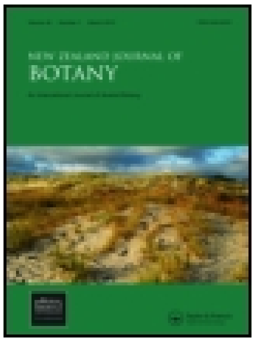


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# Sophora (Fabaceae) in New Zealand: Taxonomy, distribution, and biogeography

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# *Sophora* (Fabaceae) in New Zealand: taxonomy, distribution, and biogeography

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**Abstract** A taxonomic treatment is provided for the *Sophora microphylla* complex in New Zealand. *Sophora microphylla* sens. str. is endemic to New Zealand, and includes those plants with a distinct divaricating and/or strongly flexuose juvenile phase, orange-brown to yellow-brown juvenile stems, and distant leaflets. *S. chathamica* is reinstated at species rank, *S. fulvida* is a new combination provided for the taxon previously known as *S. microphylla* var. *fulvida*, and *S. godleyi* and *S. molloyi* are described as new species. *S. chathamica*, *S. fulvida*, *S. godleyi*, and *S. molloyi* lack a divaricating and/or strongly flexuose juvenile phase and are each distinguished by a number of leaf characters. *S. fulvida* and *S. godleyi* have distinctive leaf hairs. *S. chathamica* is a predominantly coastal species in Northland, Auckland, Waikato, Wellington, and the Chatham Islands, *S. fulvida* occurs in Northland and North Auckland on volcanic rock outcrops, *S. godleyi* occurs on calcareous mudstone and sandstone in eastern Taranaki, King Country, Wanganui, and Manawatu, and *S. molloyi* is restricted to extremely dry and exposed bluffs and rock outcrops of southern North Island headlands, Kapiti Island, and several islands in Cook Strait.

Cluster analyses of 11 leaf and 4 growth habit characters provide additional support for the revised classification, and variation in 7 leaf characters is evaluated with box plots. A key is provided to *Sophora* in New Zealand, hybridism is discussed, an assessment of each species' conservation status is made, and biogeography is reconsidered in view of the new taxonomic treatment.

**Keywords** Fabaceae; *Sophora*; *S. cassioides*; *S. chathamica*; *S. fulvida*; *S. godleyi*; *S. longicarinata*; *S. microphylla*; *S. microphylla* var. *fulvida*; *S. molloyi*; kowhai; taxonomy; biogeography; conservation; New Zealand flora

## INTRODUCTION

The taxonomy of *Sophora* (kowhai) in New Zealand has had a complex and problematic history that is embodied in the following quote from Bentham (in Hooker 1853, p. 52): "I cannot find any character to distinguish the New Zealand *Edwardsiae* from each other, even as varieties: the leaves ... show every gradation from the one to the other; so that I have in vain attempted to sort your specimens into varieties, without making one for almost every specimen." Nearly 90 years later, the genus was still taxonomically difficult, and Bentham's musings were endorsed by Simpson & Thomson (1942, p. 24), who, when describing *S. longicarinata*, commented "We had prepared a description for a beautiful plant from Haulashore Island, Nelson, ... and one for an equally fine plant of Piha, Auckland, ... but ... we hesitate to make distinctions. The genus is much in need of study to separate the many forms."

The early flora treatments for *Sophora* in New Zealand clearly reflect these problems, with Hooker (1853, 1867), Kirk (1899), and Cheeseman (1906) all treating *S. microphylla* Aiton as a variety of *S.*

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*tetraptera* J.S.Mill., or its synonym *S. grandiflora* Salisb. Cheeseman (1925), in the second edition of the *Manual of the New Zealand Flora*, accepted *S. microphylla*, *S. tetraptera*, and *S. prostrata* Buchanan at species rank.

