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Pollinator limitation of seed set in *Fuchsia perscandens* (Onagraceae) on Banks Peninsula, South Island, New Zealand

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Abstract *Fuchsia perscandens*, which has ornithophilous flowers, may be prone to pollinator limitation on the New Zealand mainland where pollinating birds are often scarce. To investigate this possibility, we hand pollinated flowers on plants at two sites on Banks Peninsula and compared their reproductive success with unmanipulated flowers on the same plants. In the 1999 season at Buckleys Bay, fruit initiation was 3.3 times higher on hand-pollinated flowers (66.6% of flowers) than unmanipulated flowers (20.0%), and fruit set was 2.7 times higher (47.9% versus 18.0%, respectively). In developed fruit, seed set per fruit was higher for hand-pollinated (70.9% of ovules) than unmanipulated flowers (48.0%). The results indicate that 34% of ovules from hand-pollinated flowers, but 9% of ovules from unmanipulated flowers, set seed. Germination rates did not vary significantly among treatments. In the 2000 season, at both sites, fruit set of hand-pollinated flowers was at least 1.7 times higher than unmanipulated flowers ($P = 0.028$), and fruit set of unmanipulated flowers did not differ significantly from that of bagged flowers from which all pollinators were excluded ($P = 0.98$). These results agree with other studies of ornithophilous plants on the New Zealand mainland and suggest that pollinator limitation is a frequent consequence of the rarity of honeyeater birds.

Keywords bird pollination; *Fuchsia perscandens*; Meliphagidae; Onagraceae; plant reproduction; pollinator limitation

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INTRODUCTION

A general trend toward simple and despecialised flowers exists within the New Zealand flora (Webb & Kelly 1993), but the long tubular flowers on *Fuchsia perscandens* (Onagraceae) suggest that this species may be specialised for bird pollination. Historically, New Zealand had three native honeyeaters (Meliphagidae) that commonly visited flowers: tui (*Prosthemadera novaeseelandia*), bellbirds (*Anthornis melanura*), and stitchbirds (*Notiomystis cincta*). Of these, stitchbirds are now absent from the entire mainland; tui are rare in the east of the South Island, and bellbirds are absent from the northern North Island. In areas where honeyeaters have recently declined in population, pollinator limitation has been reported for at least two other bird-pollinated plant species (Robertson et al. 1999). The purpose of this study was to determine whether pollination or resources limit fruit set in a population of *Fuchsia perscandens* growing in a highly fragmented habitat with decreased bird populations. We investigated this by monitoring fruit set, seed set, and germination for hand-pollinated and unmanipulated flowers over two seasons.

Determining what factors limit seed production in flowering plants may yield insights into the causes of reproductive failure in declining plant populations (Aizen & Feinsinger 1994; Robertson et al. 1999). Seed production may be limited by a shortage of acceptable pollen, inadequate resources for seed development, or losses due to herbivory or pathogens (Willson & Burley 1983). Pollinator limitation of female reproduction occurs when an inadequate supply of pollen limits seed set below the level possible given the plant's available resources. Pollinator limitation may occur on the scale of individual flowers, entire plants, or whole populations (Burd 1994), and may be detected by determining whether seed set is increased by treating receptive flowers with supplemental pollen (Bierzychudek 1981).

Although plants in theory are expected to be on average equally limited by pollination and resources (Haig & Westoby 1988), there are several non-exclusive reasons for the occurrence of pollinator limitation. First, pollinator limitation could occur if apparently excess flowers increase male fitness (Sutherland & Delph 1984). Second, in a stochastically fluctuating pollinator environment, production of more flowers than are likely on average to be pollinated may increase fitness if there is some chance of a high proportion of flowers being visited (Burd 1994). Third, chronic pollinator limitation may result from declines in pollinator abundance (Robertson et al. 1999) or changes in pollinator behaviour due to fragmentation or other causes (Aizen & Feinsinger 1994; Jules & Rathcke 1999; but cf. Kelly et al. 2000) over a time scale too short for a population to readjust its allocation of reproductive resources.

A decline in pollinator visitation to a plant population will be especially likely to result in pollinator limitation for plants that are non-apomictic and lack the ability to self-pollinate due to self-incompatibility, dichogamy, or herkogamy (see Bond 1994). Whether pollen limitation results in a decline in population density (e.g., Robertson et al. 1999) depends on the extent to which populations are seed limited (Crawley 1990; Turnbull et al. 2000) and are unable to compensate by vegetative reproduction or other means (Bond 1994).

