

Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae

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Abstract We tested the relative frequency of pollen limitation and dispersal limitation for two bird-pollinated and bird-dispersed New Zealand mistletoes, *Peraxilla tetrapetala* and *Alepis flavida*, at a South Island site where the bellbird (*Anthornis melanura*) is the sole pollinator and disperser. There was no evidence of dispersal limitation for *P. tetrapetala* over four seasons or *A. flavida* over two seasons. Few ripe fruits were present on plants at any one time (usually <5%), and more than 90% of the fruit crop was removed. *A. flavida* was not pollen limited, but *P. tetrapetala* was significantly pollen limited in 6 of 10 years. The presence of pollen limitation but not dispersal limitation, despite both services depending on the same bird, is influenced by the much faster rates of flower ripening per day compared with fruit ripening (15–54 times faster in *P. tetrapetala*). In New Zealand, pollination failure probably threatens at least as many plant species as dispersal failure. In theory, dispersal should threaten fewer plant species, because dispersal usually involves more animal species, makes smaller quantitative demands on the dispersers (fewer fruits

ripening per day, and fruits can wait longer for attention), and may be less obligate for at least some reproduction to occur.

Keywords agents of decline; *Alepis flavida*; bird dispersal; disperser limitation; frugivory; Loranthaceae; mistletoe; mutualisms; *Peraxilla tetrapetala*; pollinator limitation

INTRODUCTION

Plants may rely on animal mutualists for a range of services, of which the most common are pollination and dispersal. Bond (1994) argued that the failure of either of these two mutualisms could increase the risk of plant extinction. It is therefore important to determine the level of mutualist service, and the factors affecting this. Pollinator limitation is widespread in nature (Larson & Barrett 2000); Burd (1994) found evidence for seed production being limited by a shortage of suitable pollen in 62% of 258 studies. In contrast, well-documented examples of dispersal limitation are uncommon, and examples of this having serious consequences for the plant are extremely rare (Wheelwright 1991). Perhaps the best example is the replacement of native ants by the Argentine ant in South African fynbos, which greatly reduces seed burial of a range of ant-dispersed Proteaceae, with consequent higher seed predation and lower seed survival after fire (Bond & Slingsby 1984). Similarly, in English oak woodlands, burial of acorns by jays and squirrels greatly reduces rodent predation and enhances seed survival (Crawley 1990). However, in other cases the loss of even a whole guild of dispersers seems to have merely led to new dispersers taking over (Janzen & Martin 1982).

This leads to the question of whether dispersal is inherently less susceptible to disruption than pollination. There are several reasons why theoretically we might expect this to be so. There are more specialised pollination systems than specialised dispersal systems (Wheelwright & Orrians 1982),

although there are still many generalist pollination systems (Herrera 1996; Waser et al. 1996). Specialised dispersal systems are uncommon both because there are fewer benefits to the plant from specialisation, and because it is more difficult to exclude some potential dispersers from fruits than pollinators from flowers. This means that there may be more animals involved in dispersal and naïve animals (such as introduced bird species) may be capable of performing the dispersal role (although work in New Zealand suggests they do not often do so; Williams & Karl 1996). Secondly, the magnitude of the task for dispersal will usually be smaller, because only a percentage of flowers make fruits (Sutherland 1986)—sometimes a very small percentage, e.g., 0.1–16% in Proteaceae (Hermanutz et al. 1998). If dispersal is a numerically smaller job, a lower density of animals may suffice, and poor mutualist service is less likely.

However, Clout & Hay (1989) considered that in New Zealand, there was a greater risk from failure of dispersal mutualisms than of pollination mutualisms. They said that only about 30 species of native plant had their flowers visited by birds, and argued that “it is unlikely that any New Zealand plant is threatened by a lack of specialised bird pollinators. Few, if any, plants are exclusively pollinated by birds and there is no evidence of tight coevolution between particular bird species and particular flowers” (Clout & Hay 1989, p. 29). In contrast, they argued that “the

most important bird-plant interactions in New Zealand forests today (and probably also the most important in prehistoric forests) are those hinging on avian frugivory and seed dispersal” (Clout & Hay 1989, p. 30), largely because there is now a fairly small number of effective dispersing bird species, with six large-seeded trees entirely dependent on the kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*). Similar arguments were advanced by Lee et al. (1991).

In this paper, we measure the relative levels of pollination and dispersal service to the two mistletoes *Peraxilla tetrapetala* and *Alepis flavida* (Loranthaceae) at Craigieburn, central South Island. These species are interesting test cases for several reasons. Both species are bird-pollinated and bird-dispersed, and a single bird species, the bellbird (korimako, *Anthornis melanura*: Meliphagidae) is the principal mutualist at Craigieburn for both pollination and dispersal of both mistletoes (Ladley & Kelly 1996; Ladley et al. 1997). The features of their flowers and fruits are listed in Table 1. The two plants vary in their degree of dependence on pollinator visitation: *P. tetrapetala* has explosive flowers which are opened only by native birds (Ladley & Kelly 1995) and, less often, by native solitary bees (Kelly et al. 1996). Pollen limitation has been shown over three out of four seasons at Craigieburn (Robertson et al. 1999), apparently because of a low density of bellbirds, even though

Table 1 Characteristics of mistletoe flowers and fruit at Craigieburn affecting pollination and dispersal of *P. tetrapetala* and *A. flavida* (means \pm 95% C.I.). Source: 1, Ladley & Kelly (1996); 2, Ladley et al. (1997); 3, Robertson et al. (1999); 4, Murphy & Kelly (2003); 5, this paper. *, 1997–2003 inclusive.

