

Gynodioecy, sexual dimorphism and erratic fruiting in *Corynocarpus laevigatus* (Corynocarpaceae)

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Abstract. The New Zealand karaka tree, *Corynocarpus laevigatus* J.R. & G.Forst., is shown to be gynodioecious. Flowers on female plants have large but empty anthers and many set fruit. Flowers on male plants produce pollen and each has a fully developed ovule. On most male plants, a low proportion of flowers set fruit. Inflorescences and flowers on male and female trees are similar in overall appearance, except that the flower parts on males are larger and flowers open more widely. Even the gynoeceia on male plants are larger in most respects. We also report that although trees retain their gender, their intensity of fruiting varies from year to year. Some observations indicate that other species of *Corynocarpus* in Australia and the south-western Pacific might also be gender dimorphic.

Introduction

Gender dimorphism (Sakai and Weller 1999) among flowering plants is unevenly distributed with respect to geography, ecology and taxonomy. First, gender dimorphism is found in most floras, but is more common on islands, e.g. Hawai'i (14.4% of genera, Sakai and Weller 1999) and New Zealand (23% of genera, Webb *et al.* 1999). Second, gender dimorphism seems to be associated with traits such as perenniality and woodiness, size, abiotic pollination and fleshy, vertebrate-dispersed fruit (Renner and Ricklefs 1995). Third, gender dimorphism is more widespread in some families (Yampolsky and Yampolsky 1922) and rare in others such as Brassicaceae (Bateman 1955; Garnock-Jones 1991). However, in spite of all of these recognised associations, knowledge of the distribution of gender dimorphism is still incomplete, even for countries such as New Zealand that have been centres of intensive study (see reviews by Godley 1979; Webb *et al.* 1999; Newstrom and Robertson 2005). Here, we add the Australasian family Corynocarpaceae to families that are known to exhibit gender dimorphism by reporting and describing gynodioecy in the New Zealand endemic *Corynocarpus laevigatus*.

Corynocarpus has five extant species, and is found in New Guinea, New Zealand, Queensland, the Solomon Islands, Vanuatu and New Caledonia (Molloy 1990; Wagstaff and Dawson 2000). *C. laevigatus* (Maori name: karaka) is a small tree endemic to New Zealand, with small white flowers and large orange aromatic fleshy drupes. Our attention was drawn to its breeding system by our observations that some trees regularly set abundant fruit whereas others fruit poorly or not at all. This has been noticed before, but not explained. Moore (1986) reported that an isolated tree at Warkworth produced apparently perfect flowers with 'androecium and gynoecium both well developed' and 99% stainable pollen, but set no fruit. Molloy

(1990) noted 'some trees clearly are better producers of fruit than others'. Our study examines variation in fruit production among trees and among years, which were reported also by Pigott (1927).

Materials and methods

We studied 18 cultivated, roadside *Corynocarpus laevigatus* trees in Kelburn, Wellington, New Zealand, in spring and summer of 1998. Growth rings on one tree and examination of historical street photographs in the Alexander Turnbull Library indicated the oldest trees were planted between ~1940 and 1957. Some small trees are likely to be much younger replacements of trees that have died. The findings of this study are not invalidated by the focus on cultivated plants (see also Rivers 1971 on *Dodonaea*), especially since *Corynocarpus* is most readily propagated from seed rather than cuttings or grafts (Metcalf 1995). In addition to *C. laevigatus*, we also examined flowers from one plant each of *C. rupestris* (Australia) and *C. dissimilis* (New Caledonia) from trees cultivated in Christchurch, New Zealand, by B. P. J. Molloy (pers. comm.).

Plants were observed at flowering and their gender determined by examining flower morphology and pollen production. The sexed plants, 13 polliniferous (male) and five pollen-sterile (female), the locations or which were carefully and unambiguously noted by using street addresses and a global positioning system, were assessed later for their level of fruit production.

