

## Pollinator behaviour, not increased resources, boosts seed set on forest edges in a New Zealand Lorantheaceous mistletoe

BENJAMIN R. MONTGOMERY<sup>1</sup>\*

DAVE KELLY<sup>1</sup>†

ALASTAIR W. ROBERTSON<sup>2</sup>

JENNY J. LADLEY<sup>1</sup>

<sup>1</sup>Department of Plant and Microbial Sciences  
University of Canterbury  
Private Bag 4800  
Christchurch, New Zealand

<sup>2</sup>Ecology Group  
Institute of Natural Resources  
Massey University  
Private Bag 11222  
Palmerston North, New Zealand

\*Present address: Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109-1048, USA.

**Abstract** The endemic New Zealand mistletoe *Peraxilla tetrapetala* (Loranthaceae) has previously been shown to be pollinator limited, and to experience higher fruit set in increasingly fragmented habitats, but the mechanism for higher fruit set on edges has not been studied. Edges could affect plant resources (through higher light) and/or pollinator behaviour. This study measures the degree to which pollination and resource limitation affect female reproductive success along a gradient of increasing exposure to the forest edge. Forty-two plants in pairs at varying distances from the forest edge were selected from within two *Nothofagus* forest fragments in the 1999/2000 season; and on one plant in each pair, all ripe undamaged flowers were hand-pollinated. Light levels and the degree of edge exposure were measured for each plant, and path analysis was used to determine the relationship of

these variables to proportion fruit set. In agreement with previous studies, unmanipulated plants were found to be strongly pollen limited, especially in shady locations. However, on plants receiving hand-pollination, fruit set was uniformly high and was unaffected by edge exposure or light levels. Direct observation of flower visitation rates by birds in the 2000/01 season showed that edge flowers were visited twice as often as interior flowers. These results show that the higher fruit set on edges is due to visitation patterns of pollinators, and not due to greater resource availability on edges. This improved pollination on edges may help to buffer this declining plant against local extinction.

**Keywords** bird pollination; edge effects; fragmentation; Loranthaceae; mistletoe; *Peraxilla*; pollinator limitation; resource limitation

## INTRODUCTION

*Peraxilla tetrapetala* Tiegh (Loranthaceae), one of six Loranthaceous mistletoes endemic to New Zealand (Ladley et al. 1997), has declined in range and density since the European colonisation of New Zealand around 1840 (Norton 1991). Introduced mammalian herbivores and widespread habitat loss are each partly responsible (de Lange & Norton 1997; Norton 1997; Ogle 1997). Additionally, pollination failure has been implicated in the decline. *P. tetrapetala* is pollinated primarily by native honeyeater birds (Ladley & Kelly 1995a), although several native solitary bees, including *Hylaeus agilis* and *Leioproctus* sp., may also act as pollen vectors (Kelly et al. 1996). Ripe *Peraxilla* flowers remain closed until opened by a pollinator, and only a low percent of unopened flowers set fruit (a mean of 2.4% at three sites over 6 years; Robertson et al. 1999; A. W. Robertson, D. Kelly, & J. J. Ladley unpubl. data). Because non-native birds and bees rarely or never open flowers, *P. tetrapetala* seed set depends on visitation from a small group of pollinators. Consequently, seed set is sensitive to

†Author for correspondence.  
Email: dave.kelly@canterbury.ac.nz

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changes in pollinator distribution or behaviour (Kelly et al. 2000). Since European colonisation, honeyeater bird populations have declined throughout New Zealand, and both *P. tetrapetala* and *Peraxilla colensoi* have been shown to be pollen-limited at several locations, suggesting that pollination failure has contributed to reductions in *P. tetrapetala*'s distribution (Robertson et al. 1999).

A previous study of *P. tetrapetala* found that flower herbivory decreased and pollination increased among four increasingly fragmented habitats, suggesting that at some spatio-temporal scales, fragmentation may improve *P. tetrapetala* reproductive success (Kelly et al. 2000). This result concurs with the suggestion of Kuijt (1964) that fragmentation could indirectly benefit mistletoes by benefiting avian mutualists, but contrasts with the finding of Norton et al. (1995) that mistletoes are less common along fragmented corridors in Western Australia due to the deleterious effects of fragmentation on birds. The degree of fragmentation may be crucial to whether any effects are positive or negative (Kelly et al. 2000).