Stage	Variable	<i>P. tetrapetala</i>	<i>A. flavida</i>	Source
Pollination	Flower colour	Red	Yellow	2
	Corolla length (mm)	26.6 \pm 1.0	16.2 \pm 0.8	2
	Nectar sugar content per flower (mg)	4.64 \pm 0.27	0.59 \pm 0.3	4
	Self-compatibility	self-compatible, not autonomous	autonomously selfing	2, 3, 5
	Fruit set, pollinators excluded (% , with <i>n</i> years)	0–5.0% (7*)	65–90% (2)	2, 3, 5
Dispersal	Ripe fruit colour	Green	Orange or red	1
	Wet fruit weight (mg)	93.5 \pm 10.3	91.5 \pm 7.2	5
	% of wet weight in pulp	57.5	74.8	5
	Pulp % sugar (w/w)	25.2	12.4	5
	Pulp % water	47.0	78.7	5
	Sugar content per fruit (mg)	13.5 \pm 10.2	8.8 \pm 3.0	4, 5
	Germination inside flesh	0%	0%	1

the birds spend much of their foraging time on flowers when these are available (Murphy & Kelly 2001, 2003). In contrast, *A. flavida* readily self-pollinates and is able to produce high fruit set even inside bags (Table 1), rendering it insensitive to pollinator service.

Secondly, the two mistletoe species are at particular risk of dispersal limitation. Since bellbird densities are too low for pollination of *P. tetrapetala*, and bellbirds are also the principal disperser, there may be too few bellbirds for adequate dispersal. At this site, Ladley & Kelly (1996) showed that mutualist service (fruit removal) of both species appeared to be inadequate in the 1993 season. Also, the ripe fruits of *P. tetrapetala* are green and hard, whereas those of *A. flavida* are swollen, fleshy, and brightly coloured (orange or red; Ladley & Kelly 1996; Table 1). Most bird-dispersed fruits are fleshy and brightly coloured (usually red), supposedly to provide maximum visual contrast for the birds. This may mean that *P. tetrapetala* fruits are unattractive or easily overlooked.

Also, the consequences of inadequate dispersal could be severe for these two mistletoes. Like all the New Zealand Loranthaceae, the seeds of *P. tetrapetala* and *A. flavida* cannot germinate until they are removed from the fruit, which in the field happens only by bird ingestion (Ladley & Kelly 1996). Also, the seed must be removed from the fruit to expose the viscin layer which glues the seed to a host branch. Thirdly, because the mistletoes are stem parasites, the seeds have to be dispersed to a branch on a new host tree before the current host dies. Unlike in most plants, it is not an option for undispersed mistletoe seeds to fall below the parent and germinate there. In combination, these attributes mean that successful establishment of new mistletoe plants is absolutely dependent on birds handling the fruits. Finally, Robertson et al. (1999) argued that reproduction in these mistletoes is likely to be seed-limited.

Therefore, the aims of this study were to answer these questions:

- 1 What is the frequency of pollen limitation in *P. tetrapetala* and *A. flavida* at Craigieburn?
- 2 What is the frequency of dispersal limitation in *P. tetrapetala* and *A. flavida* at Craigieburn?
- 3 At a given density of birds, is pollination more likely to fail than dispersal?
- 4 What features of the flowers and fruits affect the probability of mutualism failure? For example, are *P. tetrapetala* fruits unattractive to dispersers, and less well dispersed as a result?

METHODS

Study site

The site (171°42.5'E, 43°9.1'S) is 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 almost pure *Nothofagus solandri* var. *cliffortioides* forest and is largely undisturbed. Both mistletoes, *Peraxilla tetrapetala* and *Alepis flavida*, parasitise *N. solandri*. The study site was the same one at Craigieburn used by Ladley & Kelly (1996). For both species, flowering occurs at this site in January, with fruit set in autumn or winter, so "1993" refers to the 1992/93 season.

Levels of pollination service

To measure pollination effectiveness in *P. tetrapetala*, between 1993 and 2003 we measured fruit set (% of flowers ripening into a single-seeded fruit) under three treatments. "Natural" flowers were unmanipulated and accessible to pollinators. "Hand-pollinated" flowers were individually pollinated when receptive with a paintbrush carrying a mixture of pollen from several other mistletoe plants. "Bagged" flowers were enclosed in muslin bags before opening to prevent any pollinator visitation. All three treatments were performed on the same plants, except in 1995 when hand pollination was applied to entire plants to test for cryptic self-incompatibility (see Robertson et al. (1999) for details). The results were analysed within each year using a Generalised Linear Model with binomial error distribution and logit link function, and chi-square significance tests when the residual deviance was between half and twice the value of the residual d.f., or an *F*-test otherwise. Predictors were plant as a block effect entered first, and treatment. If treatment was significant, a post-hoc means comparison was performed on the natural and hand-pollinated treatments to test for significant pollen limitation.

Pollination service to *A. flavida* was measured at this site in 1993 and 1997 by Ladley et al. (1997), who showed that this species can routinely self-pollinate (Table 1).

Fruit sugar reward

To determine the relative rewards offered by fruits of the two mistletoe species, 15 ripe fruits of each species were collected at Craigieburn in May 1996. Juice was squeezed from each fruit and its sugar

content measured using a refractometer. The seed and pulp were separated and the wet and dry weights determined for each component; for dry weights, the seeds were combined in lots of five before drying for 24 hrs at 50°C.

Fruit ripening and removal rates: 1995 season

In 1995, ripening of *P. tetrapetala* fruits was recorded on bagged plants. On 12 small *P. tetrapetala* plants, all flowers were hand pollinated in January 1995 with self or outcross pollen. Once the resulting fruits started to ripen, the plants were enclosed inside muslin bags to exclude frugivorous birds, and ripe fruit inside the bags was removed by hand at each visit for germination experiments (Robertson et al. 1999). There were 10 visits altogether between 3 April and 29 November. From 23 June onwards, the number of ripe and over-ripe fruits was recorded at each visit. Ripe *P. tetrapetala* fruits were identified by a dark ring at the distal end, and a softening of the fruit pulp; over-ripe *P. tetrapetala* fruits show darkened, wrinkled flesh over the whole surface of the fruit (Ladley & Kelly 1996). From these data, the fraction of fruits going from unripe to overripe in a month in the absence of dispersal or predation could be determined.