Gender estimates (Fig. 1) were calculated by the formula of Lloyd (1979). These estimates are based on fruit and pollen production, and include an equivalence factor that takes into account the necessary equality of male and female genetic contributions at the population level. Male production of each

tree was estimated as the number of functional anthers per flower (five for male trees, zero for female trees). Gender plots are often crude estimates, but they are nevertheless an effective way to show distribution of gender in populations. First, male reproductive success is difficult to measure, and most gender plots assume that males contribute genes through pollen in equal proportions. Female success is often easier to measure; however, in gynodioecious populations where females produce no pollen, they all contribute 100% of their genes via ovules, regardless of the number or proportion of their flowers that produce seeds. Thus, gender plots are best for describing the relative performance of those plants that reproduce both through pollen and ovules. Additionally, in trees such as *Corynocarpus*, it is difficult to measure the numbers of fruits on males. Although both male and female performances are estimates, they can be used to make a population gender plot that gives a picture of the distribution of gender in the population.

Flower samples (16 trees) were collected and preserved in 70% ethanol for later study. Fruit samples (9 trees) were examined fresh. Measurements of flower and fruit characters were made for statistical comparison between males and females by using Welsh's *t*-test to account for unequal variances. Stigma receptivity was tested on a few flowers by immersing stigmas for ~5 min in 1% aqueous KMnO_4 , which stains receptive stigmas brown (Robinson 1924). We checked the presence of fertile pollen by squashing an anther in Alexander's differential stain (Alexander 1969), which stains pollen walls green and putatively viable cytoplasm magenta. Terminology of flower parts, for which the homology of some whorls is not easily interpreted, follows the detailed study by Philipson (1987). In particular, the outer and inner parts of bipartite structures comprising the whorl internal to the petals are referred to as petaloid scales and nectaries, respectively.

We also report field-notebook observations of fruit production in *Corynocarpus* across several seasons for several populations in the Wellington area, New Zealand. Voucher specimens of the plants studied are deposited in

WELTU and grid references are available from the authors on request.

Results

Flowering

Flower buds of *C. laevigatus* appeared in June in Wellington and flowering occurred in November at least in 1998 (in subsequent years the same trees have also been seen in flower in September and October). Few flowers remained open at the end of November 1998; however, a few male trees had late flowers in mid-December. Fruit development was rapid, with enlarged ovaries apparent within days of anthesis and fully enlarged but green fruit present in mid-December. Molloy (1990) recorded fruit ripening in late summer to winter. We did not see pollinator visits to the flowers; however, in a suburban setting, the flower visitors are unlikely to reflect the original pollinators of *C. laevigatus* before European contact.

Gender dimorphism

Corynocarpus laevigatus exhibits gender dimorphism. Trees could be readily assigned to male or female gender on the basis of flower morphology and fruit production. We follow Lloyd (1979) and Lloyd and Bawa (1984) in referring to polliniferous plants in dimorphic populations as males even though many set fruit (but see Sakai and Weller 1999, pp. 7–8). This reflects their functional gender as sires of all the seed produced in the population. In our sample, five trees were female and 13 were male.

Flowers on male trees produced copious well stained pollen and each had a well formed ovule. Such flowers were relatively large (mean diameter 5.65 mm, Table 1, Fig. 2) and opened quite widely. Stigmas were coated with abundant pollen. The stigmas did not stain well in KMnO_4 , but we observed some pale staining,