Fuchsia perscandens (Onagraceae) is a gynodioecious endemic shrub or liane, and is uncommon despite its broad distribution (Godley & Berry 1995). Natural hybrids frequently occur between *F. perscandens* and the closely related tree fuchsia, *F. excorticata*, and the pendent flowers of the two species are very similar (Allan 1961; Godley & Berry 1995). Both are protogynous (a form of dichogamy) and herkogamous, with the stigma hanging below the anthers. Flower colour changes from green at anthesis to crimson when the flower is post-reproductive. Access to nectar is restricted by the tubular hypanthia, which in *F. perscandens* are 10–20 mm long, with the nectary located at the base. *F. excorticata* is self-compatible but, because flowers are solitary and sparse, geitonogamy via wind pollination is unlikely, and dichogamy and herkogamy limit autogamous selfing; the same is probably true of *F. perscandens*. Bellbirds, tui, and stitchbirds are the primary pollinators of *F. excorticata* (Delph & Lively 1989). No pollinators of *F. perscandens* have ever been recorded, but its strong floral similarities to *F. excorticata* suggest that *F. perscandens* may depend on the same pollinators.

Populations of honeyeater birds have decreased markedly in abundance on Banks Peninsula since the 1830s (Wilson 1992). The inaccessibility of the nectary to short-tongued animals may discourage most potential alternative pollinators, making *F. perscandens* particularly likely to suffer from pollinator limitation in the absence of honeyeaters.

To determine whether pollination limits maternal reproductive success in this population, fruit set, seed set, and germination rates of hand-pollinated and unmanipulated flowers were determined for plants in an area with low honeyeater densities. Additionally, the fruit set of flowers apparently damaged by nectar robbers was compared with that of undamaged flowers. At the same time, plants were observed in an effort to determine the identity of pollinators.

METHODS

The study was conducted at two sites on the Port Hills, Canterbury. Buckleys Bay Scenic Reserve (43°36.0′S, 172°44.1′E; 200 m a.s.l.) was used in 1999 and in 2000. The reserve consists of 9.4 ha of steep slopes above Lyttleton harbour (Wilson 1992). Prior to human settlement, the Port Hills were primarily forested, but the reserve now supports ungrazed pasture interspersed with second-growth native bush containing *F. perscandens* and *F. excorticata* as well as hybrids and backcrosses of these species (Wilson 1992). A second site was selected in the 2000 flowering season on private farmland at the Tors, on the summit of the Port Hills (43°35.6′S, 172°41.6′E; 380 m a.s.l.), 3.2 km east of Buckleys Bay. At the Tors, *F. perscandens* plants were growing among boulders and low shrubs surrounded by grazed pasture. The area is much more exposed to wind than Buckleys Bay, and the *F. perscandens* plants were low in stature but showed no signs of grazing damage.

During late October 1999, nine flowering *F. perscandens* plants (one female and eight hermaphrodites) were located at Buckleys Bay. Most plants were already in flower upon initiation of the study. Hermaphroditic flowers were considered receptive to pollination if anthers had dehisced recently or were still undehisced and the stigma still appeared moist. Female flowers were considered receptive if the hypanthium and sepals were still in their green or purple colour stage and if the stigma still appeared moist.

In total, 98 flowers were selected on 7 plants (including the 1 female) and were tagged around the penduncle with coloured wire between 31 October and 10 November 1999. On all plants with two or more receptive flowers, hand-pollinated or unmanipulated treatments were assigned by pairing flowers and randomly choosing treatments within each pair. Treatments were assigned randomly to unpaired flowers. Forty-eight flowers were hand pollinated, and 50 control flowers were labelled but left unmanipulated. Due to differences in flower production among plants, the number of flowers per plant used in this study ranged from 2 to 28. Hand pollinations were performed with a paintbrush using a mix of pollen from at least four plants, usually separated by tens of metres, and sometimes including self pollen. Due to a shortage of pollen donors, dehisced anthers from hand-pollinated flowers were occasionally collected. When this was necessary, no more than four of the eight anthers were removed, and none was removed from flowers in the unmanipulated treatment.

A narrow elongate slit, probably created by nectar robbers, was apparent in the sides of many flowers. In order to determine whether these slits were associated with low fruit set, five plants were searched for open flowers on November 23, and the presence or absence of a slit was noted for a total of 23 flowers not used in the earlier study. Flowers were then labelled with coloured wires, and fruit set was determined in mid January.