Allan (1961) also accepted *S. microphylla* at species rank, but recognised an additional two varieties (Table 1). One of these, *S. microphylla* var. *longicarinata* (G.Simpson et J.S.Thomson) Allan, was a new combination for the species first described by Simpson & Thomson (1942) and recently reinstated by Heenan (1998a). The other, *S. microphylla* var. *fulvida* Allan, was a new variety considered to be restricted to parts of the western Waitakere coast, North Auckland (Allan 1961). The distinctiveness of *S. microphylla* var. *fulvida* was first recognised by H. H. Allan who "suggested ... that the tree ... which occurs in a restricted area around Anawhata, near Auckland, is either a variety of *S. microphylla* ... or a distinct species" (Briggs & Mangan 1948, p. 1889). Briggs & Mangan were prompted by Allan to investigate the seed alkaloid compounds of this then unnamed *Sophora*, and they concluded that the results "support the classification of this plant as a new species". Earlier, Petrie had collected *S. microphylla* var. *fulvida* from the Waitakere Ranges (e.g., WELT 19452, "the only form found thereabouts"), and he cultivated it at his daughter's farm at Pukeatua, west Taupo (e.g., WELT 19456A). A description of the Waitakere plants was also prepared by Simpson and Thomson but not published (Simpson & Thomson 1942).

A contribution to *Sophora* taxonomy was also made by Cockayne (1902, pp. 279, 319), when he named the Chatham (Rekohu) Islands plants as *S. chathamica*. Cockayne also considered *S. chathamica* to be common in the Auckland area (Cockayne 1927, p. 97; Cockayne & Phillips Turner 1928, p. 51), and he noted that the kowhai from Chatham Islands, the Auckland area, and Chile were similar in lacking a juvenile growth form (Cockayne 1899, p. 373; Cockayne 1912, fig. 1, 2). Godley (e.g., 1975, 1979a, 1979b; Godley & Smith 1977; Sykes & Godley 1968), in a study of habit-heteroblasty in *Sophora* from throughout New Zealand, also reported that races from Northland, Auckland, Chatham Islands, Chile, and Gough Island in the South Atlantic lacked a juvenile form typical of *S. microphylla*. In addition, Godley (1975, 1979a, 1979b) reported that *S. microphylla* var. *fulvida*, and other plants from the Whanganui River and Ohingaiti (Rangitikei River, North Island), also lacked the distinctive juvenile phase.

The Whanganui River plants of *Sophora* were treated as a distinct geographic race in a study of the phenolic compounds of *Sophora* (Markham & Godley 1972), but their taxonomic status was not investigated. The first collection of the Whanganui River/Rangitikei form was by W. Colenso in December 1848 from the Oroua River, on the western flanks of the Ruahine Range (Colenso Herbarium 2319, WELT 23904; unpublished letter to W. J. Hooker, June 1850). In obvious reference to the distinctly hairy leaves, Colenso, in his letter to Hooker, called it "E. velutina n.sp. W.C.", and the WELT herbarium sheet is labelled as "Edwardsia velutina".

Most recently, another form of *Sophora* that is shrubby, sometimes prostrate, and particularly leafy



**Table 1** Comparison of taxonomic treatments of *Sophora* in New Zealand.

| Current revision | Allan (1961) | Yakovlev (1967) | Tsoong & Ma (1981) |
|---|---|---|---|
| *S. chathamica* | synonym of *S. microphylla* | *S. microphylla* subsp. *microphylla* var. *chathamica* | *S. chathamica* |
| *S. fulvida* | *S. microphylla* var. *fulvida* | *S. microphylla* subsp. *microphylla* var. *fulvida* | – |
| *S. godleyi* | – | – | – |
| *S. longicarinata* | *S. microphylla* var. *longicarinata* | *S. microphylla* subsp. *microphylla* var. *longicarinata* | – |
| *S. microphylla* | *S. microphylla* var. *microphylla* | *S. microphylla* subsp. *microphylla* var. *microphylla* | *S. microphylla* |
| *S. molloyi* | – | – | – |
| *S. prostrata* | *S. prostrata* | *S. microphylla* subsp. *microphylla* var. *prostrata* | *S. prostrata* |
| *S. tetraptera* | *S. tetraptera* | *S. tetraptera* | *S. tetraptera* |

has been reported from several islands in Cook Strait (Atkinson & Bell 1973; Walls 1979, 1981, 1982, 1986; Ogle 1983). This shrubby form is often cultivated as an ornamental species in New Zealand, and the growth habit of a mature cultivated plant has been described (Heenan 1992).