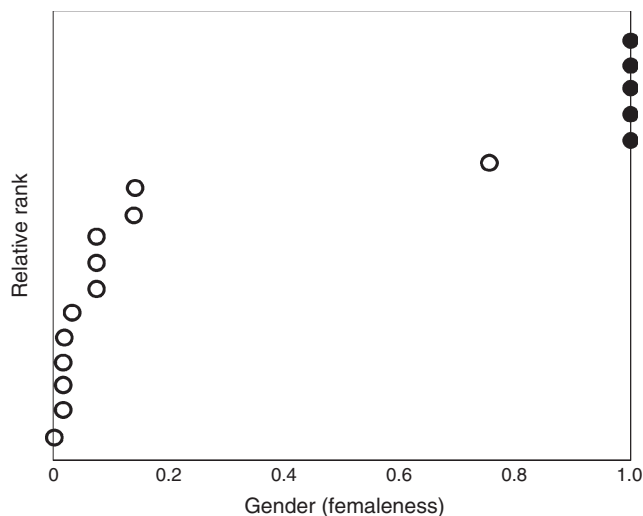


Fig. 1. Gender plot (femaleness plotted against relative rank, see Lloyd 1979) for *Corynocarpus laevigatus* at Kelburn, New Zealand. Open circles, male plants; filled circles, female plants.

Table 1. Sexual dimorphism in flower ($n=5$ female, 13 male) and fruit ($n=4$ female, 5 male) morphology in *Corynocarpus laevigatus* at Kelburn, New Zealand

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., no significant difference

Character (mm)	Female (mean \pm s.e.)	Male (mean \pm s.e.)	<i>t</i>	d.f.
Flower diameter	4.08 \pm 0.15	5.65 \pm 0.15	7.9***	12
Sepal length	2.54 \pm 0.10	3.14 \pm 0.11	4.0***	12.8
Sepal width	2.26 \pm 0.12	2.71 \pm 0.12	3.0*	12.4
Petal length	2.40 \pm 0.04	3.18 \pm 0.12	6.4***	11.7
Petal width	1.66 \pm 0.13	2.09 \pm 0.14	2.4*	12.6
Petaloid scale length	1.62 \pm 0.11	2.40 \pm 0.15	4.6***	13.9
Petaloid scale width	0.82 \pm 0.09	1.00 \pm 0.06	1.8 n.s.	7.6
Nectary length	0.78 \pm 0.05	1.16 \pm 0.05	6.3***	12
Nectary width	0.76 \pm 0.05	1.12 \pm 0.04	6.1***	8.1
Anther length	0.78 \pm 0.05	0.82 \pm 0.04	0.7 n.s.	9.2
Filament length	1.61 \pm 0.07	2.34 \pm 0.04	10.1***	8.4
Ovary length	1.26 \pm 0.05	1.99 \pm 0.06	10.3***	13.5
Ovary width	0.80 \pm 0.02	1.25 \pm 0.04	10.9***	13.9
Style length	0.85 \pm 0.08	1.14 \pm 0.06	3.1**	10.6
Stigma width	0.32 \pm 0.05	0.36 \pm 0.01	0.8 n.s.	4.4
Ovule length	0.67 \pm 0.04	0.97 \pm 0.03	6.4***	10.9
Fruit length	28.9 \pm 2.44	32.92 \pm 1.08	2.3 n.s.	4.3
Fruit width	18.43 \pm 1.25	22.51 \pm 1.07	2.8*	6.5