However, pollination is only one of several factors that could cause fruit set rates to vary. The failure of some ovules to develop into seeds may arise from an inadequate supply of suitable pollen (pollen limitation), inadequate resources to develop all ovules into seeds (resource limitation), damage occurring during seed production by herbivores or pathogens (herbivore limitation), or some combination of these (Delph 1986; Schemske & Horvitz 1988; Ackerman & Montalvo 1990; Burd 1994; Timmerman-Erskine & Boyd 1999; Larson & Barrett 2000).

The degree of pollination or resource limitation to female reproductive output may differ in importance among individuals in a population (Haig & Westoby 1988), due to variation in plant age or size (Zimmerman & Aide 1989; Lawrence 1993), herbivore damage (Janzen 1976; Lawrence 1993), water availability (Delph 1986), or nutrient or light availability (Niesenbaum 1993; Cunningham 1996; Timmerman-Erskine & Boyd 1999). Similarly, individuals are likely to differ in the level of pollinator service they attract, due to differences in phenotype, size, floral neighbourhood, or micro-habitat (e.g., Galen 1985). Hence, some members of a population may experience pollen limitation while others experience resource limitation.

Whether resources or pollen limit seed set may be determined by hand-pollination experiments. If the seed set of hand-pollinated flowers is greater than

that of unmanipulated flowers, then pollen is limiting for that plant; otherwise resources are limiting (Bierzychudek 1981).

Within a population, edge exposure may influence reproductive success by affecting resource availability or pollinator behaviour. If plants near edges experience higher light levels and light is a limiting resource, edge plants should have more resources available to invest in seed development. Similarly, if pollinators preferentially forage near to or far from edges and pollen is limiting, then plants would differ in the amount of pollinator service they receive, depending on their proximity to edges. The goal of this study was to determine for two populations of *P. tetrapetala*, whether the proportion of flowers that set fruit varied among plants with different levels of edge exposure and, if so, whether resource levels or pollinator service (or both) vary among these plants. We considered light to be the principal resource to mistletoes likely to vary across the edge gradient, because of previously published work (e.g., Niesenbaum 1993) and because variation in water and nutrient availability to the host *Nothofagus* trees is likely to be unresponsive to edge effects because the trees all reach the canopy.

By hand-pollinating all ripe flowers on a subset of plants, we investigated whether edges influenced seed set by affecting the degree of resource limitation. By monitoring seed set on unmanipulated plants, we investigated whether variation in edge exposure influenced proportion seed set by influencing pollinator behaviour. Finally, by directly observing bird behaviour we tested whether flower visitation rates differed in relation to proximity of edges.

## METHODS AND MATERIALS

The study was performed in two fragments of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest about 11 km apart near Lake Ohau, central South Island, New Zealand (see map in Kelly et al. 2000). Round Bush (44°12'S, 169°49'E) was a 5.3-ha fragment of predominantly older trees with little *Nothofagus* regeneration evident. The edges of the Round Bush fragment abutted the lake shore, a rocky stream bed with low shrubs, or pasture; in all cases an edge was clearly discernible. The second site, North Branch of Temple Stream (44°06'S, 169°48'E) was a 690-ha fragment located on the flood plain and neighbouring slopes of Ram Hill. Forest edges at North Branch were clearly discernible along

the riverbank and where the forest adjoined pasture and tussock-lands. At our study sites, bellbirds (*Anthornis melanura*, Meliphagidae) were the only honeyeater birds present. *P. tetrapetala* was abundant, and bellbirds were observed at both sites but their abundance was not monitored.

Floral observations and manipulations were performed in mid December of 1999. At Round Bush, 34 *P. tetrapetala* individuals, each with fewer than 500 flowers, were selected and divided by proximity into groups of two or three. Within each pair (or triplet), one plant was randomly allocated to the hand-pollination treatment and the other(s) to the unmanipulated (control) treatment. The 16 groups were 14 pairs and 2 groups of 3. At North Branch, four pairs were selected, and in each pair one plant was hand-pollinated and one unmanipulated. Allocating treatments within these groups helped to ensure that a similar range of microhabitats was included in both the unmanipulated and hand-pollinated treatments.