Several authors from outside of New Zealand have contributed to the taxonomy of the New Zealand species of *Sophora*. A revision of *Sophora* sect. *Edwardsia*, to which the New Zealand species belong, was provided by Yakovlev (1967) (Table 1). He accepted *S. tetraptera* at species rank and, in a rather unconventional treatment, recognised a number of varieties of *S. microphylla*. The most recent treatment of the New Zealand species was provided by Tsoong & Ma (1981), who accepted *S. prostrata*, *S. microphylla*, *S. tetraptera*, and *S. chathamica* (Table 1).

*Sophora microphylla* sens. lat. has often been considered to occur in Chile and on Gough Island in the South Atlantic (Pizarro 1959; Markham & Godley 1972; Hoffmann 1982; Rodriguez et al. 1983), and for this reason is of considerable biogeographic interest (Guppy 1906; Wace & Dickson 1965; Sykes & Godley 1968; Markham & Godley 1972; Peña et al. 1993; Peña & Cassels 1996; Hurr et al. 1999). Several studies have attempted to establish relationships between the different geographic forms of *S. microphylla* sens. lat. In a study of the seed and leaf phenolic compounds of *S. microphylla*, Markham & Godley (1972) concluded that plants collected from Chile, Gough Island, and New Zealand were all referable to *S. microphylla*. These biochemical data did support a particularly close relationship between plants from Gough Island and Chile. A recent phylogenetic analysis of 11 species of *Sophora* sect. *Edwardsia* was undertaken using morphological and biochemical characters (Peña & Cassels 1996). In this study, Chilean plants were treated as *S. macnabiana*, a species these authors considered to be different from, but related to, *S. microphylla*. The morphological characters distinguishing *S. macnabiana* and *S. microphylla* were primarily those of the leaves. The revision presented here treats the Chilean and Gough Island plants as a different species, and their legitimate name is *S. cassioides* (F.Phil.) Sparre (Heenan 2001). The monophyly of *Sophora* sect. *Edwardsia* has been demonstrated using cpDNA (Hurr et al. 1999), but this study was unable to adequately resolve relationships among different populations of *S. microphylla* sens. lat. and other species of *Sophora* dispersed around the southern oceans.

When reinstating *S. longicarinata* and in selecting a lectotype for *S. microphylla* (Heenan 1998a), it was necessary to critically examine a large amount of plant material of *S. microphylla* sens. lat. During that study, it became apparent that *S. microphylla* sens. lat. exhibited distinct patterns of variation in leaf and growth-habit characters. The results of subsequent field, herbarium, statistical, and cultivation studies of the *S. microphylla* complex are reported in this paper.

## MATERIALS AND METHODS

Field studies of *Sophora* have been made throughout New Zealand by PBH and PJdL during the 1990s. In particular, during August 1997 field work was undertaken on *S. chathamica*, *S. fulvida*, and *S. microphylla* in the Waitakere Ranges at Anawhata, Armour Bay, Cornwallis, Huia, Little Huia, Omanawanui Ridge, Oratia Stream, Piha, Mill Bay, Whatipu, and Whites Beach; and near Whangarei at Mt Manaia, Bream Head, and Whangarei Heads. Observations have also been made on *S. microphylla* and *S. chathamica* in the North Island at Green Bay, Auckland; near Warkworth at Mahurangi Heads and Ti Point; Helensville, Woodhill; Tuakau, Port Waikato, Raglan, Aotea, and Kawhia harbours; the Mokau and Tongaporutu rivers; Kaiaua, Miranda, Coromandel Peninsula, and Thames; Kapiti Island, Cook Strait, Wairarapa, and Wellington. Field studies were made of *S. chathamica* on the Chatham Islands during 1996, and of *S. longicarinata* in Nelson and Marlborough between 1993 and 1997 (Heenan 1998a). Field observations have been made on *S. godleyi* and *S. microphylla* between 1997 and 2000 in the catchments and tributaries of the Pohangina, Rangitikei, Turakina, Mangaweka, Whanganui, and Waitotara rivers. *S. molloyi* has been studied at several sites near Cape Palliser and Cape Terawhiti and on Kapiti Island. *S. tetraptera* has been studied from East Cape to Cook Strait. In the South Island observations have been made on *S. microphylla* and *S. prostrata* between 1990 and 2000. Herbarium specimens from many of these sites have been deposited at AK and CHR, and herbarium specimens at AK, AKU, CHR, NZFRI, WELT, and WAIK were examined.

