

Sexual arrangements in kohekohe (*Dysoxylum spectabile*, Meliaceae)

J.E. Braggins, M.F. Large and D.J. Mabberley

Abstract

Braggins, J.E.¹, Large, M.F.² and Mabberley, D.J.³ (¹Plant Science, School of Biological Sciences, University of Auckland, Auckland, New Zealand; ²Institute of Molecular BioSciences, Massey University, Palmerston North, New Zealand; ³National Herbarium of The Netherlands, University of Leiden, The Netherlands, and Royal Botanic Gardens, Sydney, NSW 2000, Australia) 1999. *Sexual arrangements in kohekohe* (*Dysoxylum spectabile*, Meliaceae). *Telopea* 8(3): 315–324. Detailed examination of floral structure in *Dysoxylum spectabile* (Forst. f.) Hook. f. from New Zealand reveals that individual trees are either exclusively female with flowers lacking pollen, or are male or rarely hermaphrodite with flowers producing pollen and seldom, if ever, fruit. Floral structure is described for both forms.

Introduction

Kohekohe (*Dysoxylum spectabile* (Forst. f.) Hook. f.) is a striking cauliflorous/ramiflorous tree restricted to the North Island and northern South Island of New Zealand (Fig. 1), where it flowers from late autumn to winter; it is found in primary forest and persists in cleared areas forming a major component of the canopy, besides being planted in parks as an amenity tree. Its flowers, which have a creamy white staminal tube, pale green calyx and corolla, with nectar produced from a disk around the ovary (Fig. 3, 4), are visited by insects and birds which may be pollinators.

Kohekohe is the only member of the mahogany family, Meliaceae, to be found in New Zealand and is the most southerly species in a genus of some 80 species found from Sri Lanka and southern China through Malesia east to Niue (Mabberley 1995).

Mabberley (1995) records that *Dysoxylum* species are 'dioecious, more rarely with hermaphrodite flowers', the family including trees which are dioecious, polygamous, monoecious, or with only bisexual flowers (Mabberley 1997). Styles (1972) established that many members of the Meliaceae have functionally unisexual flowers, but that each male or female flower also has well formed though sterile rudiments of organs of the opposite gender. Pennington and Styles (1975) examined representatives from all known genera and showed that only *Turraea* L. and related genera have exclusively hermaphrodite individuals.

The sexual arrangements in *Dysoxylum* species had not been examined in the field before 1990 when DJM visited New Zealand to examine living kohekohe material and, with JEB and MFL, made some pilot studies. Since then investigations on pollen morphology in the genus (Large & Mabberley 1994) as well as studies on *D. pachyphyllum* Hemsl. from Lord Howe Is. (unpublished) also indicate dioecy in the genus, although this is not always obvious.

These observations lend support to earlier reports by Styles (1972, table 1) who describes *Dysoxylum fraserianum* (A. Juss.) Benth. from Australia and the red bean of Australia, *D. muelleri* Benth., a synonym of the Malesian *D. mollissimum* Blume (Mabberley 1994) as dioecious.

