

Table 5. Independent assortment v. linkage, dominance v. recessiveness, and their effects on sex-ratios. *Truly dioecious (Lewis 1941)

Mutant states	INDEPENDENT ASSORTMENT				LINKAGE			
Male development suppressor	DOM	DOM	rec	rec	DOM	DOM	rec	rec
Female development suppressor	DOM	rec	DOM	rec	DOM	rec	DOM	rec
Possible "M": F ratios	1:1 2:1	1:1 4:3 2:1	1:1 2:1	1:1 4:3 2:1	1:1 2:1	1:1* 2:1	1:1* 2:1	1:1 2:1

ratios in four of the six possible crosses. This may be the case in populations 5 and 9 which do not vary significantly from equality of sexes. Populations with ratios intermediate between 2:1 and 1:1 could result from cross 4, or more probably from mixed crosses, involving crosses 4 and/or 6 with the others in varying amounts.

Alternative Models

Other possible models were considered where the two genes for sex-expression were linked, and/or where either or both of these genes were dominant.

Table 5 summarizes the alternative states of the two genes and the possible ratios of the sexes in offspring derived from seeds of a single parent plant.

In most of these models, intermediate ratios between 1:1 and 2:1 in *whole populations* could arise from mixed crosses, as is likely the case in some of the populations studied. However, in the case of seeds from *individual crosses* (rather than whole populations) the variable production of neuters (ovule or seed abortion) as seen in the fairly good correspondence between observed and predicted in plants 12, 13 and 18 in Table 4, together with the evidence in the graphs of Fig. 4 showing two different levels of reduction in seed-production in population 2, suggests a model with no linkage, with the female determinant recessive and the male determinant either recessive or dominant, permitting ratios of male to female, from the offspring of individual plants, of 4:3.

While in theory there is nothing to chose between the two models which predict a ratio of four "males" to three females in the offspring of individual plants, the

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postulation of a model in which the male determinant is recessive would, on the principle of Occam's razor, be the better choice, as dominance for 'M' would probably require "selection of modifying genes or alleles" (Lewis, *op. cit.*) and would be of no selective advantage over both male and female being recessive suppressors (evolutionarily the more primitive condition). Weak linkage could also produce 'M' : F ratios intermediate between 1:1 and 2:1 but unlikely to be consistently 4:3. Again there seems to no need to add this complication in the choice of a preferred model.

Evolutionary considerations

The genetic mechanism postulated for *Geniostoma* may not be uncommon in the New Zealand native flora. Of 126 plants in a population of *Coprosma spathulata*, 42% were females, a figure comparable with some of the *Geniostoma* populations examined in this paper. Godley (1964) found that 10 out of 16 populations of N.Z. native species he examined showed a preponderance of males. Females in some ranged from about one-third to nearly one-half, as in *Geniostoma*.

The greater numbers of pollen-bearing plants in some gender-polymorphic species may be related to the seemingly-primitive evolutionary status of flower development in a flora where long-tongued native bees are absent, so that complex co-evolution of flower structure with pollinators is not highly developed, and pollination therefore more haphazard. Godley (*op. cit.*) suggests that "an excess of males may have arisen by selection to compensate for inefficiencies in pollination, in situations where seed production is limited by the availability of pollen and not by the number of ovules".

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Sex ratios of some trees native to New Zealand

Rhys Gardner

Introduction

Godley (1964) examined populations of 16 dioecious native plant species with respect to sex ratio, that is, their proportion of male to female plants. The sex ratios of some florally dimorphic native members of the Apiaceae were investigated by Webb and Lloyd (1980), and those of *Gaultheria* (Ericaceae) by Delph et al. (2006). That work is continued here with respect to some apparently gynodioecious trees of northern New Zealand.

In gynodioecious species one morph has hermaphrodite (sometimes termed 'perfect') flowers and the other, female (male-sterile) flowers. In dioecy, where there are just male and female morphs, a 1:1 sex ratio is expected (though not always found). In gynodioecy the theoretical ratio is harder to predict, since it is dependent on several genetical and ecological factors. These include: genetic mechanism; degree of inbreeding depression; allocation of resources to vegetative growth versus reproduction; and in the hermaphrodites, degree of maleness (e.g., Rattenbury 1980, 2011; Richards 1997; Barrett 1998; Seger & Stubblefield 2002; De Jong & Klinkhamer 2005; Burt & Trivers 2006; McCauley & Bailey 2009). For example, if male-sterility is caused, as is often the case, by a maternally-transmitted cytoplasmic gene, even females of high fitness may become disadvantaged if the pollen-supplying hermaphrodites become too uncommon.