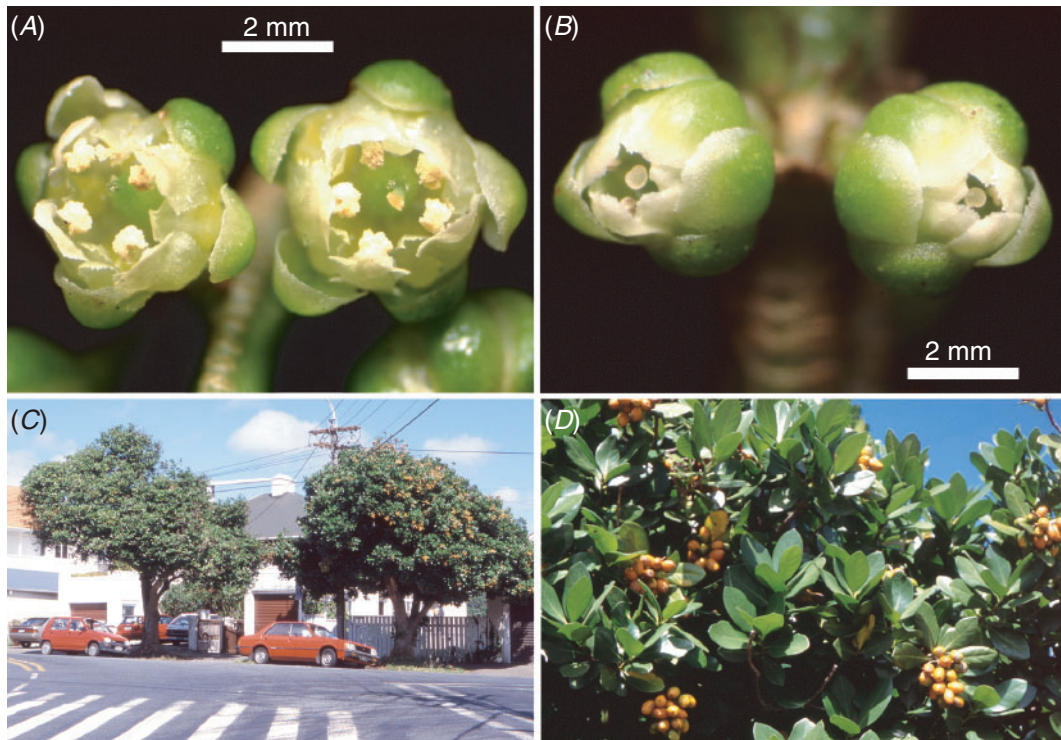


Fig. 2. *Corynocarpus laevigatus*, showing (A) flowers from a male tree, (B) flowers from a female tree (W.M. Malcolm, MicroOptics Ltd, Nelson, New Zealand), (C) male tree (left) and female tree (right), and (D) fruiting branches on a female tree.

suggesting that poor stigma function might be a factor in reduced fruit production on males. We observed no floral scent, but small quantities of nectar were present. Male trees mostly set small quantities of fruit; however, the percentage fruit set per tree could not accurately be quantified.

Flowers on female trees had fully formed anthers, but these contained no pollen and were thus classed as staminodes. Each flower had a well formed ovule. Such flowers were smaller than the flowers on male trees (mean diameter 4.06 mm, Table 1, Figs 2, 3) and smaller in nearly all organs, including ovaries and ovules. They did not open widely, but retained a globular shape and opened only far enough to expose the small stigma (Fig. 2). Stigmas were papillate, pinkish when fresh, and stained well in KMnO_4 . We observed no floral scent, but small quantities of nectar were present. Female trees set copious quantities of fruit (Fig. 2).

The gender distribution in the population is shown in a gender plot (Fig. 1), which shows the population is dimorphic, with two gender classes, constant females and inconstant males (Lloyd 1979). Five female trees had a femaleness score of 1. Only one male tree had a score of 0 (constant male); the rest had low levels of fruit maturation. One polleniferous tree had a gender estimate close to that of the female trees.

Our flower samples of both *C. dissimilis* and *C. rupestris* had well formed ovaries and pollen grains, so we cannot infer from them whether populations are dimorphic. However, in wild populations of *C. similis*, *C. dissimilis*, *C. cribbianus* and *C. rupestris*, only some trees bore fruit, and seedlings were present only under fruiting trees, which indicates this pattern is constant from year to year (B. P. J. Molloy, pers. comm.).

Sexual dimorphism

Sexual dimorphism occurred in most flower parts (Table 1, Figs 2, 3). Flowers on male trees were larger in most characters associated with display; however, anther length and stigma width were not significantly different between the sexes. The ovules in flowers on male trees were larger than in flowers on female trees. The lengths, but not the widths, of the petaloid scales were significantly greater in flowers from male trees.