Several environmental variables were measured for each plant. The distance of each plant to the nearest forest edge (*edge distance*) was measured. Additionally, the proportion of the host tree's canopy edge not abutting a neighbouring canopy (*edge*), the proportion of canopy cover of the ground within a 10-m radius of the mistletoe (*canopy*), and the light level on a scale of 0 to 10 (*light*) were estimated visually for each plant. A *light* score of 10 would be assigned to a mistletoe whose entire foliage was exposed to full sunlight throughout the day, and a score of 0 would be assigned when the entire foliage was in dense shade throughout the day. Intermediate scores were assigned according to the proportion of the foliage that was likely to experience shading and the proportion of time shading was likely to occur.

Light levels were also measured using diazo-paper chemical light meters (Friend 1961; Baars 1995). Light meters were exposed on or just above each plant for six days, then collected and kept in darkness until they were processed. This paper is coated in a light-sensitive chemical that bleaches with exposure to sunlight and which, in the unbleached form, reacts with ammonia causing the paper to darken on exposure to ammonia vapour. Layers of sheets of this paper make up the meters and are successively bleached by exposure to sunlight. The light level (*diazo*) was measured by counting the number of fully bleached sheets and the fraction of the degree of bleaching of the bottom-most exposed sheet in each pad of photosensitive paper. We had expected that the diazo measurements

would be more accurate and would be used in preference to the visual light estimates. The two variables were significantly correlated ( $R^2 = 0.603$ , d.f. = 40,  $P < 0.001$ ). However, the visual estimates explained more of the variance than the diazo measurements in both the GLM (Table 1), and the path analysis (see Fig. 2). Diazo light sensors provided a measure of light intensity over only one small area (1 cm<sup>2</sup>) of the entire plant, whereas the visual estimate was able to include the entire plant. Additionally, due to logistical constraints, light sensors were often placed nearer to the *Nothofagus* trunk than most of the mistletoe foliage, possibly resulting in measurements that were over-responsive to shading by the trunk. Hence, we present data only for the visual light estimates. The path analysis diagrams calculated using *diazo* instead of visual estimates were similar to those presented in Fig. 2.

Previous research has demonstrated that *P. tetrapetala* flowers damaged by larvae of the moth *Zelleria maculata* rarely set fruit (Kelly et al. 2000). Consequently, on all plants, any flower that was observed to have a *Zelleria* entrance hole, frass, or other evident damage was removed before counting or pollinating flowers. For hand-pollinated plants, each flower that was already open prior to treatment was marked with coloured wire. Unopened ripe flowers were opened by hand, and the stigma was pollinated using a paintbrush by the application of a mixture of pollen from at least four mistletoes growing on other trees. Unripe flowers were revisited four to six days later and all possible additional pollinations were performed. Flowers that remained unripe were labelled with a wire of another colour and left unmanipulated on the plants. Overall, a mean of 77% of flowers in our treatment group were hand-pollinated and 94% were either hand-pollinated or naturally opened, for which there is a high probability of pollination. Counts were made of undamaged flowers on all unmanipulated plants.

Fruit set was determined by recording the number of swelling ovaries two months later (February 2000). Ovaries that exhibited no enlargement by then were deemed to have failed (Ladley et al. 1997; Robertson et al. 1999). Since fruits contain a single seed, fruit set equals seed set in *Peraxilla*. On hand-pollinated plants, counts of fruit developing from flowers that opened prior to, or that ripened after, our pollinations were excluded from this analysis.

Generalised linear models (GLMs) were used to examine the influence of treatment, site, and edge effects on the proportion of fruit set. Because fruit set was measured as a proportion, the GLMs used a

binomial error distribution and logit link function. The first analysis performed included data from both the hand-pollinated and unmanipulated plants, and it examined only the effects of treatment, site, and an interaction effect on fruit set. Subsequent analyses, which were performed separately on hand-pollinated and unmanipulated plants, initially included site and the indicators of light and edge exposure. Model construction was performed by initial inclusion of all variables of interest, followed by stepwise removal of variables lacking significant explanatory power.