General observations and statistical analyses of leaf measurement data were made on a large collection of *S. microphylla* sens. lat. of known provenance that was established by E. J. Godley at the Landcare Research (then DSIR Botany Division) experimental nursery. As these plants are grown under similar environmental conditions, they provide a means to assess whether leaf morphological variation is due to environmentally induced phenotypic variation or whether it has a genetic basis. The fundamental premise of this type of study is that plants gathered from different sites and grown under uniform environmental conditions are unaffected by any irregularities that occurred in different natural habitats. Included in this collection are 35-year-old plants of *S. cassioides*, *S. chathamica*, *S. fulvida*, *S. godleyi*, *S. longicarinata*, *S. microphylla* sens. str., *S. molloyi*, *S. prostrata*, and *S. tetraptera*.

Leaf hairs were observed with the Oxford CT1500 cyrostage of a scanning electron microscope (SEM). For the SEM examination fresh leaves were frozen in liquid nitrogen, sputter-coated with gold, and viewed at −180°C in a Leica S440 SEM.



### Statistical analysis

Eleven leaf and four growth habit attributes were measured for 68 specimens of *Sophora* from New Zealand, Chatham Islands, Chile, and Gough Island (Atlantic Ocean), that were cultivated under uniform conditions at the Landcare Research experimental gardens, Lincoln, Canterbury (Appendix 1). Leaf and growth habit characters measured include:

1. Leaf length (mm).
2. Leaflet number per leaf.
3. Leaflet length (mm).
4. Leaflet width (mm).
5. Leaflet thickness (mm).
6. Leaflet hair density (hairs per 1-mm line).
7. Petiolule length (mm).
8. Leaf colour. 1, green; 2, dark green; 3, grey.
9. Leaflet overlap. 1, present; 2, absent.
10. Leaflet taper. 1, present; 2, absent.
11. Hair type. 1, appressed; 2, spreading; 3, curly/twisted.
12. Juvenile growth habit. 1, present; 2, absent.
13. Growth form. 1, tree; 2, shrub.
14. Adult branches. 1, interlaced; 2, not interlaced.
15. Underground stems or rhizomes. 1, present; 2, absent.

Five mature leaves were measured from the outside of each plant. For each leaf the quantitative measurements were taken from five leaflets from the middle third of the leaf. Exploratory data analysis was carried out for the leaf measurements to check for errors, outliers, and normality for each character. The quantitative characters (1–7) exhibited non-normal distributions and, furthermore, the distribution varied between characters and within a character when it was separated into species groups. Cluster analysis and single box plots are therefore presented as they do not require assumptions of normality or homogeneity of variance.

Cluster analysis was undertaken to assess overall phenetic relations of the individual plants based on the average value of the leaf characters (characters 1–11) for each plant, and the average value of the leaf characters (characters 1–11) with the addition of four growth habit characters (characters 12–15). For each cluster analysis Gower's (1971) general coefficient of similarity was used to construct a similarity matrix from which a phenogram was produced using the average linkage clustering method (UPGMA) (Sneath & Sokal 1973). Box plots were generated from the individual leaf measurement data for characters 1–7 to show character distribution for each species and examine character variation. The box plots depict the median (central line in each box), 25% and 75% quartiles (upper and lower limits of each box), the maximum point within 1.5 times the interquartile range from the quartiles (indicated by the whiskers), and outliers (i.e., points greater than 1.5 times from the quartiles) indicated by lines outside of the whiskers. All analyses were made using S-Plus (Statistical Sciences 1998).

### Species concept

In this study we recognise *S. fulvida*, *S. godleyi*, *S. chathamica*, *S. microphylla*, and *S. molloyi* at species rank following the Ecological Species Concept (van Valen 1976; Andersson 1990). This concept advocates closely examining morphological variation and correlating this with different adaptive zones. The application here of the Ecological Species Concept further highlights its utility in solving complex taxonomic problems among closely related, and often difficult to discriminate, sibling species.