For the hand-pollinated and unmanipulated flowers, fruit initiation was monitored in mid December 1999 and fruit set was monitored in mid January 2000, when fruits were observed to be swollen and either turning from green to purple or already purple, which is indicative of being ripe (Godley & Berry 1995). At this stage, all remaining fruits were collected. Some fruits had been naturally removed prior to our collection. We were able to differentiate between ripe removed fruits and aborted fruits by observing the status of the peduncle with the attached wire. The peduncles of ripe removed fruits remained green and were stained purple at their apical end from the pigment in the berries, while peduncles of aborted fruits turned brown and were not purple at their apical end. Ripe removed fruit were included as set fruit.

To determine seed-set within ripened fruits, berries arising from both the hand-pollinated and unmanipulated treatments were collected from two hermaphroditic plants and the sole female plant. Counts of seeds and undeveloped ovules were made for each collected fruit from these plants. Seed and ovule counts were either performed soon after collection, or fruits were preserved in 70% ethanol until counts were performed. When examined with a dissecting microscope, developed seeds were easily distinguished from undeveloped ovules or aborted seeds. Developed seeds were larger than undeveloped ovules, and had dark, roughly textured seed coats. Undeveloped ovules lacked dark seed coats and were largely transparent. No attempt was made to differentiate between unfertilised ovules and aborted seeds.

To determine germination rates, one or two apparently healthy and ripe berries from both hand-pollinated and unmanipulated treatments were selected from the same three plants. After counting of seeds and ovules, developed seeds were rinsed and separated from ovules. Seeds were kept separate according to plant and treatment within each plant, but when multiple berries from each plant-by-treatment combination were available, seeds from these berries were mixed together. For each plant-by-treatment combination, 120 seeds were selected, rinsed in distilled water, and divided equally into two 85-mm plastic petri dishes lined with moistened filter paper. The filter paper was re-moistened on a weekly basis. Germination, defined as emergence of the hypocotyl from the seed coat, was monitored for 22 weeks, which was 4 weeks after germination had ceased in all dishes.

In 2000, pollination treatments were performed on all available flowering plants at both Buckleys Bay and the Tors. At Buckleys Bay, this included the sole female and six hermaphrodites (including one hermaphrodite not used in 1999), and at the Tors this included five hermaphrodites. At Buckleys Bay, on each plant 10 flowers were allocated to each of 3 treatments: unmanipulated (naturally pollinated) flowers; hand cross-pollinated; and bagged to exclude all pollinators. The same method was used at the Tors, but some plants had too few flowers to allocate 10 to each treatment. In total on the 5 plants, 37 unmanipulated, 35 hand-pollinated, and 21 bagged flowers were used. Treatments were set up in late September and fruit set was determined in early November 2000.

Analyses of fruit initiation, fruit set, seed set, and germination were performed with S-Plus 2000 (MathSoft Inc.), using binomial generalised linear models (GLM), which employ the logit link function. Since we could not test for differences between the sexes with only a single female plant, in 1999 all plants were combined in these analyses, with notes in the results where the single female differed from the hermaphroditic plants. In 2000 the female plant was not included in the analysis, because the sample size for hermaphroditic plants was higher, and because the female would be predicted to respond very differently from hermaphrodites to the bagged treatement used in that season. Each model included the following independent variables: plant, treatment, and, when the experimental design allowed, an interaction effect between these variables. In the second year the model also included site as a factor. Interaction effects that did not improve the models were dropped. A post-hoc comparison of means test was used to determine which treatments differed when a GLM revealed a significant effect of treatment among three treatments. For the nectar robbing study, the fruit set of robbed flowers was compared with that of undamaged flowers using the Fisher exact test with individual flowers as the experimental unit.

In an effort to identify *F. perscandens* pollinators, in 1999 five plants at Buckleys Bay were videotaped for a total of 7.7 hours. Six hours and 15 minutes of this time were filmed from about 5 m away, a distance that would allow observation of whether birds visited the plant but not whether birds probed flowers. For 1.5 hours of this time, a few flowers were filmed from about 1 m away, which was close enough to allow observation of the behaviour of any birds or large invertebrates that visited the flowers.