Of nine trees for which fruits were measured, male trees produced significantly ($P < 0.05$) wider fruits; although the males' fruits were longer, the difference was not significant in these small samples (Table 1).

Fruiting

In 1998, fruiting performance of 17 trees that had been sexed at flowering was estimated. Female trees typically set large numbers of fruit on every inflorescence, although many of these fruits fell before ripening. Male trees varied in their fruit set. Only one male tree set no fruit at all, but several set very low numbers. One male tree set fruit in quantities close to that observed in all the large female trees, and two small female trees set lower numbers of fruit than other trees in the population. Although we studied only one population in detail, others in the Wellington region (and elsewhere, Moore 1986; Molloy 1990) also set very variable amounts of fruit per tree. An unusually large tree at York Bay, Eastbourne, had scattered large fruit, although a single branch was crowded with small fruit.

Intensity of flowering in *C. laevigatus* is not consistent from year to year. A mature female tree outside 32 Upland

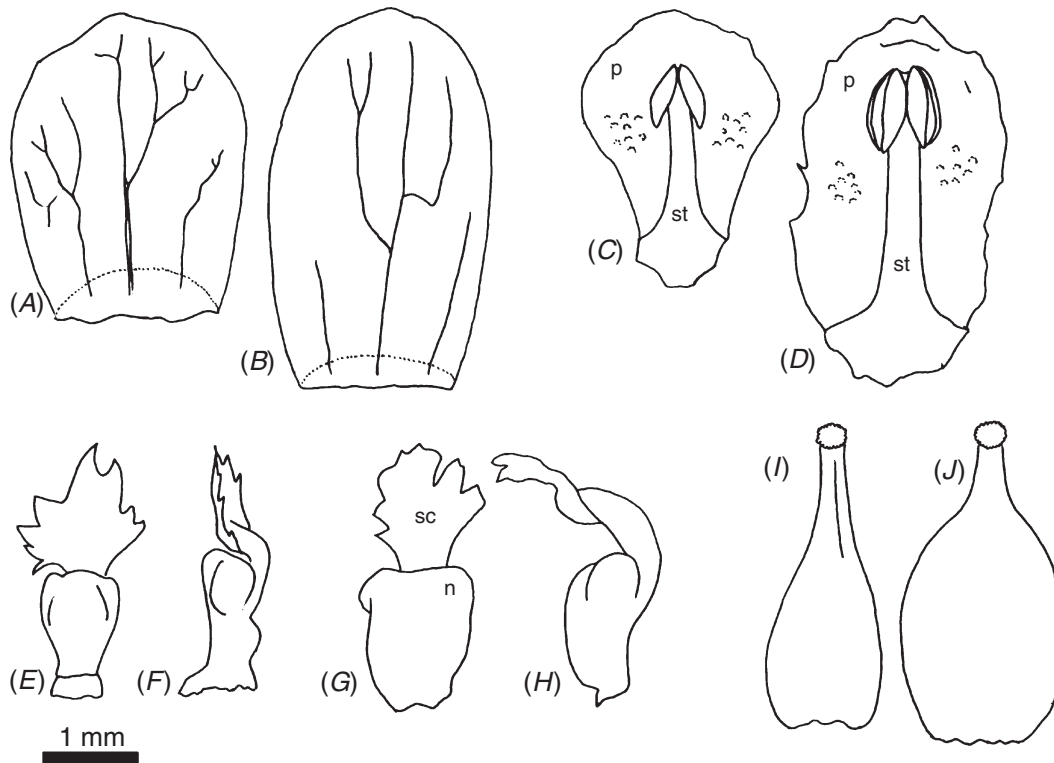


Fig. 3. Sexual dimorphism in *Corynocarpus laevigatus* showing (A) sepal from female tree; (B) sepal from male tree; (C) petal (p) and staminode (st) from female tree; (D) petal (p) and stamen (st) from male tree; (E, F) scale (sc) and nectary (n) from female tree; (G, H) scale (sc) and nectary (n) from male tree; (I) pistil from female tree; and (J) pistil from male tree.