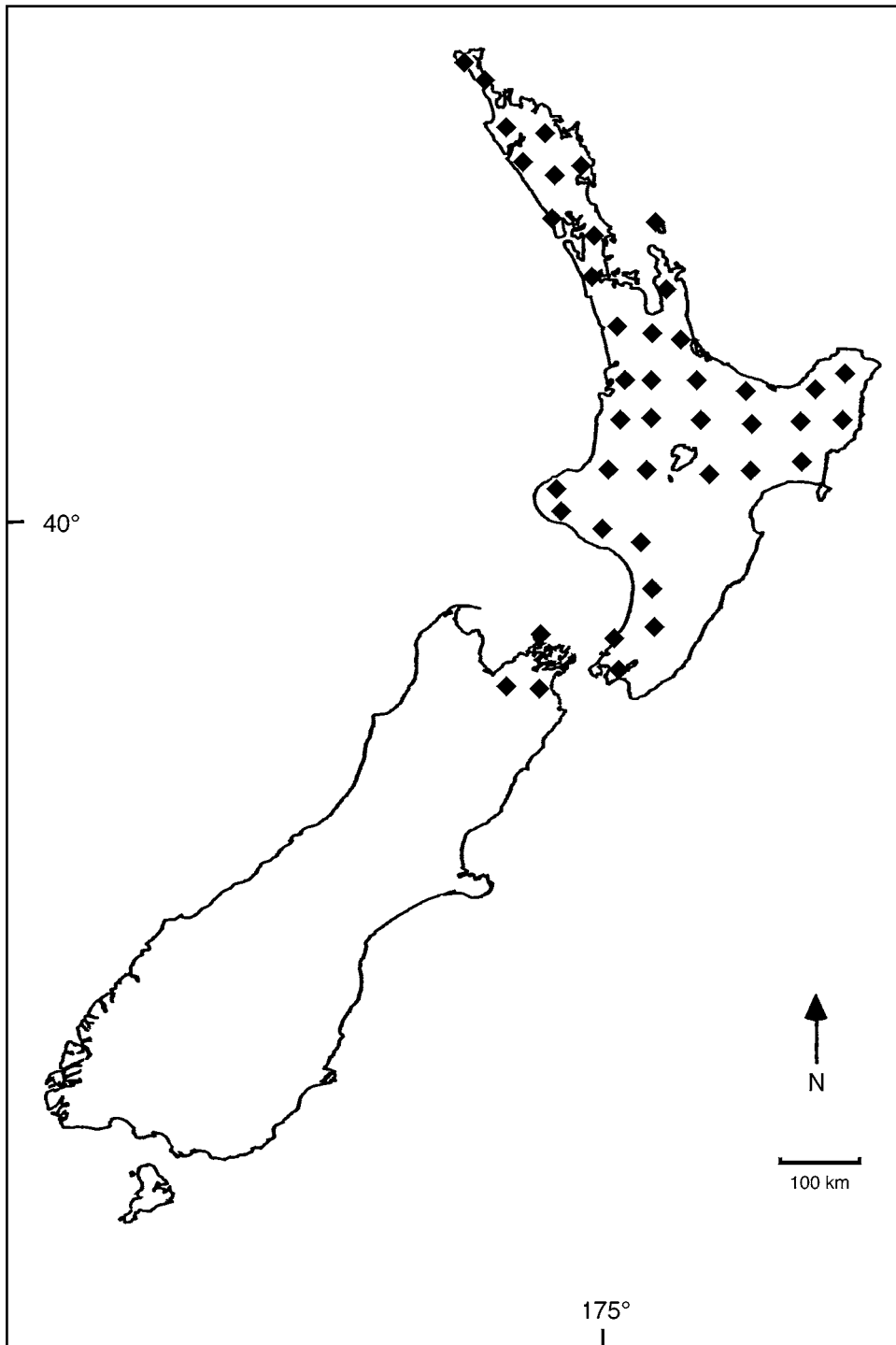


Fig. 1. Map showing the distribution of *Dysoxylum spectabile* in New Zealand. This information is based on herbarium material and the following sources: Allan 1961; Cheeseman 1925; Crowe 1992; Dawson 1988; Salmon 1980.

However, despite investigations devoted to the ecology of *D. spectabile*, e.g. Court and Mitchell (1988, 1989), its dioecious nature appears not to have been previously appreciated. Kohekohe has also been the subject of many taxonomic treatments and features in most texts on New Zealand trees and other flowering plants, e.g. Allan in the New Zealand Flora (1961: 462) states that the flowers are 'perfect'. Nonetheless in several cases it is illustrated in sufficient detail that the sex of the flowers can be discerned, e.g. that in Salmon (1970: 118) being male.

Understanding the floral biology of kohekohe has been further complicated by the majority of specimens lodged in herbaria being male (a full list of material studied is available from the authors, though a representative one is presented in the Appendix).

Materials and methods

In this study carried out by JEB and MFL, fresh material of kohekohe was examined from throughout its New Zealand range with the aims of understanding and describing its functional floral biology. A list of the living subject trees is available from the authors. Herbarium vouchers are deposited in AKU.

Flowers

Flowers were collected from fruit-bearing and non fruit-bearing trees and examined for their reproductive structures. Trees were monitored throughout the flowering period (March–June) for three successive seasons (1996–1998). Calyx, corolla and staminal tube measurements were made (Fig. 2), those of the tube with a pair of electronic callipers (Mitutoyo digimatic, Mitutoyo corporation model CD-6").