To determine natural fruit removal rates by frugivores at Craigieburn in 1995, 109 unripe *P. tetrapetala* fruits were mapped on 13 May on unbagged branches on 9 additional plants. The fruits were observed at each monthly visit and the fate of each fruit (unripe, ripe, overripe, or gone from the plant) was recorded. Since 30% of fruits had ripened

on the bagged plants by this date, the starting percentage on 13 May was set to 70%. This experiment allowed us to calculate the natural removal rates of fruits, and also record how long undispersed ripe fruits remained ripe.

Fruit ripening and removal rates: 1996–1998 seasons

To determine fruit ripening rates and removal rates in 1996, 1997, and 1998, all fruits were counted on small (<70 cm in each dimension), low-growing (<2 m height), isolated *P. tetrapetala* plants ($n = 10$ in 1996, 5 in 1997, and 9 in 1998). At regular intervals, the number of unripe, ripe, and overripe fruits on each plant was counted as in 1995. In the 1996 season, there were 8 visits between 27 March 1996 and 5 January 1997; for the 1997 season, 8 visits between 2 April 1997 and 8 January 1998; for 1998, 13 visits between 13 March and 11 October. Visits were fortnightly in April and approximately monthly thereafter.

In the 1995 season, when fruits disappeared from the plants it was not known whether they had been dispersed by a bird, or had fallen off the plant. To determine this, in 1996–1998 a 2 m × 2 m piece of fabric was laid out underneath each plant used for dispersal to catch any seeds which fell off. The number of whole undispersed fruits caught on the fruit trap underneath each plant was recorded at each visit. The traps also caught a number of seeds which had been eaten and then voided by birds; these are not presented as it is not known from which plant they came.

Table 2 Significance tests of pollination treatments on fruit set of *P. tetrapetala* at Craigieburn, from binomial GLMs. Predictors were plant (except in 1994/95) entered first, and treatment (hand-pollinated, natural, or bagged). Post-hoc means tests were run comparing natural versus hand treatments if the treatment effect was significant. NS, not significant; *, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.001$; N/A, not applicable as in 1995 treatments were applied to different plants.

Year	<i>n</i> plants	Plant effect (% deviance)	Treatment effect (% deviance)	Significance hand versus natural
1993	6	73.6 ***	7.7 NS	—
1995	35	N/A	58.3 ***	***
1996	7	52.4 ***	29.8 ***	*
1997	5	17.3 ***	78.9 ***	*
1998	7	35.7 ***	52.0 ***	NS
1999	10	25.8 **	68.6 ***	*
2000	10	35.0 **	52.7 ***	NS
2001	10	46.0 **	34.5 ***	NS
2002	10	25.9 *	59.4 ***	*
2003	8	53.2 *	40.4 **	*

In 1997 and 1998, the same method was used to record ripening and dispersal of *Alepis flavida*, on 5 and 10 plants, respectively, each with fruit traps placed on the ground underneath them. *Alepis* fruits are green when unripe, glossy red or orange when ripe, and wrinkled and brownish when overripe. To check for loss of fruits after they had fallen onto the traps, another similar trap was laid out away from any *A. flavida* plant and 20–50 hand-picked ripe fruits placed on them at each of five visits during the 1998 season. At the next census, the fruits still present were removed and counted, and the percentage retrieved after each interval was averaged over all five intervals.

The duration of the ripe phase in *A. flavida* fruits was determined at this site in 1998 by Bach & Kelly (unpubl. data) who found that only 2 of 214 fruits which ripened while examined at weekly intervals went from unripe to overripe between censuses, and that very few fruits fell off while unripe or ripe. They estimated that fruits take about a week to ripen (from yellow to orange or red) and another 5 days to become overripe. Ripe fruits almost never spontaneously fell off plants that were protected from animals.

Three summary statistics were calculated for dispersal service. For all visits, excluding those at the end of the season when fewer than 5% of initial fruits remained on the plants, the mean % of all initial fruits which were on plants in the ripe state was calculated (i.e., a mean of the instantaneous percentage of fruits which were ripe). In the same way, the mean percentage of overripe fruits was calculated. Also, the total number of non-dispersed fruits caught on the seed traps through the whole season was tallied and expressed as a percentage of the starting number of fruits on that plant.

Flower and fruit densities and flower ripening rates

To compare flower densities and ripening rates with fruit densities and rates, flowering information was collected on permanently tagged plants of *P. tetrapetala* in 1995–98 ($n = 42\text{--}80$ plants) and *A. flavida* in 1997–98 ($n = 50$). The plant size and flower production of each plant were recorded and expressed as flowers per m^3 of mistletoe plant; these were averaged across all plants each season. The average fruit set (%) for naturally pollinated flowers each season was determined from tagged branches on the plants where the number of flowers and later the number of fruits was recorded, using the methods of Ladley et al. (1997) and Robertson

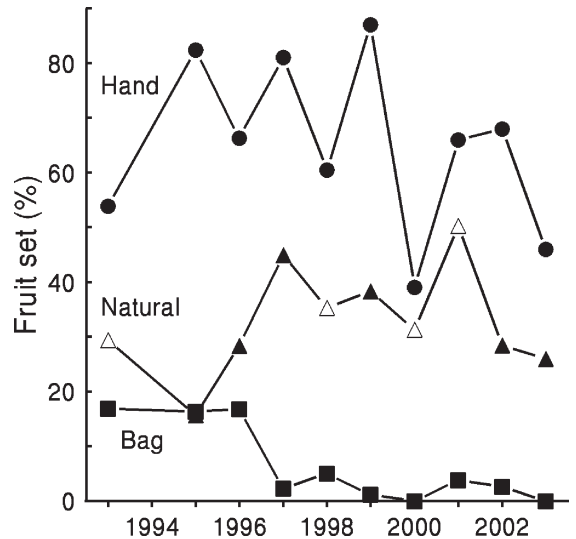


Fig. 1 Pollination limitation of fruit set in *Peraxilla tetrapetala* at Craigieburn. Natural (unmanipulated) flowers had significantly lower fruit set than hand-pollinated flowers in 6 of the 10 years (solid triangles), see Table 2. Since flowering is in January, “1993” refers to the 1992/93 season.

et al. (1999). The rate of ripening of unripe flowers was determined in 1995 (*P. tetrapetala*) and 1998 (both species) by repeated visits every few days to a subset of the marked plants, to count the total number of unripe buds, ripe flowers, and abscised flowers on tagged branches. The time elapsed between bud ripening and petal abscission was determined by following mapped flowers.