Additionally, path analysis was used to examine inter-relationships among our measures of edge exposure and light, which were partially cross-correlated, and fruit set. Path analysis allows examination of direct and indirect effects of predictor variables on dependent variables, allowing the correlation between dependent variables to be considered (Mitchell 1993); a mixture of direct and indirect effects seemed plausible in this case given the nature of the variables. In contrast, multiple regression only allows estimation of a predictor variable's direct causal effect on the dependent variable (Schemske & Horvitz 1988). GLMs were performed using S-Plus 2000 (MathSoft, Inc., Seattle, Washington, USA), and paths were constructed using the procedure LM on standardised transformed variables. To improve normality for unmanipulated plants in the path analysis, *edge distance* was log-transformed, and *edge* and *canopy* were arcsine-square-root-transformed. For the hand-pollinated plants, the same transformations were applied, except that *canopy* was squared instead of being arcsine-square-root-transformed.

Based on the path coefficients in any given path diagram, a matrix of the expected correlations among all of the variables may be derived and compared with the observed correlation matrix. Correlation matrices for each model are included in Appendix 1. If a model includes all potential paths, then the observed and expected correlation matrices will agree perfectly. If an expected correlation matrix derived from a model containing only a subset of the potential paths remains quite similar to the observed correlation matrix, then this model represents a more parsimonious explanation of the data (Kerlinger & Pedhazur 1973). The path model was refined by dropping the least significant term in a stepwise manner until only significant ( $P < 0.05$ ) and marginally significant ( $P < 0.10$ ) terms remained.

Direct measurements of bird visitation rates to mistletoe flowers were made the following season

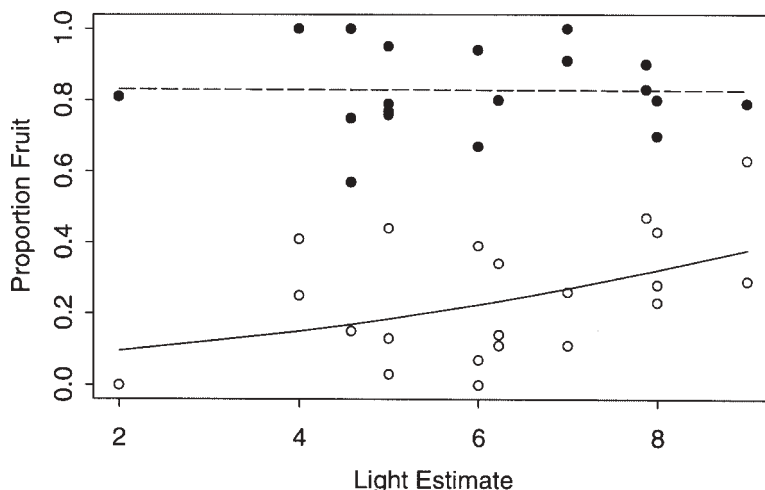
(2000/01). Observation stations were established in Round Bush and at nearby isolated host plants (see Kelly et al. 2000); at North Branch there were insufficient flowers to perform observations. Each observation station provided a view of one to several flowering mistletoes; 10 observation stations were in the interior of Round Bush, 6 were on the edge of Round Bush, and 3 were on isolated plants which were also on edges. At each station, a series of 10-minute observations was made between 5 and 9 December 2000, giving a total of 90–130 minutes per station, and 32.5 hours observation in total. For each avian flower visitor during that time, the bird species and duration of visit in seconds were recorded. The total number of available flowers at each station was counted or, for large plants, estimated independently by two observers and the mean taken. The visitation rate was expressed as seconds of bird visit per mistletoe flower per hour. The analysis was performed separately for bellbirds, and for all birds (other visitors were silvereyes, *Zosterops lateralis*, and chaffinches, *Fringilla coelebs*). Visitation rates at the edge and isolated sites were similar, so these sites were combined and compared with interior sites using a one-way ANOVA.