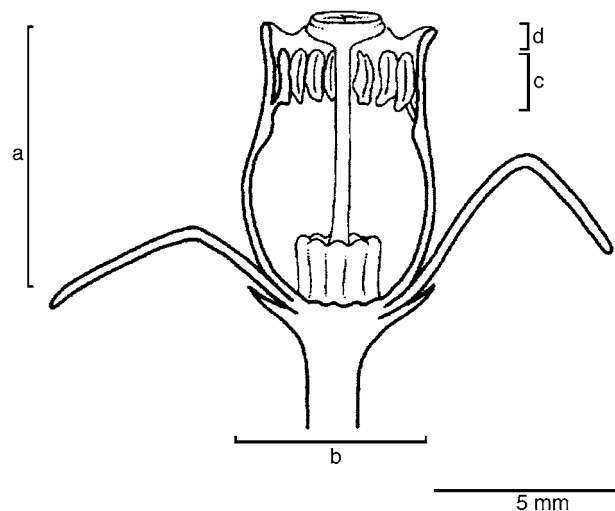


Fig. 2. Schematic LS of the flower of *Dysoxylum spectabile* indicating the positions of measurements given in Table 1. **a**, staminal tube length; **b**, staminal tube width measured at the widest point; **c**, anther length; **d**, distance of anther tip to the upper edge of staminal tube.

Table 1. Data summary on an individual tree basis, for female and hermaphrodite/male trees of *Dysoxylum spectabile*.

Sample sizes include flowers or fruits as stated sampled from three populations (2 Auckland, 1 Wellington). The sample of fruits from hermaphrodite/male trees represents all that are available from the same 3 populations. Data include mean, standard deviation and range for staminal tube length (F length); staminal tube width (F width); staminal tube length to width ratio (F L:W); number of anthers per flower (N° of anthers); anther length; distance from the tip of the anther to the top of the staminal tube (D. top of tube); style length; style head width. The level of pollen viability; number of locules per fruit; number of seeds per locule and number of seeds per fruit are also recorded.

Male	Mean	Sdev	Range	Sample size
F Length mm	7.68	0.74	5.86–9.16	75 fl.
F width mm	4.93	0.61	3.69–6.34	75
F L:W	1.56	0.16	1.20–2.08	75
N° of anthers	10.34	0.63	10–13	40 fl.
Anther length mm	1.44	0.11	1.2–1.6	40
D. top of tube mm	0.9	0.35	0.3–1.4	40
Style length mm	8.1	0.62	6.3–9.0	40
Style head mm	1.4	0.11	1.0–1.6	40
Pollen viability	96%	0.24	87–97%	50 grains × 75 fl.
N° locules	–	–	0–3	6 fruits
Seeds per locule	–	–	0–2	6
Seeds per fruit	–	–	0–2	6
Female				
F length mm	5.79	0.79	4.48–7.26	65fl.
F width mm	5.05	0.49	4.02–6.00	65
F L:W ratio	1.14	0.16	0.86–1.46	65
N° of anthers	10	0.34	10–11	30 fl.
Anther length mm	1.27	0.15	1–1.6	30
D. top of tube mm	1.0	0.28	0.6–1.2	30
Style length mm	7.1	0.62	6.2–8.2	30
Style head mm	1.3	0.18	1.0–1.7	30
Pollen viability	–	–	none	65 fl.
N° of locules	–	–	3–5	30 fruits
Seeds per locule	–	–	0–3	30
Seeds per fruit	–	–	3–7	30

Anthers and pollen

Anthers were examined for the presence of pollen. Anther number per flower, length and the distance from the anther tip to the upper edge of the staminal tube are given in Table 1. Measurements were made using a stereo dissecting microscope with a calibrated eye-piece micrometer. Pollen samples from all flowers with pollen were stained with lactophenol aniline blue and separately with fluorescein diacetate (Heslop-Harrison & Heslop-Harrison 1970) to determine levels of grain viability. Style length and style head diameter were also recorded. These data are summarised in Table 1.

Fruits

Fruits were collected from the same trees used for the floral examination. Locule number and seed set per locule were noted. Data are summarised in Table 1.