RESULTS

Levels of pollination service

For *P. tetrapetala*, both plant and treatment effects on fruit set were significant in all years, except for 1993 when treatment was marginally non-significant ($P = 0.063$) (Table 2). Mean fruit set was always low in the bagged treatment (Fig. 1), especially from 1997 when we switched to larger muslin bags which were less likely to contact the flower buds. Natural fruit set was always lower than hand-pollinated fruit set, significantly so in 6 of the 10 years (Table 2). This shows that pollen limitation was frequent for *P. tetrapetala* at Craigieburn.

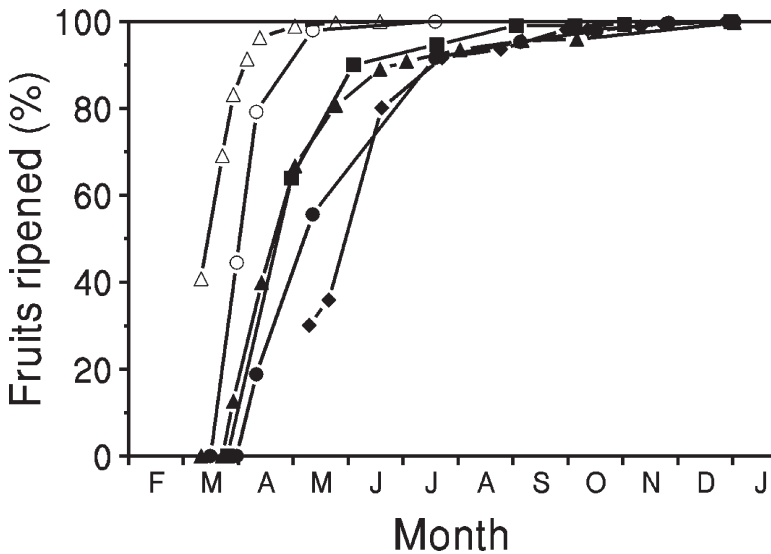


Fig. 2 Rates of fruit ripening (cumulative % of fruits which have ripened) for *Peraxilla tetrapetala* (solid symbols) and *Alepis flavida* (open symbols) at Craigieburn in 1995 (diamonds), 1996 (squares), 1997 (circles), and 1998 (triangles).

Table 3 Dispersal effectiveness for fruits of *P. tetrapetala* and *A. flavida* at Craigieburn. The mean % ripe and overripe are averages over all dates from first fruit ripening until 95% of fruits were gone, whereas % fell off is a total over the whole season. —, no data

Year	Mean % ripe	Mean % overripe	Total % fell off	Number of fruits
<i>P. tetrapetala</i>				
1995	1.4	0.6	—	109
1996	4.4	0.8	4.0	705
1997	9.5	2.4	6.5	367
1998	4.7	2.7	3.2	381
<i>A. flavida</i>				
1997	5.4	8.9	1.5	548
1998	14.8	0.7	8.0	1076

Fruit sugar reward

Although the ripe fruits of *Alepis flavida* are swollen, juicy, and brightly coloured and those of *Peraxilla tetrapetala* are dull green and relatively hard, the sugar content per fruit was higher for *P. tetrapetala* than *A. flavida* because the pulp was very high in sugar and lower in water content (Table 1).

Time of ripening and life of fruits

Fruit ripening was earlier and more rapid for *A. flavida* than for *P. tetrapetala* (Fig. 2). Most *A. flavida* fruits ripened in March and virtually all were ripe by the end of April, whereas about half the

P. tetrapetala fruits ripened after the end of April, and the last fruits did not ripen until the following summer (Nov–Jan). There was some variation among years with 1997 fruits ripening later than 1998 fruits for both species.

Once a *P. tetrapetala* fruit had ripened, it remained ripe for some time before going overripe. In 1995, of 247 ripe fruits collected at monthly intervals from bagged plants, only 5 (2.0%) had gone from unripe to overripe in a month. Of 109 mapped fruits in 1995 not protected from dispersers, most (90%) went from unripe at one census to gone at the next census. Only two fruits were seen as ripe one month and overripe the next, whereas three fruits were ripe for two consecutive months before being

dispersed. This suggests that it takes most *P. tetrapetala* fruits between 4 and 8 weeks to go from ripe to overripe. This is much slower than the 5 days estimated for *A. flavida* to go from ripe to overripe (Bach & Kelly unpubl. data), perhaps partly because *A. flavida* ripens earlier in the season when temperatures are warmer.

Rates of dispersal

The percentages of fruits which were ripe and overripe at each census are shown for both species for the 1997 season in Fig. 3. The highest instantaneous percentage of ripe fruits seen at any census for either species was in this season (28% for *P. tetrapetala* on 15 May 1997), but usually <6% of fruits were ripe at any one visit, as seen for *A. flavida*. *A. flavida* fruits ripened earlier and faster, and were removed rapidly once they became ripe. Few overripe fruits were seen in either species and few fruits were collected from the fruit traps (the cumulative percentage is shown in Fig. 3). Summary statistics for all seasons (Table 3) showed that on average there were few ripe flowers present on plants at any time, and even fewer overripe fruits. Hence, fruits rarely remained on plants long enough to become overripe.

The total cumulative percentage of fruits found on fruit traps under the plants was also low (Table 3). The highest value was 8.0% for *A. flavida* in 1998, and 71% of these fruits collected from the traps were ripe (rather than overripe) and were presumably dislodged by foraging birds. In most years nearly all fruits caught on the traps were overripe. In 1998 *A. flavida* fruits were placed on a similar fruit trap which was not under a mistletoe, and $65.1 \pm 25.7\%$ ($\pm 95\%$ C.I., $n = 5$) were recovered at the next census. The missing fruits presumably either were not noticed by the observer, had undergone secondary dispersal off the ground by birds, or had been eaten by invertebrates or introduced mammals.