## RESULTS

A GLM on the entire data set revealed a highly significant effect of treatment (hand-pollinated versus unmanipulated), and a significant treatment-by-site interaction (Table 1). The average fruit set was  $83 \pm 3\%$  (mean  $\pm$  SE) for hand-pollinated plants, but only  $25 \pm 4\%$  for unmanipulated plants. While the average percent fruit set did not vary between sites for unmanipulated plants ( $F = 1.414$ , d.f. = 1, 20,  $P = 0.248$ ), it did for hand-pollinated plants ( $F = 6.332$ , d.f. = 1, 17,  $P = 0.022$ ), accounting for the significant treatment-by-site-interaction in Table 1. Average fruit set for hand-pollinated plants was 86% at Round Bush, but only 70% at North Branch.

Among the unmanipulated plants, *light* was the only environmental measure that explained a significant proportion (19%) of the variance in proportion fruit set in a GLM (Table 1; Fig. 1). For the hand-pollinated plants, only the effect of site was significant (Table 1). Neither light levels nor any measure of degree of edge exposure was found to explain a significant proportion of the variance in seed set for hand-pollinated plants (Fig. 1).

**Fig. 1** Relationship between light level (visual estimate) and proportion fruit set for hand-pollinated (filled circles, dashed line) and unmanipulated (open circles, solid line) flowers of *Peraxilla tetrapetala*, Lake Ohau, South Island, New Zealand. Each point represents the mean for one plant. The binomial regression is significant for unmanipulated plants but not for hand-pollinated plants (see Table 1).

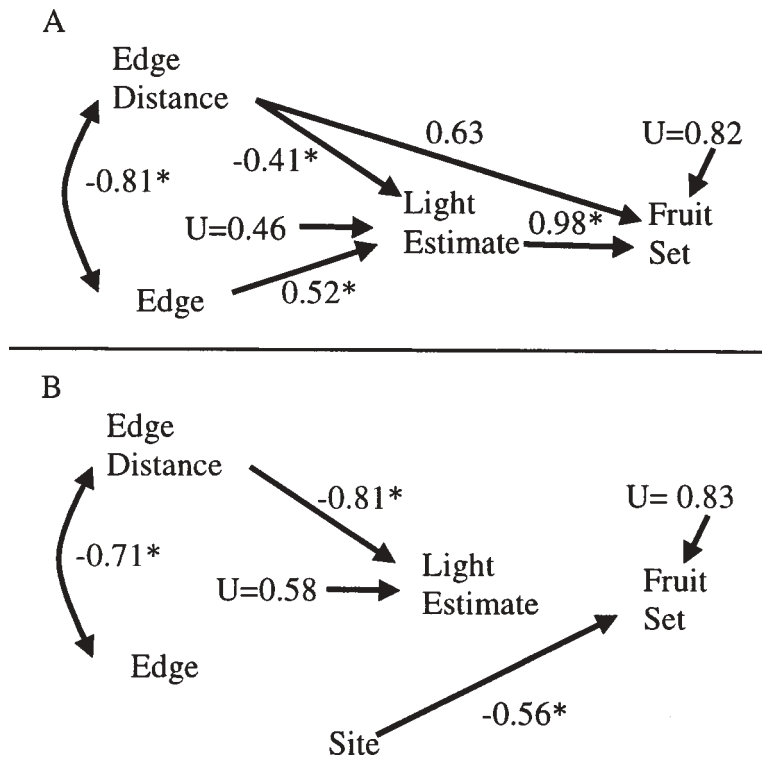


**Table 1** GLM of effect of predictor variables on fruit set for *Peraxilla tetrapetala* at Lake Ohau, 1999–2000. For all plants, effect of site and treatment on entire data set; for unmanipulated plants only, the effect of site, and measures of edge exposure on proportion fruit set; for hand-pollinated plants, the effect of site, and measures of edge exposure on proportion fruit set. Variables included in model for unmanipulated and for hand-pollinated plants before stepwise removal: *site, canopy, edge, light*.