Observations

Flowers

The shortly pedicelled flowers occur in thyrses of variable length (c. 50–530 mm long) with, in general, more per inflorescence in the male/hermaphrodite than in the female. Calyx lobes are very small (c. 3.5 mm) while the corolla is longer (c. 10 mm) with 4 to 5 linear petals. The staminal tube is cylindrical, fleshy and its margin crenate (Figs 3–8). There is some variation in length and width (Table 1). However, male flowers tend to have longer and narrower staminal tubes than do females. This is illustrated by the staminal tube length to width ratios (also summarised in Table 1) of 1.56 in the male and 1.14 in the female. Nectar is present in both kinds of flower and is produced in similar quantities.

Anthers and pollen

All flowers from all the trees examined in this study contained 10–13 anthers per flower. Anthers are shortly stalked and borne on thickened filaments emerging from the staminal tube (Figs 3, 4, 7, 8).

Of the trees studied, 40% to 50% consistently produced flowers with anthers which did not contain pollen. In these female flowers (Figs 4, 6, 8), anthers shrink at anthesis and are often dry in appearance. The remaining trees produced swollen anthers which open before anthesis. In these male flowers (Figs 3, 5, 7), pollen grain viability measured with fluoresceine diacetate ranged from 88% to 97% in any one tree.

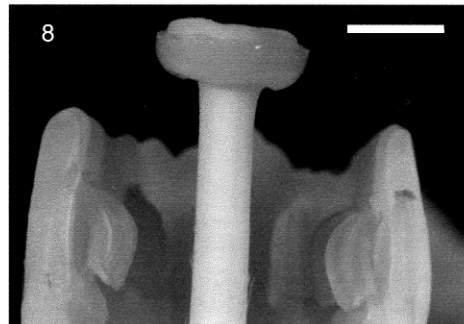
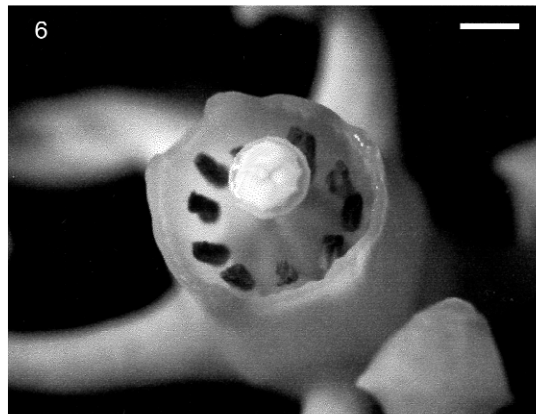
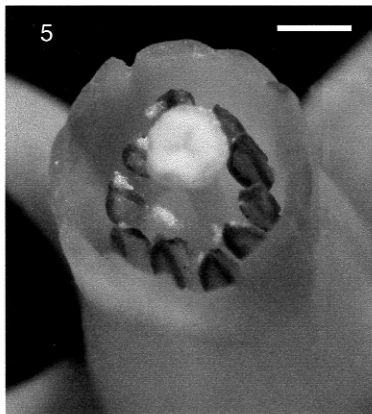
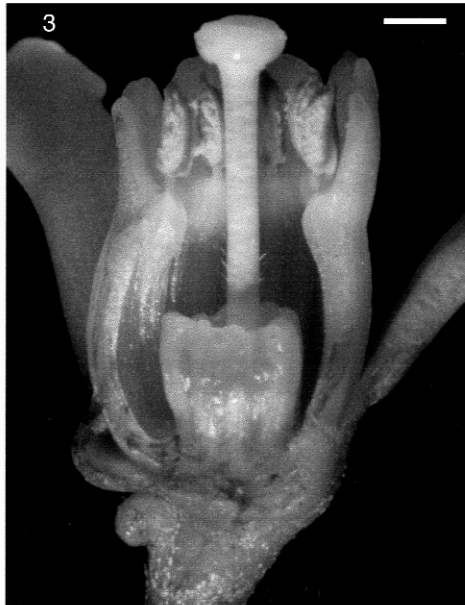
A detailed study of pollen of this and other species within *Dysoxylum* is reported by Large and Mabberley (1994: table 1, fig. 2). In *D. spectabile* pollen grains are spherical in equatorial view and 3–4-colpate. Colpi are narrow and short, reaching about half of the grain diameter. Exine ornamentation is slight, usually scabrate or granulate. Size (measured fresh and mounted in silicone oil): mean diameter = 35 $\mu\text{m} \pm 1.70$, range 29–40, sample size = 50.