Road bore thousands of fruit in 1995–1996 and again in 1996–1997, none at all in 1997–1998, and more than 3000 fruit in 1998–1999. Hundreds of mature *Corynocarpus* trees beside the State Highway 2 between Ngauranga and Petone produced a heavy crop of fruit in March 1979, but only 14% of them bore fruit in March 1999, with none carrying more than 100 (Table 2).

Table 2. Observations of fruiting intensity in several Wellington populations of *Corynocarpus laevigatus* (at Kapiti coast, Lower Hutt, Orongorongo Valley, Hutt Motorway, Eastbourne and Kelburn, New Zealand)

Season	No. of sites observed	Fruiting intensity
1976–1977	7	Heavy
1977–1978	6	Abundant
1978–1979	3	Very heavy
1979–1980	4	Heavy
1980–1981	2	Very poor
1981–1982	1	Fruiting
1983–1984	1	Fruiting
1994–1995	3	Very heavy
1995–1996	3	Poor
1996–1997	1	Heavy
1997–1998	3	Poor
1998–1999	2	Heavy

Discussion

Gender

The New Zealand flora is particularly rich in species with gender dimorphism; 23% of the genera have separate male and female plants (with or without male inconstancy) (Webb *et al.* 1999). Webb *et al.* (1999) predicted that additional large-fruited New Zealand trees that are currently listed as gender monomorphic might turn out to be either self-incompatible or gender dimorphic. The present report, and another for *Dysoxylum spectabile* (Braggins *et al.* 1999), present data in support of their prediction. It seems that the North Island flora has not been as closely examined for gender dimorphism as the South Island flora, perhaps because most of the researchers studying gender dimorphism in New Zealand plants have been based in the South Island (e.g. E. J. Godley, D. G. Lloyd, C. J. Webb, H. E. Connor, B. F. Shore). Study of other North Island species is recommended; e.g. Merrett (2005) reported gynodioecism in the shrub *Teucrium parvifolium* (Verbenaceae).

The present study is the first report of gender dimorphism in *Corynocarpus*. *Corynocarpus* flowers were described as bisexual in recent descriptive treatments (Allan 1961; Moore and Irwin 1978; Salmon 1986; Eagle 2006) and the species was not listed among native dimorphic species by Webb *et al.* (1999). The appearance of the flowers is deceptive because female flowers have anthers that appear fully formed, but these contain no

pollen. Similarly, the flowers on male plants have a fully formed gynoecium, but it seems from stigma-staining reactions that the stigma is at best only partly functional. This is similar to the cryptic gynodioecism in *Geniostoma ligustrifolium* (Endress *et al.* 1998; M. E. Endress, A. Igersheim and P. J. Garnock-Jones, unpubl. data.). Pigott (1927), Heine (1937), and Castro and Robertson (1997) recorded the species as entomophilous, although Gravatt (1970) and Castro and Robertson (1997) reported occasional honeyeater visits to flowers.

The presence of fruit on most male trees indicates that *Corynocarpus* is gynodioecious, rather than dioecious or subdioecious, at least in the population studied (see Lloyd 1979; Sakai and Weller 1999 for functional definitions of plant breeding systems). The one polleniferous tree with a high femaleness score probably is a result of overestimation of fruit production in most male trees and does not indicate that tree is an inconstant female.

Our quantitative gender research was conducted on a small roadside population and augmented by observations of other populations. In spite of limited sampling, our conclusions are consistent with other observations on this species (Moore 1986; Molloy 1990). Gender plots from other locations would be useful, especially as populations in gynodioecious species can evolve towards dioecy by reduced fruit set on males and towards cosexuality by extinction of females (Webb 1979, 1999).