RESULTS

In 1999 fruit initiation was more than three times higher and fruit set was more than two times higher in hand-pollinated flowers than in unmanipulated flowers (Table 1). For both fruit initiation and fruit set, the effect of treatment was significant but the effect of differences among plants was not (Table 2). The female plant contributed to this general pattern, although its overall levels of fruit set (30.8% for hand pollinated and 13.3% for unmanipulated flowers) were lower than the mean for hermaphrodites (54.2% and 20.0%, respectively), as would be expected since self-pollination is impossible in females. Nectar robbing had no significant effect on fruit set, with slightly over half the flowers setting fruit whether they had slits (5 of 8 flowers) or did not (8 of 15 flowers; $P = 1.0$). The average proportion seed set in successful fruit was higher ($P = 0.053$) for hand-pollinated flowers than for unmanipulated flowers, but hand pollination did not significantly increase germination rates (Tables 1 and 2).

In the second season, pollen limitation of fruit set was apparent at both sites (Table 3). Among hermaphrodite plants, both treatment and site were significant (Table 4), with fruit set on hand-pollinated flowers being higher than on unmanipulated flowers (d.f. = 19, $t = 2.388$, $P = 0.028$). Fruit set on unmanipulated flowers did not differ from bagged flowers ($t = 0.028$, $P = 0.98$). The single female plant at Buckleys Bay again showed the same pattern as hermaphrodites (fruit set was 50% for hand-pollinated flowers, but 0% for both unmanipulated and bagged flowers).

During the nearly 8 hours of videotape in 1999, only one bird was observed to alight in *F. perscandens*. A silvereye (*Zosterops lateralis*)

Table 1 Effect of hand pollination on reproduction of *F. perscandens* at Buckleys Bay Scenic Reserve in 1999. Seven plants were used for flower to fruit measurements, and three plants for seed set and germination. For details of the significance tests, see Table 2.

	Hand pollinated	Unmanipulated	*P*
No. of flowers	48	50	
Fruit initiation (%)	66.6	20.0	0.004
Fruit set (% of flowers)	47.9	18.0	0.045
No. of berries	9	8	
Seed set (% of ovules)	70.9	48.0	0.053
Germination (% of seeds)	90.6	82.5	0.227

Table 2 Significance tests of effect of plant and pollination treatment (GLM with binomial error and logit link function) on four stages in reproduction of *F. perscandens* at Buckleys Bay in 1999.

	d.f.	Deviance explained	d.f.	Residual deviance	*F* Value	*P*
Fruit initiation						
Null			13	55.17		
Plant	6	18.93	7	36.24	2.37	0.159
Treatment	1	27.21	6	9.03	20.41	0.004
Fruit set						
Null			13	30.76		
Plant	6	7.33	7	23.43	0.72	0.657
Treatment	1	10.70	6	12.73	6.35	0.045
Seed set						
Null			16	1262.34		
Plant	2	67.84	14	1194.50	0.51	0.612
Treatment	1	301.37	13	893.13	4.54	0.053
Germination						
Null			5	0.51		
Plant	2	0.36	3	0.15	5.94	0.144
Treatment	1	0.09	2	0.06	2.97	0.227

Table 3 Mean fruit set (% of flowers ripening fruit) of hermaphrodite *F. perscandens* at Buckleys Bay and the Tors in 2000. For significance testing see Table 4.

Site	Bagged	Unmanipulated	Hand-pollinated	No. of plants (No. of flowers)
Buckleys Bay	46.7	40.0	70.0	6 (210)
the Tors	20.0	28.9	50.0	5 (93)

Table 4 Effect of plant, site, and pollination treatment (tested with a GLM with binomial error and logistic link function) on fruit set of hermaphrodite *F. perscandens* at Buckleys Bay and the Tors in 2000.

	d.f.	Deviance explained	Residual d.f.	Residual deviance	*F*	*P*
Null			31	95.6		
Site	1	8.95	30	86.7	4.38	0.050
Plant	9	27.23	21	59.45	1.48	0.224
Treatment	2	15.70	19	43.75	3.85	0.040

landed near three open flowers, but it did not contact the flowers. While at the Buckleys Bay study site, we observed one bellbird land in a flowering *F. perscandens*, but we could not see whether it visited any flowers. Bellbirds were commonly heard at Buckleys Bay but they appeared to be foraging mainly on flowers of kowhai (*Sophora microphylla*) higher up in the reserve. No invertebrates were observed visiting *F. perscandens* during the 1.5 hours of close-up filming. During searching of plants for receptive flowers and performing pollinations, honeybees and a variety of other insects were seen in the area, but none was observed to visit flowers. In 2000 no birds of any kind were seen to visit plants at the Tors, and no bellbirds or silvereyes were seen at this site either during 40 minutes of direct observation or during the 6–8 hours spent doing hand-pollination work.