Gynoecium

Styles are slender with disciform style heads. The upper surface of the style head is finely papillate, with papillae longer and slightly more developed in female flowers. The pollen receptive surface appears to be the margin and ventral surface which is wet and sticky in both male (Fig. 7) and female flowers (Fig. 8), but particularly so in the latter.

The fruit is an obovate pendulous capsule up to 25 mm long in the female with 3–5 (usually 4) locules each with 0–2 or very rarely 3 seeds (total 4–7 per fruit) which have orange to scarlet arils containing a white sticky latex. Carpels are present in the male flowers but ovules within these are usually absent. Very rarely, fruits may be developed on 'male' trees; a total of 6 fruits only were observed throughout the three years of this study. These are smaller than the fruits produced by the females, being 1–3 locular to 20mm long with 0, 1 or 2 seeds (0–2 per fruit).

Locules seen in both male and female trees were often empty. The maximum number of ovules observed per locule in fruits obtained from female trees was three (or two in the fruits developed on male trees) indicating that seed number in all of the populations studied from 1996–1998, was well below potential levels.



Discussion

All flowers examined in this study contained ovaries and anthers. However, there is a distinction between trees with exclusively female flowers (without pollen) and trees with male, or rarely hermaphrodite, flowers (both with pollen).

In the populations studied the ratio of male to female trees was approximately 1:1. However, male to female ratios in natural populations of kohekohe are difficult to assess. Plants often only bear flowers on upper branches. When growing in crowded stands, these branches may become intertwined complicating determination of the source of flowering material. Assessment of the proportion of females by examining fruit set may also be misleading and underestimate natural levels. This is complicated by the rare setting of fruits by 'male' trees and the fluctuating yearly production of fruits by female trees. In any year an individual may have few flowers and thus set few fruits.

Flowering varies from year to year, with heavy flowering seasons usually followed by lighter ones. Male trees may be especially floriferous carrying more inflorescences and more flowers per inflorescence than female trees. This probably explains the bias in herbarium material towards male specimens. Individual flowers from female trees have a shorter and wider staminal tube (see Table 1) than do flowers on male trees. This difference is more pronounced in populations of kohekohe in the southern parts of its range.

The sexual arrangement exhibited by kohekohe can be described as a modified form of androecy. Although it may be easy to recognise female flowers (and consequently female trees) by the absence of pollen and shorter staminal tube, it is not as easy to understand the true functional and effective gender of the few trees with flowers which produce pollen and occasional fruits. Lloyd (e.g. 1974 a & b, 1975, 1976, 1980) argues that a continuum from hermaphroditism through gynodioecy to dioecy may exist, and points out that sexual arrangements are not always obvious from morphology.

Although this is the first time any member of the genus, or indeed of the family, has been examined for sexual arrangements for so long a period over such a wide range, it is sobering to consider that even as well known a tree as the red maple (*Acer rubrum* L.) in North America had many surprises (see Primack & McCall 1986). It is clear that further detailed work is required to verify the complete reproductive story for kohekohe and the genus *Dysoxylum* in general. When dioecy has only lately been recorded for the first time in the widespread Labiatae–Viticoideae in no less than the common Old World tropical *Premna serratifolia* L. (Mabberley 1992) it is also clear that the phenomenon may be much more widespread than even Bawa et al. (1985) have indicated.

Fig. 3. (Opposite page) LS of male flower of *Dysoxylum spectabile* with part of the calyx, corolla and anther tube removed so that the form and position of the anthers, gynoecium and nectar-producing disk can be seen. Scale bar = 1 mm **Fig. 4.** LS of female flower of *Dysoxylum spectabile* with part of the calyx, corolla and anther tube removed and showing the staminal tube with dry pollen-less anthers. The nectar-producing disk is visible surrounding the ovary at the base of the style. Scale bar = 1 mm **Fig. 5.** Male flower of *Dysoxylum spectabile* showing swollen anthers and pollen. Dehiscence occurs in late bud stage only. In very young buds the anthers are closed. Scale bar = 1 mm **Fig. 6.** Female flower of *Dysoxylum spectabile* showing dried, shrunken, indehiscent anthers. Scale bar = 1 mm **Fig. 7.** Enlargement of stigma and anthers from male flower of *Dysoxylum spectabile*. Anthers are large and releasing pollen. The wet pollen receptive surface on the margin and ventral surface of the style head is visible. Scale bar = 1 mm **Fig. 8.** Enlargement of stigma and anthers from female flower of *Dysoxylum spectabile*. Anthers are shrunken and without pollen. The wet pollen receptive surface on the margin and ventral surface of the style head is visible. Scale bar = 1 mm