The taxonomic distribution of gynodioecious species in the New Zealand higher-plant flora was part of the floral biology surveys by Godley (1979) and Webb et al. (1999). Subsequently there have been some unexpected additions to the country's gynodioecious element, notably *Dysoxylum spectabile* (Braggins et

al. 1999; Gardner 2009), *Toronia toru* (Gardner 2008a, b), and *Corynocarpus laevigatus* (Garnock-Jones et al. 2007). Sex ratio in these three species, and in three other native woody plants of northern New Zealand (*Geniostoma ligustrifolium*, *Leptecophylla juniperina*, *Pittosporum crassifolium*), is reported on here, along with observations on floral morphology and fruit set. The discussion offered is speculative, mainly consisting of suggestions for future work on these and other florally dimorphic native species.

Methods and Materials

Sampling for sex ratio was carried out in various localities in the Auckland region during flowering periods in 2008-2010. This was done just as opportunity allowed, and no attempt was made to sample every individual in a population or repeat the sampling from year to year on the same individuals. During most samplings it was not unusual to find that some trees would be "resting", that is, with few or no flowers. However, in sampling the two relatively low-stature trees, *Leptecophylla juniperina* and *Pittosporum crassifolium*, the finding of a fertile plant did stimulate effort to examine all adjacent conspecifics.

Assessment of relative fruit set in the sexes during survey of each population was noted but not quantified. Animal flower-visitors, i.e., potential pollinators, were noted.

Information about location and habitat is given in the Appendix. Nomenclature of plant species and familial placement is as in de Lange & Rolfe (2010). No voucher specimens were made.

Table 1: Sex ratios of plant populations in some Auckland localities.
ns = no significant deviation from 1 : 1 male : female ratio (chi-square test, $P=0.05$)

Species	Locality	Date	Hermaphrodites	Females	Females (total) %
<i>Corynocarpus laevigatus</i>	Sylvan Park	08/10/08	31	13	
	Oakley Creek	19/10/08	12	4	
	Gribblehurst Park	26/10/08	14	13	
	Waikaraka Park	30/09/09	30	25	39 %
<i>Dysoxylum spectabile</i>	Dingle Dell	05/06/08	30	0	
	Dingle Dell	09/06/09	15	4	
	Dingle Dell	09/06/10	18	1	
	Kepa Road	05/06/08	25	6	
	Kepa Road	10/06/09	30	5	
	Sylvan Park	08/06/09	41	6	
	Sylvan Park	16/06/10	36	12	15 %
<i>Geniostoma ligustrifolium</i>	Avondale S. Dom.	30/09/08	26	16	
	Avondale S. Dom.	01/10/08	17	19	
	Avondale S. Dom.	03/10/08	45	29	
	Craigavon Park	09/10/08	19	11	
	Smith's Bush	08/10/08	46	24	
	Waikumete	04/10/08	40	24	
	Western Springs	23/09/09	101	60	38 %
<i>Leptecophylla juniperina</i>	Cornwallis	30/08/09	16	16	
	Kendall Bay	03/09/09	29	23	
	Kendall Bay	03/09/10	47	45	
	Avondale S. Dom.	03/09/10	44	48	49 % ns
<i>Pittosporum crassifolium</i>	Western Springs	23/09/10	27	18	40 % ns
<i>Toronia toru</i>	Kendall Bay	16/09/08	34	30	
	Kendall Bay	17/09/09	50	30	
	Kendall Bay	27/09/10	35	20	40 %

Results

The six species investigated are long-lived woody plants, without any capacity to propagate vegetatively (that is, they are trees, not shrubs). All are diploid (Dawson 2000). Individual plants were found to bear flowers of only one kind.

The sex ratio counts obtained with respect to locality and year of sampling are shown in Table 1.

Floral morphology of these species (Fig. 1) and the sex ratio counts are summarized as follows, in alphabetical order by genus.

Corynocarpus laevigatus J.R. & G. Forst.
(Corynocarpaceae) (Fig. 1a)

Morphology: Flowers are hermaphrodite (corolla mouth wide at anthesis, anthers pollen-filled, ovary and ovules well-formed), or female (mouth narrow, anthers not opening and without well-formed pollen). Both morphs produce nectar and a spicy scent ("like aniseed"; B. Maxwell pers. comm.).
Flower visitors: Only dipteran flies were seen.

Sex-ratio: Pooled results (four populations, two seasons) total: 87 hermaphrodite : 55 female.