Relative ripening rates of flowers and fruits

Flowering density per m^3 of mistletoe plant was higher in *P. tetrapetala* than in *A. flavida* (Table 4). The very high value for 1995 is probably an artefact due to plants being selected and initially tagged in that year on the basis of being in flower, but this bias should not affect the flower to fruit comparison since there is no evidence of resource limitation in *P. tetrapetala* even when whole-plant hand pollination treatments are applied (Robertson et al. 1999; Montgomery et al. 2003). After 1995, all plants were measured regardless of their flowering status and the

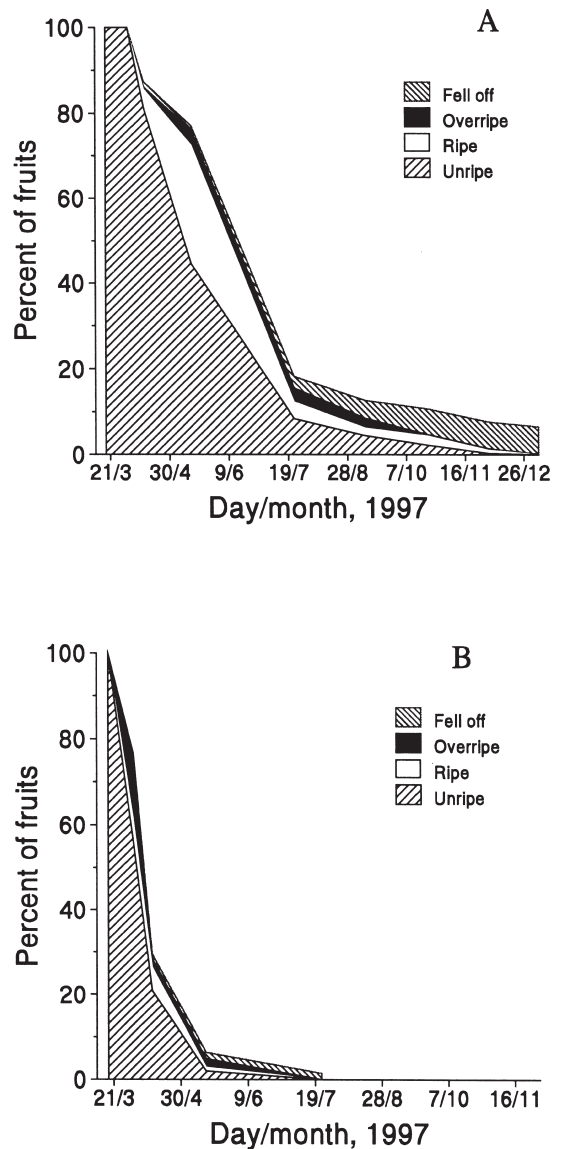


Fig. 3 Unripe, ripe, and overripe fruits through 1997 for unbagged plants of **A**, *Peraxilla tetrapetala* and **B**, *Alepis flavida*. Values are for the current census except for “fell off” where numbers are cumulative through the season.

flowering densities should be relatively unbiased. Flower ripening rates (% per day) were very much higher than fruit ripening rates. In both species, the majority of flowers ripened over about 3 weeks with nearly 10% ripening per day at the peak, compared with 6 weeks to 6 months for fruit ripening (Fig. 2) and <3.5% ripening per day at the peak. Moreover,

especially in *P. tetrapetala* the low fruit set means that there were always many fewer fruits per m³ than flowers per m³. Flower life (between ripening and petal abscission) of 6–9 days in *P. tetrapetala* and 6.4 ± 0.4 days in *A. flavida* ($n = 149$) was also much shorter than the persistence of ripe fruits at least in *P. tetrapetala* (see above). The net effect of all this is that at their peak seasons, flowers are coming ripe faster than fruits by a factor of 5 for *A. flavida* and a factor of 15–54 times for *P. tetrapetala* (Table 4), and in *P. tetrapetala* fruits can also wait 7 times longer for attention.

DISCUSSION

Is dispersal less limiting than pollination for mistletoes at Craigieburn?

Over the period 1995–1998, it appears that *P. tetrapetala* and *A. flavida* were not dispersal limited at Craigieburn. *A. flavida* was not pollination limited in 1997 (Ladley et al. 1997), and because of autonomous selfing should never be. In contrast, during this time, *P. tetrapetala* was repeatedly pollen limited.

The data show that both mistletoes received good dispersal service. Very few fruits (8%) ended up on the fruit traps below the plant, so we conclude that almost all fruits (92–98.5%) were taken by a disperser. The estimates of the number of non-dispersed fruits could be increased by 53% (100/65.1) to correct for the 65% recovery rate of fruits that were placed on fruit traps. However, the true correc-

tion factor is probably less than that, since some of the losses from the traps could be secondary dispersal. Also, naturally falling fruits onto the traps could fall any time during the interval, so would on average only be at risk of disappearing for half as long as the hand-placed fruits. In any case, even in the worst scenario (*A. flavida* in 1998 allowing for 53% greater losses) at least 88% of fruits were removed by dispersers. The conclusion of very effective dispersal is supported by the rapid rates of removal of fruits as they ripened, and the small percentage of fruits which had time to over-ripen.

These removal rates at Craigieburn are at the high end of the range in the literature. Herrera (1984) found total removal rates of 89–100% for seven species of shrub at a site in Spain, although another four species with fruits that were larger than the gape size of the dispersing birds had very poor removal rates (<20%). In Australia, the shrub *Coprosma quadrifida* had 84% of fruits removed by a collection of 14 bird species (French et al. 1992). In South Carolina removal rates averaged 72% across 22 species (range 30.0–99.1%; McCarty et al. 2002). Davidar & Morton (1986) found removal rates of 46–79% of fruit crops.

