zealand mistletoes has interesting consequences, as it was previously thought our members of the family were unspecialised and primitive. Differing degrees of specialised bird-plant mutualisms for pollination between *P. tetrapetala* and *A. flavida* may show how explosiveness may have evolved in New Zealand.³ These species have similar shaped flowers, but *A. flavida* can open itself when ripe, and thus, is not nearly as reliant on birds for pollination as the *Peraxilla* spp. Furthermore, since birds are continually competing for first access to nectar, honeyeaters may try to prematurely open *A. flavida* buds. Therefore, explosive opening may have been selected in *Peraxilla* to attract honeyeaters to their nectar when flower buds ripen, thus assisting pollination.

Such evolved partnerships between plant and bird may promote pollination efficiency but may also render the plants susceptible to a breakdown in the mutualism. Dave Kelly and his co-workers believe that *T. adamsii* may have suffered such a breakdown.² They suggest that reduction of honeyeaters may have been the major influence causing extinction. Comparison of other mistletoe pollination mechanisms suggest that *T. adamsii* also had explosive flowers and relied upon native birds for pollination and subsequent fruit-set. It could have been greatly

Figure 4. Tui foraging in *P. colensoi*



affected by the decrease in honeyeaters due to introduced predators, causing the decline and eventual extinction of the mistletoe.

Both *Peraxilla* spp. have also declined dramatically since European colonisation of New Zealand in the mid-1800's, and are now on the "vulnerable species" list. Reductions of tui and bellbird numbers are now thought to have serious effects on *Peraxilla* in some areas of New Zealand, as pollen limitation reduces the number of seeds produced and dispersed.¹²

Self-compatibility

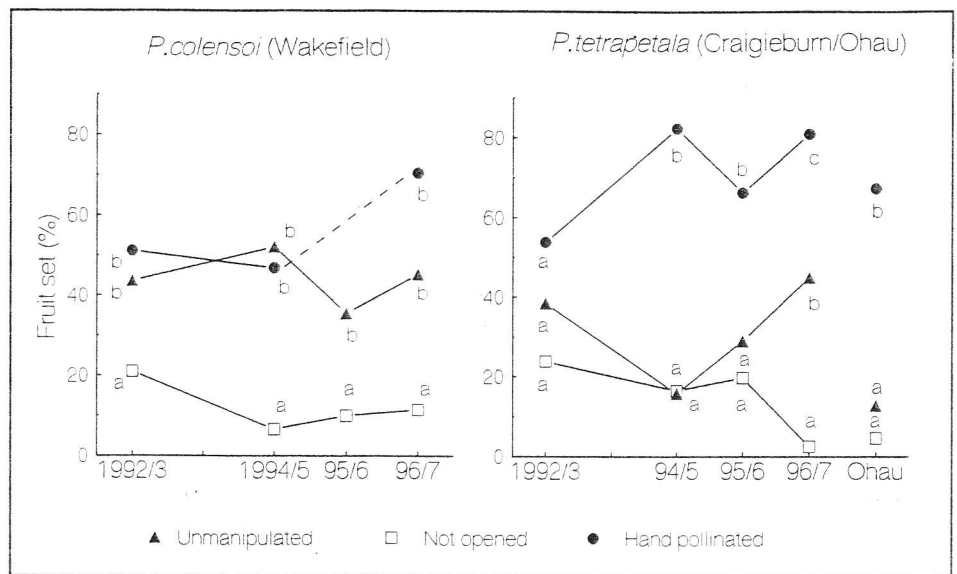
Some New Zealand mistletoes have high levels of self-compatibility and regularly self-pollinate while others do not. Self-pollination means the ability of a plant to successfully make seeds using its own pollen without the need for a pollen vector. For instance, Jenny Ladley found *I. micranthus* does not always need insects for pollination, as it set seed when pollinators were excluded.² *A. flavida* is also extremely self-compatible. It produced many seeds even when birds were artificially excluded in pollination experiments. In this species, anthers contact the stigma while still enclosed within the bud.²

Peraxilla spp. sometimes also self-pollinates 11 to 22% of bagged buds set seed.^{2,12} Some fruit would thus be made if tui and bellbirds completely disappeared. In addition, native bees also open and pollinate some flowers (see Box 2).

Craigieburn, Wakefield and Ohau experiments

The team has been conducting experiments at Craigieburn and Wakefield (near Nelson) since 1992. Fruit set has been consistently pollen limited at Craigieburn (Figure 5). Every year, far less fruit has been produced in unmanipulated buds than that achieved

Figure 5. Fruit set in *P. colensoi* at Wakefield and *P. tetrapetala* at Craigieburn over five seasons, and in *P. tetrapetala* at Lake Ohau in two seasons



by hand-pollination, and in only one season has it significantly exceeded that of bagged buds which occasionally self-pollinate.¹² Results from Lake Ohau show the same pattern. In contrast, the *P. colensoi* plants at Wakefield have been able to consistently set as much fruit as that achieved by hand-pollination, showing that there is not a lack of pollinators at that site. Importantly, tui and bellbirds were recorded visiting plants significantly more often at Wakefield than at Craigieburn and Lake Ohau.

At Craigieburn, despite wide seasonal fluctuations in flowering effort, fruit production has remained remarkably constant (Figure 6). The team suggests this result indicates a limit imposed by the birds on the numbers of flowers that can be pollinated per season.

Regional surveys

Another important aspect of the work on *Peraxilla* spp. has been to record the rate of bud-opening at different sites within New Zealand. The method for this procedure is relatively simple. On

Box 2. Can bees become pollinator substitutes?

Peraxilla buds are opened most often by tui and bellbirds. However, Kelly et al. observed native small, solitary bees opening *P. tetrapetala* buds at Craigieburn and Lake Ohau in 1994-95. It is the first record worldwide of both bees and birds opening an explosive flower.²¹ *Hylaeus agilis* (Colletidae) and *Leioproctus* sp. (Halictidae) use their mandibles to attack bud tips. However, this is costly in terms of time, (20-40 seconds per bud), and effort, due to the large size of buds (27 mm long) in relation to the size and mass of native bees (7 mm body length, 0.01 grams). It seems amazing that such little bees could open large mistletoe flowers. (In fact, they are too small to regularly open the even bigger *P. colensoi* buds, length 42 mm).

However, native bees are not as efficient as birds at pollinating *P. tetrapetala*. They fly from flower to flower collecting pollen, but are too tiny to frequently touch stigmas.²¹ They still assist mistletoes, though, by doubling fruit-set if tui and bellbirds are not available.

Although native solitary bees may help *P. tetrapetala* persist in areas of declining tui and bellbirds, they cannot entirely replace honeyeaters in their mutualism with mistletoes as they are less efficient at pollination, and unable to help with dispersal (see page 9). However, more work needs to be completed to understand the importance of the bee-mistletoe relationship.