Fruiting: No assessment of relative levels of fruiting was made, but in both seasons studied most trees had heavy crops.

Dysoxylum spectabile (G. Forst.) Hook.f.
(Meliaceae) (Fig. 1b)

Morphology: Flowers are hermaphrodite (anthers pollen-filled, ovary and ovules well-formed) or female (anthers without pollen). Both morphs produce nectar and a honey-like scent. To a slight to moderate (varying ?) degree there is a secondary pollen-presentation mechanism: the anthers dehisce in late bud, and in newly-opened flowers it is not unusual to find self-pollen around the stigma's sticky perimeter.
Flower visitors: Honey-bees; honey-eater birds (tui, *Prothemadera novaeseelandiae*).

Sex ratio: Pooled results (three populations, three seasons) total: 195 hermaphrodite : 34 female.

Fruit set: Female trees generally set abundant fruit; hermaphrodites, very much less (seed appears to be viable).

Geniostoma ligustrifolium J.R. & G. Forst.
(Loganiaceae) (Fig. 1c)

Morphology: Flowers are hermaphrodite (large pollen-filled anthers, ovary and ovules well-formed, stigma long-papillose) or female (vestigial anthers, stigma short-papillose). Both morphs produce nectar and emit a strong spicy odour like that of cumin. There is a secondary pollen-presentation mechanism: in late bud the anthers dehisce to deposit groups of pollen (often seen as 5 or 10 distinct clumps) around the equatorial part of the stigma.

Flower visitors: Only dipteran flies were seen.

Sex ratio: Pooled results (four populations, two seasons) total: 294 hermaphrodite : 183 female.

Fruit set: No instance was seen of a hermaphrodite plant making fruit or bearing the remains of last year's fruit. Rattenbury (2011) claimed that such fruits, with apparently viable seed, do occur, but very rarely.

Leptecophylla juniperina (J.R. & G.Forst.)
C.M.Weiller (Ericaceae) (Fig. 1d)

Morphology: Flowers are hermaphrodite (anthers large and pollen-filled, ovary and ovules well-formed) or female (anthers smaller, opening but pollen lacking). Both morphs produce nectar and a honey-like scent.

Sex ratio: Pooled results (three populations, two seasons) total: 136 hermaphrodite : 132 female.

Flower visitors: None seen.

Fruit set: Female trees mostly set abundant fruit, hermaphrodites very much less. The viability of the seed of the latter was not investigated.

Pittosporum crassifolium Banks & Sol. ex A. Cunn.
(Pittosporaceae) (Fig. 1e)

Morphology: Flowers are hermaphrodite (anthers large and pollen-filled; stigma and ovary relatively small but ovules well-formed) or female (anthers shrunken). Both morphs produce nectar and a pleasant sweet scent that is perhaps most intense near dusk.

Sex ratio: For the one population (one season): 27 hermaphrodite : 18 female.

Flower visitors: None seen.

Fruit set: Female trees set abundant fruit (old capsules are persistent on the twigs, and the ovaries of the current crop swell rapidly). Only one of the hermaphrodites showed capsules from the previous year and its ovaries were not swelling; hermaphrodites are therefore judged to have a low level of fruit-set.

Toronia toru (A. Cunn.) L.A.S. Johnson & B.G.Briggs
(Proteaceae) (Fig. 1f)

Morphology: Flowers are hermaphrodite (stigma relatively small, ovules relatively few) or female (anthers vestigial). Both morphs produce nectar and a honey-like scent.

Flower visitors: None seen.