However, earlier work at Craigieburn did show a large fraction of fruits not being removed from plants in 1993 (Ladley & Kelly 1996), especially for *P. tetrapetala*, whose fruits did not seem to ripen normally that year. This conclusion was subsequently reinforced by the difference in measured fruit weights between 1993 (64 mg; Ladley & Kelly 1996) and 1996 (94 mg; Table 1). These seasonal differences may be caused by weather variations, to

Table 4 Fruit and flower ripening rates for *P. tetrapetala* and *A. flavida* at Craigieburn. *, no data for that season, so value (or mean of values) from other season(s) used.

Year	Flowers /m ³	Flower ripening rate (max %/day)	Max flowers ripening/ m ³ /day	Fruit set (%)	Fruits/m ³	Fruit ripening rate (max %/day)	Max fruits ripening/ m ³ /day	Ratio of flowers to fruits to fruits ripening per day
<i>P. tetrapetala</i>								
1995	2152	7.1	153	9.0	194	1.47	2.85	53.6
1996	578	(7.9)*	46.0	30.4	176	1.78	3.13	14.7
1997	435	(7.9)*	34.6	31.5	137	1.71	2.34	14.8
1998	423	8.8	37.2	19.5	88.7	1.71	1.52	24.5
<i>A. flavida</i>								
1997	366	(9.0)*	33.3	62.5	207	3.15	6.52	5.1
1998	330	9.0	30.0	72.3	257	2.37	6.08	4.9

which *P. tetrapetala* may be especially susceptible as it ripens from late autumn through winter when Craigieburn sometimes has snow lying for weeks on end. Another possible factor affecting fruit removal rates for both mistletoes is reduced bellbird densities due to a mast-seeding-related outbreak of stoats (King 1983). There was a moderate *Nothofagus* mast year at Craigieburn in 1991 (Schauber et al. 2002), which would be predicted to lead to elevated stoat densities in the summer of 1992/93, but we have no data on stoat or bird numbers at that time.

The efficient dispersal of *P. tetrapetala* is noteworthy given that the small green fruits are so cryptic. The signal that the fruit has ripened is very subtle, being a slight darkening of the green at the distal end of the fruit (Ladley & Kelly 1996). However, the fruits have a large sugar reward, and clearly bellbirds regularly find them. At Craigieburn the diet of bellbirds is dominated by mistletoe fruits when these are available (Murphy & Kelly 2001, 2003).

One caveat is that we have shown good dispersal quantity (a high percentage of mistletoe fruits are taken by birds), but have no information on dispersal quality (germinability, location that seeds are dropped, etc.; Schupp 1993). In this case, however, dispersal quantity should be highly correlated with overall dispersal success, since seeds not taken by birds have zero fitness, the forest is a monoculture of the preferred host tree, and the absence of multiple dispersers means no inter-specific variation in bird behaviour patterns or gut treatment. All seeds swallowed by bellbirds should have equal, albeit small, chances of landing on a suitable host branch.

Our conclusion is that for these two mistletoes, dispersal was not limiting for either species over the study period, whereas pollination was usually limiting for *P. tetrapetala*. These results can be explained partly by the biology of the species: pollen limitation is less likely in autonomously selfing species (Larson & Barrett 2000) such as *A. flavida*. However, pollination for *P. tetrapetala*, and dispersal for both species, does require the service of a mutualist. Thus, it seems that dispersal is functioning effectively at bellbird densities which are insufficient for adequate pollination of *P. tetrapetala*. Both fruits and flowers are preferred foods for bellbirds when they are available (Murphy & Kelly 2003). The failure of pollination, but not dispersal, seems to be because the rates of service required for pollination are higher than those required for dispersal.

In theory, should dispersal be less limiting than pollination?

It seems worthwhile, therefore, to consider whether this result could apply to pollination and dispersal generally. Bond (1994) argued that the failure of pollination and/or dispersal mutualisms between plants and animals could have serious consequences for the risk of plant extinction. Bond identified three variables that affect the risk of plant extinction from mutualism failure, which we call mutualist service, mutualist-dependence, and seed-dependence. Here we evaluate the relative risks from of the three variables to pollination and dispersal (Table 5).

Table 5 Relative risks that failed dispersal and pollination mutualisms will threaten plant populations with reduced density or local extinction.

Factor	Dispersal	Pollination
Risk of poor mutualist service	Moderate: dispersal usually unspecialised, involves multiple, often unrelated, animals; fruits usually require lower processing rate (fruit number is often << flower number, individual fruit life > individual flower life, fruiting season > flowering season)	High: pollination systems more specialised, may involve single animal; flowers must usually be processed at a higher rate
Mutualist-dependence of reproduction	Moderate: dispersal benefits usually not absolute; germination enhancement widespread but usually not absolute; predator escape variable	High: plant species often require outcross pollen or pollen vector for seeds to be set
Seed-dependence of population maintenance	Usually low: colonisation of new sites important over long time scales and for pioneer species, but establishment usually possible adjacent to parent	Variable: most likely to be important in short lived plants and open habitats

The first variable is **mutualist service**: the risk of the mutualist(s) giving inadequate service to the plant. This is affected by how specialised the mutualism is, how many species are involved on each side, and whether other organisms can step in as replacements. Mutualist service can be readily quantified by the rate of flower or fruit visitation. For dispersal, this is a measure of dispersal quantity (Schupp 1993). Because dispersal usually involves more species of less specialised animals (Wheelwright & Orians 1982; Jordano 1987), and lower processing rates of fruits per day, on average dispersal should be less at risk than pollination (Table 5).

In relation to processing rates per day, it is noteworthy that the short flower life and long fruit life in *P. tetrapetala* seem to not be unusual. Ashman & Schoen (1996) reviewed flower longevity in 280 species and found that 73% had flowers lasting ≤ 5 days, and 91% lasting ≤ 10 days. McCarty et al. (2002) measured ripe fruit persistence on 22 plant species in South Carolina; even though the fruits were exposed to removal by vertebrates, the mean fruit life was 62 days, the range of species means was 3 to 152 days, and 25% of species had fruits persisting more than 88 days on average.