From limited descriptive accounts, we consider it likely that other species of *Corynocarpus* from Australia and south-western Pacific are also gender dimorphic. Wagstaff and Dawson (2000) presented a phylogenetic hypothesis for *Corynocarpus* that was consistent with a migration from the tropics into New Zealand. It is likely that gender dimorphism is more widespread in the genus and possible that all species of the genus exhibit gender dimorphism, but whether this is dioecy or gynodioecy is at present unknown. If so, gender dimorphism in *Corynocarpus* probably did not evolve in New Zealand, and is thus consistent with many of the other New Zealand gender-dimorphic genera (Godley 1979; Webb *et al.* 1999). From a recoding of *Corynocarpus* as gender dimorphic in the cladogram of Cucurbitales presented by Zhang *et al.* (2006), it seems gender dimorphism is probably a synapomorphy of a large clade, comprising the whole order except the Anisophyllaceae, but with reversals to monomorphic conditions in Begoniaceae, some Cucurbitaceae and Coriariaceae.

Sexual dimorphism

Schultz (2003) tested the idea that many floral-size traits in dimorphic species are pleiotropic and related to stamen length. In dioecious *Sidalcea hirtipes*, Schultz (2003) found that most traits covaried with stamen length, except for style length, which was orthogonal to stamen length in a principal components analysis. In *Corynocarpus*, male flowers were larger in all traits measured, although the differences were not significant in several traits (Table 1). Most length measurements, but fewer width measurements, were significantly greater in flowers from male trees (widths of petals, petaloid scales and styles were not significantly different between the sexes). Schultz (2003) argued that this is an expected and common pattern in gynodioecious species, where gender dimorphism is thought

to be recently evolved and there has been insufficient time for natural selection to counter pleiotropy. In view of the larger sizes in the gynoecium of males of *Corynocarpus*, it would be interesting to examine whether emasculation of male flowers results in smaller female organs. Larger floral display in males is a predicted consequence of sexual selection, because males can increase their fitness more than females by increasing the number of pollinator visits to flowers (Delph *et al.* 1996). In trees such as *C. laevigatus*, geitonogamous selfing is likely in males, unless prevented by self-incompatibility or reduced fruit set.

Fruiting

The observed low fruit set on small female trees suggests that some aspect of small plant size imposes a limit on fruit production. Thus, either limited resources associated with small size (cf. Garnock-Jones 1986) or reduced display to pollinators might be limiting to fruit set in small plants. Some fruit fall from the trees while green (Pigott 1927), perhaps because of adjustment to the resources available for further fruit maturation (Bawa and Webb 1984). Low fruit production on male trees might be explained by early acting genetic load owing to self-pollination (Kärkkäinen *et al.* 1999), early abscission of flowers that are functionally male or by competition for resources (Bawa and Webb 1984).

Male trees produced fruit that were broader than the fruit on female trees (Table 1); it might be that these trees had a good supply of resources for the few fruits that matured, allowing each to reach optimal size. Platt (2003) and Van Essen and Rapson (2005) reported larger fruit near Maori occupation sites and inferred Maori selection for fruit size. It seems unlikely that Maori selection would account for larger fruits on male trees generally, since selective breeding would most likely focus on high-yielding female trees. However, previous selection might have influenced the fruit size on the particular trees in our study and so these results need to be tested with larger and wild samples.

Maori traditionally planted karaka in groups, often in circles surrounding a central tree (Molloy 1990); it was probably known that isolated trees would not bear fruit. The erratic fruiting of karaka had profound effects on pre-contact Maori. Colenso (in Skey 1872) wrote 'As the same karaka woods did not bear alike plentifully every year, the years of barrenness were to the tribe seasons of calamity and want, the karaka being one of their staple vegetable articles of food'. Sawyer *et al.* (2003) showed *Corynocarpus* is widespread in the Wellington region but noted that an association with Maori occupation sites suggests it might not be indigenous there. *C. laevigatus* is considered to be invasive in many parts of its New Zealand range and in several other countries where it is naturalised (Costall *et al.* 2006).

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