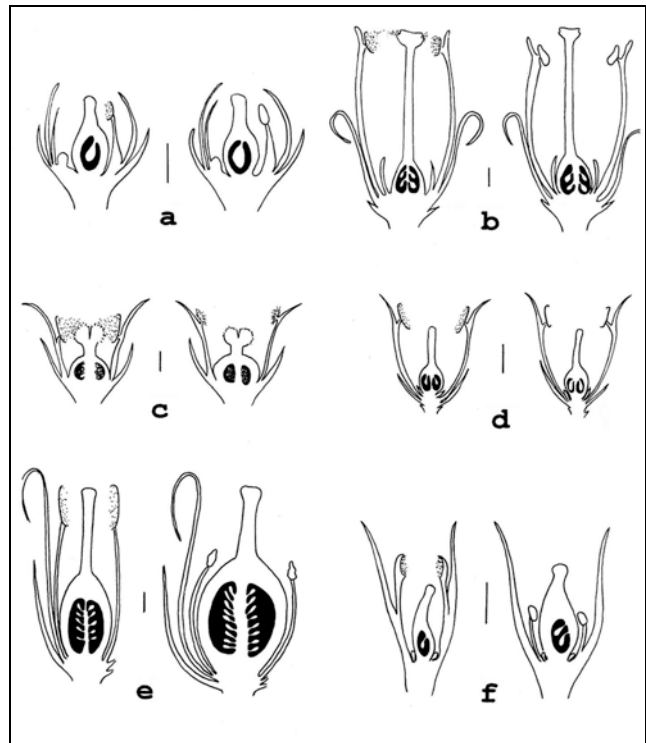


Fig. 1. Floral structure of six New Zealand native woody species (males left, females right); for details see text. Diagrammatic (symmetry disregarded). a: *Corynocarpus laevigatus*; b: *Dysoxylum spectabile*; c: *Geniostoma ligustrifolium*; d: *Leptecophylla juniperina*; e: *Pittosporum crassifolium*; f: *Toronia toru*. Scale bars 1 mm.

Sex ratio: For the one population (three seasons): 119 hermaphrodite : 80 female.

Fruit set: The proportion of female flowers that develop fruit is very low. No fruit at all has been observed on hermaphrodites (with the exception of two individuals, which are variably "intersex" in morphology; in some years these produce abundant fruit with apparently viable seed).

Discussion

The results for each species are analysed separately and speculated on. Overall, only one of these morphologically gynodioecious species, *Corynocarpus laevigatus*, appears to function in this mode; the others in their functioning approach dioecy.

For *Corynocarpus laevigatus* the sex ratio results of the present study agree with those of Garnock-Jones et al. (2007), whose only study population (cultivated trees in Wellington city but presumably seed-derived) had thirteen hermaphrodites and five females.

These authors noted substantial interseasonal and inter-morph variability in the amount of fruit made by their study population and also by other trees in the Wellington region, with hermaphrodites (their "males") usually making a lesser amount of fruit than the females. Perhaps this variability is caused by the

effect of adverse weather on the flowers and their pollinators, since Wellington lies towards the southern limit of distribution of this subtropical tree.

In *Dysoxylum spectabile*, the results of the present study, a significant excess of hermaphrodites, agree with my previous findings (Gardner 2007, 2009) on the same populations, giving some confidence that the data reflects the true local sex ratio. What might require explanation then is the low number of fruit being made by this morph. Experiments are needed to show whether this is because of a natural low level of selfing, or whether cross-pollination is absolutely required. If the latter is the case then perhaps the low fruit set might be due to the flowers getting insufficient visits from the "right" pollinators (cf. Anderson 2003; Merrett et al. 2007). That is, honey-eater birds can be hypothesized as being more effective than honey-bees in removing the obstructive self-pollen from the stigma.

In *Geniostoma ligustrifolium* the sex ratio is strongly biased towards hermaphrodites, but these make a very low amount of fruit and thus act overwhelmingly as males. This confirms the observations of Rattenbury (1980; unpublished ms.). As for *Dysoxylum*, the pollen presentation mechanism would seem likely to hinder cross-pollen from reaching the receptive part of the stigma until the self-pollen has been eroded away.

Again, details on physiological and genetic aspects of pollination in *G. ligustrifolium* are more or less unknown. Rattenbury (unpublished ms.) states that germination of self-pollen on the stigma does happen "regularly"; clearly though, self-fertilization, if it happens at all, is a rare event. One can hypothesize that the absence from the Auckland region of the two smaller honey-eater birds, the bellbird (*Anthornis melanura*) and the stitchbird (*Notiomystis cincta*), both of which feed on *Geniostoma* flowers (Castro & Robertson 1997), might be responsible for current inefficient cross-pollination of the hermaphrodites. Or perhaps a general decline in pollen-gathering insects, such as our native bees, is implicated.

Since in this species (and also in *Dysoxylum spectabile*) it seems likely that self-incompatibility is present, the question is raised: why has there been a further development to gynodioecy or subdioecy? Perhaps the pollen-presentation mechanism is partly responsible: in situations where pollination efficiencies are low, having a stigma uncluttered by self-pollen might be advantageous to any plant with female tendencies.

In *Leptecophylla juniperina* the very low amount of fruit set by the hermaphrodites is in agreement with the observed 1:1 sex ratio, that is, this morph acts overwhelmingly as male. However, all hermaphrodites examined had normal-looking ovaries and ovules,

and, since the females in the study populations are making abundant fruit, it would seem that pollen is being moved around effectively (i.e., it would be available to cross-pollinate the hermaphrodites). Perhaps the sexual condition of the species has only recently been achieved, with inefficiencies in the female (presence of anthers) more or less balanced by those in the male (presence of normal-sized ovary).