| Predictor                     | d.f. | Residual deviance | d.f. | Residual deviance | F       | P      |
|-------------------------------|------|-------------------|------|-------------------|---------|--------|
| <b>All plants</b>             |      |                   |      |                   |         |        |
| Null                          |      |                   | 40   | 20.768            |         |        |
| Site                          | 1    | 0.001             | 39   | 20.767            | 0.0072  | 0.933  |
| Treatment                     | 1    | 14.899            | 38   | 5.868             | 125.310 | <0.001 |
| Site * treatment              | 1    | 0.706             | 37   | 5.162             | 5.940   | 0.020  |
| <b>Unmanipulated plants</b>   |      |                   |      |                   |         |        |
| Null                          |      |                   | 21   | 3.677             |         |        |
| Light                         | 1    | 0.685             | 20   | 2.992             | 4.892   | 0.039  |
| <b>Hand-pollinated plants</b> |      |                   |      |                   |         |        |
| Null                          |      |                   | 18   | 2.206             |         |        |
| Site                          | 1    | 0.509             | 17   | 1.699             | 6.332   | 0.022  |

In our *a priori* model for path analysis, we hypothesised that light level would directly affect fruit set, and that the site and our three measures of edge exposure would affect fruit set directly as well as indirectly via an effect of each of these factors on light levels. This model was tested independently for the hand-pollinated and unmanipulated plants because we expected that the environmental variables affecting fruit set would differ between hand-pollinated and unmanipulated plants, thus violating the linear regression assumption that all effects are additive and linear (Mitchell 1993).

Among the unmanipulated plants, path analysis indicated that *light* had a positive effect on fruit set (Fig. 2A). In this model, *edge distance* exerted a positive, marginally significant direct effect on fruit set as well as a negative effect via the path through *light*. *Edge* had a positive indirect effect on fruit set via the path through *light*. Inclusion of the direct effect of *edge distance* on fruit set in the path model substantially improves the agreement between the observed and expected matrices (Appendix, Table A1 versus Table A2), suggesting that this effect is important, despite the path's marginal significance.



**Fig. 2** Path diagrams of effects of site and environmental variables on proportion fruit set for *Peraxilla tetrapetala* near Lake Ohau, Central South Island, New Zealand. **A**, Unmanipulated plants; **B**, Hand-pollinated plants. Variables initially included in analyses: *Site* (Round Bush versus North Branch), *edge distance* (distance to nearest forest edge), *edge* (percentage of host tree's canopy not abutting a neighbouring canopy), *canopy* (percentage of canopy cover within a 10-m radius of the mistletoe), *light* (a visual estimate light level at the mistletoe). *Fruit set* is the percent of undamaged flowers setting fruit, and *U* means unexplained variation. Transformations were applied as described in methods. Paths lacking significance or marginal significance ( $P < 0.10$ ) were dropped from model. \*,  $P < 0.05$ .

Among the hand-pollinated plants, *edge distance* was again found to have a significant effect on *light*, but neither light nor edge variables had any direct or indirect effects on fruit set. Only site was found to have a significant effect on fruit set (Fig. 2B).

Bird visitation rates were twice as high to edge mistletoes as to interior plants in December 2000, whether all birds or bellbirds only were considered (Table 2) but, due to higher variances for the bellbird data, only the means for all birds were significantly different.

**DISCUSSION**

These results demonstrate that at both sites *P. tetrapetala* was pollen-limited and capable of ripening a high proportion of fruit when entire plants were supplementally pollinated. The consistently high fruit set of hand-pollinated plants, regardless of light levels or degree of edge exposure, demonstrates that resource availability for ripening fruits is not limiting across the gradient of edge

**Table 2** Bird visitation rate to edge and interior *Peraxilla tetrapetala* flowers (seconds of visit per flower per hour) in December 2000. Data are presented for all birds (bellbirds, silvereyes, and chaffinches) and for bellbirds alone. The *F* and *P* values from a one way Anova on the data are also given. Based on 32.5 hours total observation at 19 stations where one to several mistletoe plants were observed (see text).