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Appendix Representative list of the herbarium material of *Dysoxylum spectabile* examined in this study.

The specimens listed are of flowering material only (a complete list is available from the authors): AK (Auckland Institute and Museum, NZ); AKU (University of Auckland, NZ); WELT (National Museum of New Zealand); WELTU (Victoria University of Wellington, NZ). Collector, date of collection, and location are included where available.

Herbarium No.	Collector	Date collected	Location
MALE			
AK 27565	K Wood	13 Aug 1960	Halls Res, Huia
AK 144188	P Hynes	3 July 1951	Waikawhai Park
AK 132273	DL Knowlton	12 Sept 1942	Smiths Bush
AK 11364	Herb. Kirk	–	Auckland
AK 50701	HE Powell	6 June 1948	Purewa Bush Ak
AK 31837	JS Edwards	June 1953	Waiheke Is
AK 213026	JL Barton	5 June 1960	Piccadilly Rd Kaikohe
AK 213027	JL Barton	11 May 1960	Waimatenui State Forest Tutamoe
AK 126815	RC Cooper	8 June 1966	Waipu Gorge Whangarei
AK 150638	AE Wright	25 May 1979	Fanal Is Mokohinau Gp
AK 127541	F Shakespear	1900–1902	Little Barrier Is
AK 109119	ED Smith	1892–1910	Little Barrier Is
AK 118088	ED Smith	1892–1910	Little Barrier Is
AK 104240	–	7 July 1909	Te Aroha
AK 104234	J Adams	–	Thames
AK 123109	RC Cooper	11 May 1965	Katikati Tuahu Head
AK 126839	RC Cooper	3 July 1966	Makau Pa Waitomo
AK 143110	AE Wright	27 May 1977	Abel Head Farewell Spit
AK 142240	AE Orchard	16 July 1977	M'ore Hosp Otahuhu
AK 229853	TF Cheeseman	June 1883	Orakei
AK 5051	TF Cheeseman	June 1883	Orakei
AK 229855	TF Cheeseman	June 1883	Orakei
AKU 011380	EK Cameron	3 June 1974	Exhib Dr Titirangi
AKU 011275	Ball	May 1885	Titirangi
AKU 018973	JM Moss	27 April 1985	Whangaripo Valley
WELT 63821a	Banks & Solander	1833 [sic]	New Zealand
WELT 29794	D Petrie	1904	Mt Eden Auckland
WELT 29802	D Petrie	1920	Mt Eden Auckland
WELT 29803	D Petrie	1908	Waiwera Auckland
WELT 29804	D Petrie	1909	Waiwera Auckland
WELT 29800	T Kirk	–	Auckland
WELT 29801	T Kirk	–	Auckland
WELT 29796	T Kirk	–	Auckland
WELT 58016a	J Buchanan	–	Kawau Auckland
WELT 77425	JA McMahan	1926	Double Bay
WELT 39404	WRB Oliver	–	Waikanae Wellington

Herbarium No.	Collector	Date collected	Location
ELT 62762	B Ending	1972	Waikanae Wellington
WELTU 18267	J McClean	1962	Maungaroa
WELTU 3673	GM Auther	1948	New Plymouth
FEMALE			
AK 215526	AE Esler et al.	29 June 1978	Cornwall Park
AK 208597	AJ Dakin	11 June 1973	Kirks Bush Papakura
AKU 018978	AM McCarrison	9 May 1985	Tram Valley Rd Swanson
AKU 007870	AG Simpson	Aug 1961	Bot. Garden Wellington
WELT 63821b	Banks & Solander		New Zealand
WELTU 3672	JA Hay	1949	Wellington
WELTU 3676	DA Franklin	1957	Waikanae Wellington