The second is **mutualist-dependence** of reproduction: how much seed production/dispersal relies on the mutualist. This depends on whether there are alternative mechanisms (such as self-pollination or abiotic dispersal) which can circumvent the failure of the animal-mediated process. Mutualist dependence can be quantified by recording the sensitivity of reproduction to reduced visitation rates. This is frequently measured for pollination, for example, Burd (1994) showed that many plant species require outcross pollen, or require an agent to move pollen onto the stigma (Table 5). Mutualist dependence on dispersers is much harder to measure than for pollination, because it hinges on the relative success of dispersed and non-dispersed seeds (which is affected by dispersal quality; Schupp 1993). Unfortunately, the exact destination of most removed seeds will be unknown. Many of the most important dispersal events are rare in time and remote in space, and therefore hard to measure. Also, seeds which are not dispersed usually still have some non-zero probability of success in the vicinity of the parent. To complicate matters further, some seeds processed by a disperser are dropped underneath the parent, next to any non-removed seeds. All this means that well-designed experimental tests of the effects of dispersal on reproductive effectiveness are

difficult, and this probably skews the published literature, leading to a dearth of papers documenting such effects.

The third is **seed dependence** of the population: how much the maintenance of plant population density depends on continued seed production or dispersal. Bond (1994) reasoned that long-lived clonal plants may persist for centuries even if reproduction by seed is greatly reduced. Also, plants which have strong density-dependent seedling mortality may be little affected at the population level by reduced seed output (Andersen 1989; Crawley 1990). Seed dependence must be tested differently for pollination and dispersal mutualisms. For pollination, the crucial experiment is to add seed to a population and see if extra recruitment occurs; Turnbull et al. (2000) found some evidence for seed limitation in about half of the 100 cases they reviewed, especially in short-lived plants and plants of open habitats (Table 5). For dispersal, because of the temporal and spatial difficulties referred to in the previous paragraph, it is not clear what the definitive experiment would be. However, a review of the benefits of dispersal can indicate when dispersal is most likely to affect population size.

Potential benefits from dispersal

There are three major areas of potential benefit from dispersal. The first is by colonising new areas remote from the parent plant. Generally, seeds handled by an animal disperser will have a very much greater chance of reaching a distant site. This benefit is essentially through the healthy maintenance of metapopulation dynamics, and is likely to be important on relatively long time scales, except for pioneer or early seral species which continually need to find the next gap. For most plants, however, seeds which stay near the parent may have a success rate at least as good as those which travel a long distance and most likely land in unsuitable habitats. It is not clear that non-seral plant populations would decrease rapidly if distant dispersal was prevented (Table 5).

The second major possible benefit of dispersal is through the enhancement of germination. There is an extensive literature on how the germination of fleshy-fruited species is affected by animal dispersers (reviewed by Traveset 1998). Although there has been much speculation about plants which absolutely require gut treatment by a putatively co-evolved animal, there are very few plausible claims for an obligate relationship (Traveset 1998). Most germination work concentrates on whether passage through a vertebrate gut gives a higher final

germination percentage than hand cleaning of the seed. However, hand cleaning of seeds is not a common occurrence for most field plant populations, rendering this comparison somewhat academic.

Of more interest for the ultimate success of the seeds is the final germination percentage of seeds cleaned by either method compared with those in fruits. Generally, seeds retained in the fruits have markedly lower final germination percentages compared with cleaned seeds (Bannister & Bridgeman 1991; Traveset 1998). For example, of the 46 bird-dispersed New Zealand woody species tested by Bannister & Jameson (1994), Burrows (1995a,b,c,d, 1996a,b,c,d,e,f, 1999a,b), and Trass (2000), 20% showed good germination ($\geq 50\%$) in fruits, 20% showed moderate germination (20–50%), and 60% showed poor germination ($< 20\%$) in fruits. For most of these species, germination of hand cleaned seeds was $> 90\%$.

However, a crucial question is whether the non-germinated seeds inside fruits are dead, or alive but dormant. Usually, this is not known (Traveset 1998). If the seeds are dead, then dispersed seeds have a major survival advantage over non-dispersed seeds. In contrast, if seeds in fruits are merely dormant, they may germinate later. Dispersal in space and dispersal in time are logical alternatives in plants, as shown by species with heteromorphic seeds where the better-dispersed (in space) seeds have limited dormancy while the poorly spatially dispersed seeds have stronger dormancy (Venables & Brown 1988). A delay in germination caused by the fruit flesh in fleshy-fruited species could serve as a facultative mechanism for dispersal in time when there has been no dispersal in space.

There are two problems with the experimental data showing low germination percentages of seeds retained in fruits. The first is that the experiments may not have been carried on long enough to allow full germination of dormant seeds (Burrows 1996c). Germination of *Prumnopitys ferruginea* continues for > 4 years (Beveridge & Smale 1981; Clout & Tilley 1992), but most germination experiments are terminated after a few months (Traveset 1998). Secondly, the experimental conditions (typically the fruits are on filter paper in petri dishes; Burrows 1995a; Traveset 1998) probably reduce leaching and breakdown of the fruit pulp compared with fruits on the soil surface in the field, and may hasten seed death. Therefore, the germination percentage and germination speed of seeds in fruits may be depressed in these experiments. More work under field conditions comparing cleaned and uncleaned seeds

is desperately needed. At present, the data suggest a major germination advantage from disperser cleaning of seeds in many species, but this is not absolute, as some germination is usually possible from undispersed fruits (Table 5).

The third possible benefit of dispersal is escape from predation. This forms the basis of the escape hypothesis for the diversity of tropical forests (Janzen 1970; Connell 1971). There are many tests of this hypothesis in the tropical literature, and some authors show convincingly that only seeds which are dispersed away from the parent escape predators and pathogens (e.g., Schupp 1992; Howe 1993). There are also examples from outside the tropics (Bond & Slingsby 1984; Crawley 1990; Packer & Clay 2000), so the principle may apply more widely than was first thought. One complication in evaluating this benefit is that it is not conferred on seeds handled by a disperser then dropped under the parent, in contrast to benefits from better germination.