| Site              | All birds | Bellbirds only | <i>n</i> stations |
|-------------------|-----------|----------------|-------------------|
| Edge and Isolated | 0.0272    | 0.0103         | 9                 |
| Interior          | 0.0101    | 0.0051         | 10                |
| <i>F</i>          | 4.93      | 1.32           |                   |
| <i>P</i>          | 0.040     | 0.27           |                   |

exposure. Thus, we are able to reject the hypothesis that the degree of resource limitation varies substantially across the gradient of edge exposure, in contrast to the findings of Kato & Hiura (1999) and Niesenbaum (1993) in other systems. Supplemental pollination of a subset of flowers in

only one flowering episode may cause a plant to reallocate resources towards the treated flowers. This reallocation could lead to lower fruit set in the remaining flowers within the flowering episode (Zimmerman & Pyke 1988), lower fruit set in subsequent years (but see Timmerman-Erskine & Boyd 1999), or an increased quantity of seeds or fruit without a corresponding increase in seed or fruit biomass (Janzen et al. 1980; Zimmerman & Aide 1989; Ackerman & Montalvo 1990). Because a mean of 94% of flowers were hand-pollinated or naturally opened, the potential for reallocation of resources from unmanipulated to hand-pollinated flowers was minimal. Previous studies of *P. tetrapetala* have found no evidence of decreased fruit set in subsequent years as a consequence of whole-plant pollinations (Robertson et al. 1999). Consequently, our finding of no evidence of resource limitation is unlikely to be an artefact of reallocation of reproductive resources.

Since there was strong pollination limitation throughout the population, patterns of fruit set should vary across the gradient of edge exposure in response to any variation in pollinator behaviour. The bird observations showed that birds visited edge flowers twice as often as interior flowers in the 2000/01 season. In most of the South Island, bellbirds are the primary pollinators, but the other birds recorded visiting flowers in this study (silveryeyes and chaffinches) can pollinate flowers successfully at Lake Ohau (Ladley et al. 1997). Since birds visited edge flowers more often, natural fruit set should be higher on edges. In support of this expectation, we found that among the unmanipulated plants, variation in light level explained a significant proportion of the variance in fruit set in both the GLM and path analysis. As demonstrated by the path analyses, light levels were higher for plants near edges. Our results therefore agree with earlier work in this area showing higher fruit set on edges (Kelly et al. 2000); furthermore, our results suggest that pollinator service, not limiting resources, is primarily responsible for this edge effect.

One puzzling aspect of the results is that *edge distance* apparently had a direct positive effect on fruit set, separate from its indirect negative effect via light. This implies that, given equal light levels, a mistletoe in a small clearing in the forest interior may get better pollination than one on the forest edge. It is possible that such second-level effects could arise from the activities of the other group of pollinators, solitary bees. Casual observations suggest that the bees favour flowers in sunshine, but avoid very

windy areas (see below). Work is currently under way to test this hypothesis.

The significant effect of site on the hand-pollinated treatment may be a consequence of real differences in resource limitation or differences in the application of pollen. In order to avoid any potential effects of outbreeding depression, pollen was not mixed between sites, so differences between sites in the quality of pollen collected could have influenced fruit set. Additionally, differences in weather between treatments could have affected the success rate of hand-pollinations. Despite lower fruit set of hand-pollinated plants at North Branch, pollen was limiting overall at both sites.

Our findings contrast with those of Jules & Rathcke (1999), who found decreased resource limitation but increased pollination limitation nearer to fragment edges for an insect-pollinated perennial herb. Similarly, Aizen & Feinsinger (1994) found increased pollination limitation in increasingly fragmented habitats for several entomophilous species. However, the one ornithophilous species included in Aizen & Feinsinger's (1994) study experienced reduced pollinator limitation in increasingly fragmented habitats. Together, these results suggest that bird pollinators may sometimes respond differently than invertebrate pollinators to edge exposure. Bees can also serve as pollinators of *P. tetrapetala* (Kelly et al. 1996), and casual observations suggest that bees prefer to visit plants in direct sunlight, which would provide greater insect visitation on edges. Although most flowers appear to be opened by birds rather than by bees at this site, bees and other insects make frequent visits to flowers that have been opened (A. W. Robertson, D. Kelly, & J. J. Ladley unpubl. data). This means that the fruit set response we measured may not be wholly due to the demonstrated higher bird visitation rates on edges. A study to quantify the responses of bees to edge effects is currently under way. It would be valuable to know whether plants exposed to more light produce a greater quantity or quality of nectar. If so, this would raise the possibility that pollinator response to edges is mediated indirectly by differences in the mistletoes themselves. Further study would help to elucidate each of these subjects.