In *Pittosporum crassifolium* the sex ratio shows only a weak inequality of the two morphs, and in agreement with this the hermaphrodite makes only a very low amount of fruit. Again though, there seems to be no sign of reduction in its femaleness, with the ovules appearing normally developed and about as numerous as in the females. Larger samples need to be counted; if they were to show a significant excess of hermaphrodites then here too the hypothesis of inefficient current levels of pollination might apply.

In *Toronia toru* the sex ratio is strongly hermaphrodite-biased; this morph though appears not to set fruit. In conjunction with the low amount of fruit set by females this might again suggest some general failure of the pollination process.

When they first open, the flowers of *T. toru* have a pinkish fimbriate-lobed corolla mouth, and are sweet-scented. These features bring to mind one of this tree's common associates in its kauri forest habitat, *Alseuosmia macrophylla* A. Cunn. (Alseuosmiaceae). This is a wholly or fully self-incompatible species (Gardner 1976; Merrett et al. 2007) whose level of fruit-set around Auckland is currently very low too. Perhaps both trees are affected by predation of their pollinators (moths especially?), by wasps, mice and rats.

New Zealand is well known for its high level of floral dimorphism, but as implied by Delph et al. (2006) there is still much to learn here, beginning with morphology (often hard to determine in the field, and even harder in the herbarium) and going on to sex ratio and the elucidation of incompatibility relationships and genetic mechanisms. Similarly Richards (1997) in his text on plant breeding-systems laments that such information is neglected by writers of regional Floras. This is doubly relevant in New Zealand, a biodiversity hotspot whose "official" Flora is, in part, now fifty years out of date.

In summary then: five of the six species investigated (*Corynocarpus laevigatus*, *Dysoxylum spectabile*, *Geniostoma ligustrifolium*, *Pittosporum crassifolium*, *Toronia toru*) show an excess of the hermaphrodite (pollen-bearing) morph, but only in *C. laevigatus* is much fruit made, and the hypothesis is advanced that in the other four species the current level of cross-pollination might be much lower than it was in pre-human times. The sixth species, *Leptecophylla*

juniperina, shows a 1:1 sex ratio, in accordance with the observed very low amount of fruit made by the pollen-bearing morph. This species could be regarded

as dioecious, but the presence of a normal gynoeceium in the pollen-bearing morph requires explanation.

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Appendix: Localities and habitats.

Avondale South Domain, Blockhouse Bay
36 deg 55 min 174 deg 42 min 30 m alt.
Coastal secondary growth (*Kunzea ericoides* dominant)

Cornwallis, Manukau Harbour
37 deg 01min 174 deg 36 min 50 m alt.
Coastal secondary growth (*Leptospermum scoparium* dominant)

Craigavon Park, Green Bay
36 deg 55 min 174 deg 41 min 30 m alt.
Radiata pines and secondary growth (*Kunzea ericoides* dominant)

Dingle Dell, St Heliers
36 deg 52 min 174 deg 51 min 20 m alt.
Old broadleaved forest on mudstone

Gribblehurst Park, Morningside
36 deg 53 min 174 deg 44 min 35 m alt.
Old broadleaved forest on basalt (*Alectryon excelsus* dominant)

Kauri Point, Laingholm
36 deg 59 min 174 deg 38 min 5 m alt.
Coastal scrub

Kendall Bay, North Shore
36 deg 49 min 174 deg 42 min 45 m alt.
Coastal secondary growth (*Kunzea ericoides* dominant)

Kepa Road, St Heliers
36 deg 52 min 174 deg 50 min 40 m alt.
Old broadleaved forest on mudstone

Oakley Creek, Pt Chevalier
36 deg 52 min 174 deg 48 min 10 m alt.
Forest of native and exotic trees

Sylvan Park, Takapuna
36 deg 46 min 174 deg 46 min 10 m alt.
Old broadleaved spp. forest

Waikaraka Park. Onehunga
36 deg 56 min 174 deg 48 min 5 m alt.
Old native and exotic plantings.

Waikumete Cemetery, Glen Eden
36 deg 54 min 174 deg 39 min 35 m alt.
Old *Leptospermum scoparium* scrub

Western Springs, Grey Lynn
36 deg 52 min 174 deg 43 min 20 m alt.
Self-sown native scrub under old radiata pines