When all these factors are considered, it seems that dispersal failure should usually be less likely than pollination failure (Table 5), which is congruent with the observation that dispersal limitation is less commonly reported in the literature. Clearly there are many exceptions to all the generalisations in the table; however, given specific information on these variables for a particular plant species, it should be possible to evaluate the relative risks for that species with some accuracy.

Is dispersal less limiting than pollination in New Zealand generally?

Clout & Hay (1989) argued that few New Zealand plants were exclusively pollinated by birds, and that there was no evidence of tight coevolution between particular birds and flowers. In contrast, they showed that six large-seeded trees are now entirely dependent on the kereru for dispersal. They concluded that the most important bird-plant interactions in New Zealand forests are associated with dispersal rather than pollination.

However, since their paper was published, evidence of both specialised pollination systems and possibly widespread pollen limitation has emerged. Specialised pollination systems have been shown for *P. tetrapetala*, *Peraxilla colensoi*, and *Trilepidea adamsii* (Ladley & Kelly 1995), and *Dactylanthus taylorii* (Ecroyd 1996). Pollination limitation has been shown at two Canterbury sites for *Fuchsia perscandens* (Montgomery et al. 2001). Anderson (1997) showed reduced seed set in a range of native plants (including *Metrosideros excelsa*,

Rhabdothamnus solandri, and *Sophora microphylla*) on the mainland around Auckland compared with offshore islands where bird densities were higher. A review by Anderson et al. (2004) of the above and other studies found that six of seven tested native bird-pollinated plants were pollen-limited on the mainland, the only exception being *A. flavida*. Birds have also been found to visit many more plant species than the few which show classic ornithophilous flower structures (Castro & Robertson 1997; Anderson 2003). Clearly, some New Zealand native plants are at risk from inadequate pollination service.

There are fewer data showing problems with inadequate dispersal in New Zealand. Anderson (1997) and McNutt (1998) found some evidence for slower, or less complete, fruit removal from plants on the mainland compared with islands, but the review by Anderson et al. (2004) found reduced dispersal in only three of eight fleshy-fruited species. Also, evidence of slower fruit removal shows only that the plants are getting poor mutualist service. What is more difficult is to say whether the plants are mutualist-dependent and seed-dependent. Mutualist-dependence will be highest in plants which have zero success from non-dispersed fruit, but for many New Zealand woody plants, some germination occurs from intact fruits in petri dishes (see above). If these experiments are a fair reflection of the relative germinability of dispersed and non-dispersed seeds in the field, then the numerical advantage to dispersed seeds ranges from less than 2-fold in species like *Fuchsia excorticata* and *Schefflera digitata*, to 6-fold in *Alectryon excelsus* and *Myrsine australis*, 50-fold in *Griselinia littoralis* and *Hedycarya arborea*, and an absolute need for dispersal in the 16 species that showed no recorded germination from intact fruits (Bannister & Jameson 1994; Burrows 1995a,b,c,d, 1996a,b,c,d,e,f, 1999a,b; Trass 2000). Of the six large-seeded trees now wholly dependent on kereru for dispersal, two (*Beilschmiedia tawa* and *Corynocarpus laevigatus*) have been tested and both had zero germination in fruits, so these appear highly mutualist-dependent. However, as noted above, only field experiments can clarify how strong mutualist-dependence is for bird-dispersed New Zealand plants.

The third criterion, seed-dependence (that reduced dispersal will negatively affect population size), is little studied in New Zealand. Some of the most mutualist-dependent species, such as *B. tawa*, are plants of mature forest and have strongly resprouting adults, so may be well buffered against a failure of reproduction by seed. Most of the

important forest trees do not resprout (Burrows 1994) which increases seed-dependence, but on the other hand most are not pioneer species.

Therefore, on current evidence, pollination failure could threaten at least as many species of New Zealand plants as dispersal failure (cf. Clout & Hay 1989). There are only about 30 species of native plants which appear to be primarily bird-pollinated (Godley 1979), but their level of mutualist dependence for pollination seems to be higher than was first thought, and birds may also be important to plants with smaller flowers. In contrast, some plants have a lower risk of dispersal failure because of specialisation and fruit quantity issues (Table 5), and the level of mutualist-dependence for dispersal is quite variable.

Of course, pollen limitation can interact with dispersal, and both may change in parallel since the key pollinators in New Zealand (bellbirds, and tui, *Prothemadera novaeseelandiae*) are also important dispersers. Pollen limitation may itself reduce dispersal in two ways. Firstly, any reduction in pre-dispersal seed production on average reduces *pro rata* the number of seeds arriving post-dispersal at any distance from the parent. Far from the parent, where self-thinning is unimportant, this means that pollen limitation directly reduces the chance of dispersal to a distant site (Erhlen & Eriksson 1995). Secondly, if pollen limitation reduces the size of the fruit display, frugivores may switch to an alternative food source which gives a higher energy intake rate.

Overall importance of pollination and dispersal mutualisms: relative timescales

Overall, dispersal may be generally less likely to be limiting plant populations than pollination. If we rank threats to a population of a long-lived plant, there are three different levels of threat. Any factor which kills adult plants (such as browsing by herbivores) can have an effect within a time period measured in years to decades. Any factor which prevents seed production (such as pollination failure) will have an effect as the current adults die, so may be visible within decades to centuries. Any factor which allows continued regeneration *in situ* but prevents dispersal among patches of a metapopulation (such as dispersal failure) may take millennia to show any major effect. However, if it can be shown that seeds in un-dispersed fleshy fruits in the field typically die without germinating, then dispersal failure could represent as much of an immediate threat to plant populations as pollination failure.

ACKNOWLEDGMENTS

Funding was provided by the Foundation for Research, Science and Technology. We thank the Department of Conservation for permission to work at Craigieburn, and Cathy Bach and two anonymous referees for helpful comments on the manuscript.

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