To allocate resources optimally, plants should invest in pollinator attraction and fruit provisioning in such a manner that both are simultaneously limiting (Haig & Westoby 1988). However, despite *P. tetrapetala* being pollination limited, it may not benefit from additional investment in pollinator attraction. *P. tetrapetala* already produces large

bright red flowers with copious nectar (Ladley et al. 1997) and at times flowers so heavily that the entire plant appears scarlet (Ladley & Kelly 1995b; Sessions 2000), so it is a favoured food source of bellbirds (Murphy & Kelly 2003). Instead, the pollination failure comes from greatly reduced densities of pollinating birds in New Zealand since 1840 due to introduced mammalian predators (Robertson et al. 1999; Murphy & Kelly 2001).

In this study, all flowers with identifiable damage from the moth *Zelleria maculata* were removed. By removal of this common florivore, we were able to consider pollinator and resource limitation in the absence of herbivore limitation. Previous studies have shown that *Zelleria* preferentially attack flowers away from edges (Crowfoot 1998; Kelly et al. 2000), so if damaged flowers had been included in the analysis, the differential in fruit set rates between edge and interior in unmanipulated plants would have been even greater.

This study shows that on the temporal and spatial scale examined, forest edges indirectly benefit *P. tetrapetala* fruit set by decreasing pollination limitation without influencing resource limitation. Edges might have some direct negative effects on *P. tetrapetala* by affecting other stages in the mistletoe's life history. Although higher light intensity is thought to have a positive effect on establishment of seedlings (Kelly et al. 2000), there may be negative effects such as altering the behaviour of herbivores. Possums (*Trichosurus vulpecula*) are known to damage mistletoes (Norton 1997; Ogle 1997; Sessions & Kelly 2001a,b; Sessions et al. 2001), and are known to prefer forest edge habitats (Coleman et al. 1985), but there is no evidence of recent serious effects of possums on *P. tetrapetala* at Lake Ohau (Sessions & Kelly 2001a). Overall, this study does not demonstrate that *P. tetrapetala* populations necessarily benefit overall from increased edges, but it does demonstrate that greater exposure to edges favours a mutualistic interaction leading to increased seed set. Such enhanced performance per plant on edges helps to counterbalance the large reduction in plants per km<sup>2</sup> caused by forest clearance (Kelly et al. 2000), and hence may help to reduce the risks of local extinction in this declining endemic plant.

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**Appendix** Correlation matrices of observed and expected values for the model for unmanipulated plants shown in Fig. 2A that includes at least one path linking all variables. Expected values, derived from each model, are expressed above the diagonal and observed values are expressed below the diagonal. Scores differing by more than 0.10 between observed and expected are in bold.

**Table A1** All significant and marginally significant paths used to reconstruct correlation matrix. Corresponds to all paths included in Fig. 2A.

|               | Edge distance | Expected values |                |           |
|---------------|---------------|-----------------|----------------|-----------|
|               |               | Edge            | Light estimate | Fruit set |
| Edge distance | –             | –0.81           | –0.84          | –0.19     |
| Edge          | –0.81         | –               | 0.86           | 0.32      |
| Light         | –0.84         | 0.86            | –              | 0.45      |
| Fruit set     | –0.19         | 0.39            | 0.45           | –         |

Observed values

**Table A2** Only significant paths in Fig. 2A used to reconstruct correlation matrix.

|               | Edge distance | Edge  | Expected values |              |
|---------------|---------------|-------|-----------------|--------------|
|               |               |       | Light           | Fruit set    |
| Edge distance | –             | –0.81 | –0.83           | <b>–0.37</b> |
| Edge          | –0.81         | –     | 0.86            | 0.32         |
| Light         | –0.84         | 0.86  | –               | 0.45         |
| Fruit set     | <b>–0.19</b>  | 0.39  | 0.45            | –            |

Observed values