DISCUSSION

This study suggests that at two Port Hills sites, fruit and seed set of *F. perscandens* is pollen limited. In two seasons, hand-pollinated flowers were more likely to initiate fruit than unmanipulated flowers. Post-initiation fruit abortion occurred, suggesting that resources might limit fruit set in the absence of pollinator limitation. Nevertheless, hand-pollinated flowers were still more than 2.6 times more likely to set fruit than unmanipulated flowers. Furthermore, seed set within developed fruit was higher for hand-pollinated than unmanipulated flowers. By multiplying the proportion of flowers that set fruit by the proportion of ovules that develop into seeds in fertilised flowers, our data indicate that in the first season 34% of ovules from hand-pollinated flowers set seed while only 9% of ovules from unmanipulated flowers set seed. This suggests that supplemental pollination increases the overall proportion of ovules producing seeds nearly four-fold.

The results do not necessarily indicate that *F. perscandens* is pollen limited at the level of the entire plant over its reproductive lifetime. Plants may reallocate resources for fruit development away from flowers receiving less or lower quality pollen to those with access to a better pollen supply (Janzen 1977). Consequently, the perceived degree of pollen limitation may be artificially exaggerated by supplementally pollinating only a subset of flowers on a plant and comparing the reproductive output of those flowers with unmanipulated flowers, which probably receive less pollen (Bawa & Webb 1984). Similarly, a plant supplied with supplemental pollen could allocate resources toward that season's reproduction at the expense of future reproduction, thus appearing pollen-limited within a season, but remaining resource-limited over its lifetime (Janzen et al. 1980; Chaplin & Walker 1982).

To demonstrate that this *F. perscandens* population was limited by low pollination rates, additional information about the degree of pollinator limitation and the population's demography would be necessary. First it would be necessary to demonstrate that inadequate pollination limited the reproductive output of a large proportion of plants over each plant's lifetime. Additionally, to demonstrate a population-level effect of pollen limitation, it would be necessary to determine that the population was seed limited (Crawley 1990). The lianoid habit of *F. perscandens* suggests that it may spread vegetatively, which may mean that in the short term populations are able to compensate for reduced sexual reproduction through vegetative propagation. Nevertheless, a shift from sexual to asexual reproduction could reduce the plant's ability to disperse and limit the potential for genetic recombination. Consequently, *F. perscandens* populations might not be able to compensate fully for decreased seed set from increased pollinator limitation.

Silvereyes frequently rob nectar from *F. excorticata* flowers through slits they create near the bases of the hypanthia (Delph & Lively 1985), so the presence of these same slits in *F. perscandens* flowers suggests that silvereyes rob nectar from *F. perscandens* in the same manner. As silvereyes are self-introduced from Australia and have only been abundant in most of New Zealand since 1856 (Heather & Robertson 1996), their nectar robbing may represent a new selective force on *Fuchsia* reproductive patterns. However, since we found no evidence that nectar robbing decreased fruit set, it is unlikely that nectar robbing is the cause of pollinator limitation in this population.

The degree of pollinator limitation suggested by the results is consistent with limited signs of active pollen vectors for *F. perscandens*. In the past, plentiful honeyeater birds, which have tongues adapted to gathering nectar (Heather & Robertson 1996), would probably have pollinated *Fuchsia* populations on the Port Hills. However, the recent decline of bellbirds and near extinction of tui populations in the area is likely to have led to the breakdown of this pollinator relationship. Bellbirds are still present in the Buckleys Bay area, but in spring appear to forage mainly on kowhai flowers, which are larger, more numerous, and further from predators on the ground than the flowers of *F. perscandens*. Thus, *F. perscandens* may have attracted enough pollinators when birds were more common and food relatively scarcer, but fails to attract enough pollinators today. Twenty bird species and many invertebrate species have become naturalised in the Port Hills Ecological Region in the last 150 years (Wilson 1992); however, the naturalised species lack the morphological or behavioural characteristics to gather nectar through the floral aperture. For example, on *F. excorticata*, bumblebees are known to steal nectar through slits created by silvereyes but almost never visit the floral aperture itself (Delph & Lively 1985). The evidence of pollinator limitation suggested by this study and the fact that no pollinators were directly observed visiting flowers suggests that increased pollinator limitation may have followed from declines in pollinator populations. These results concur with other studies of pollinator limitation in ornithophilous New Zealand plants (Robertson et al. 1999), and suggest that declines in populations of native pollinating birds may alter the population dynamics of plants that depend on these birds for pollinator service.

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