The application of the Ecological Species Concept in resolving taxonomic problems in New Zealand *Sophora* is exemplified by the recognition of *S. godleyi*. During an early phase of the revision, when herbarium specimens were being placed into broad morphological groups, it was noted that specimens somewhat similar to *S. fulvida* occurred in Wanganui, eastern Taranaki, and Rangitikei (North Island). These specimens occurred on calcareous mudstones, sandstones, and siltstones, whereas it had already been noted that *S. fulvida* was restricted to andesitic and basaltic volcanic outcrops in Northland and Auckland (North Island). This fundamental ecological difference prompted close examination of morphological attributes on herbarium specimens, and this resulted in

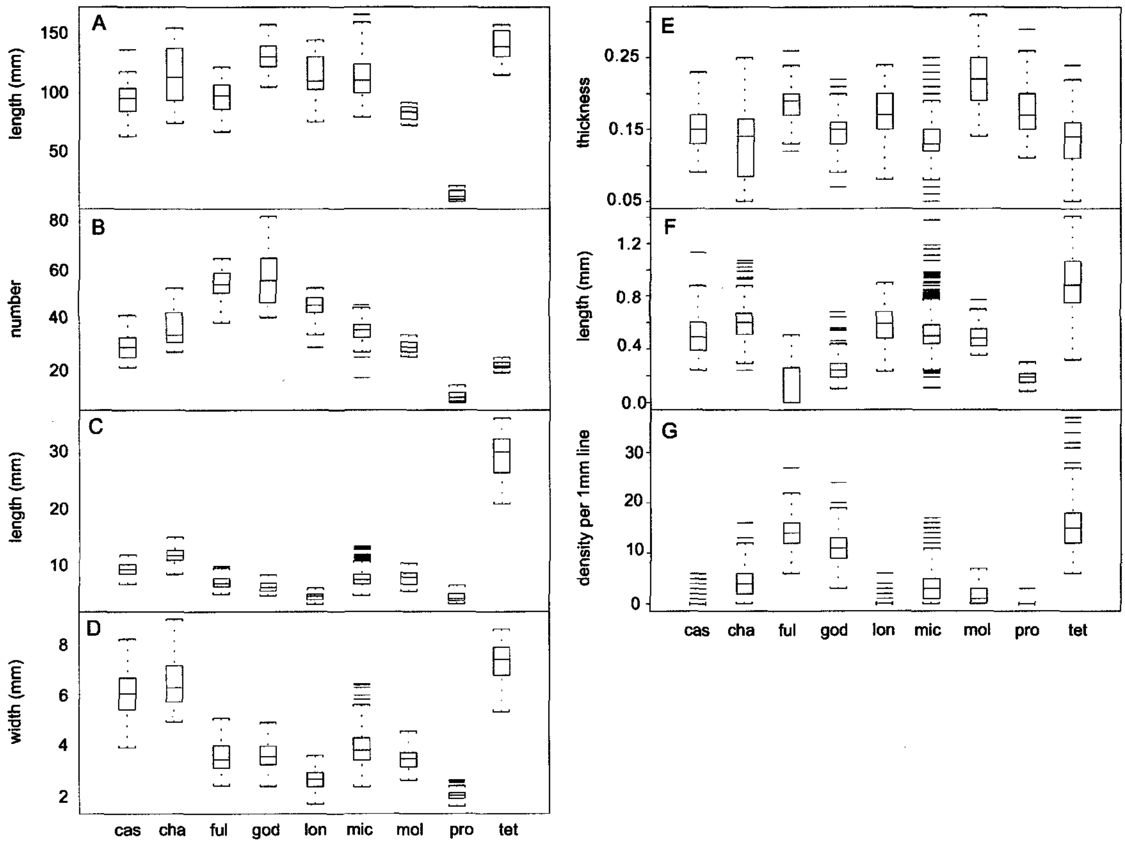



**Fig. 1** Box plots of quantitative leaf characters. Median, 25 and 75 percentiles, whiskers maximum point with >1.5× interquartile range, and outliers are represented. **A**, leaf length; **B**, leaflet number per leaf; **C**, leaflet length; **D**, leaflet width; **E**, leaflet thickness; **F**, petiolule length; **G**, hair density. Abbreviations: cas = *S. cassioides*; cha = *S. chathamica*; ful = *S. fulvida*; god = *S. godleyi*; lon = *S. longicarinata*; mic = *S. microphylla*; mol = *S. molloyi*; pro = *S. prostrata*; tet = *S. tetraptera*.

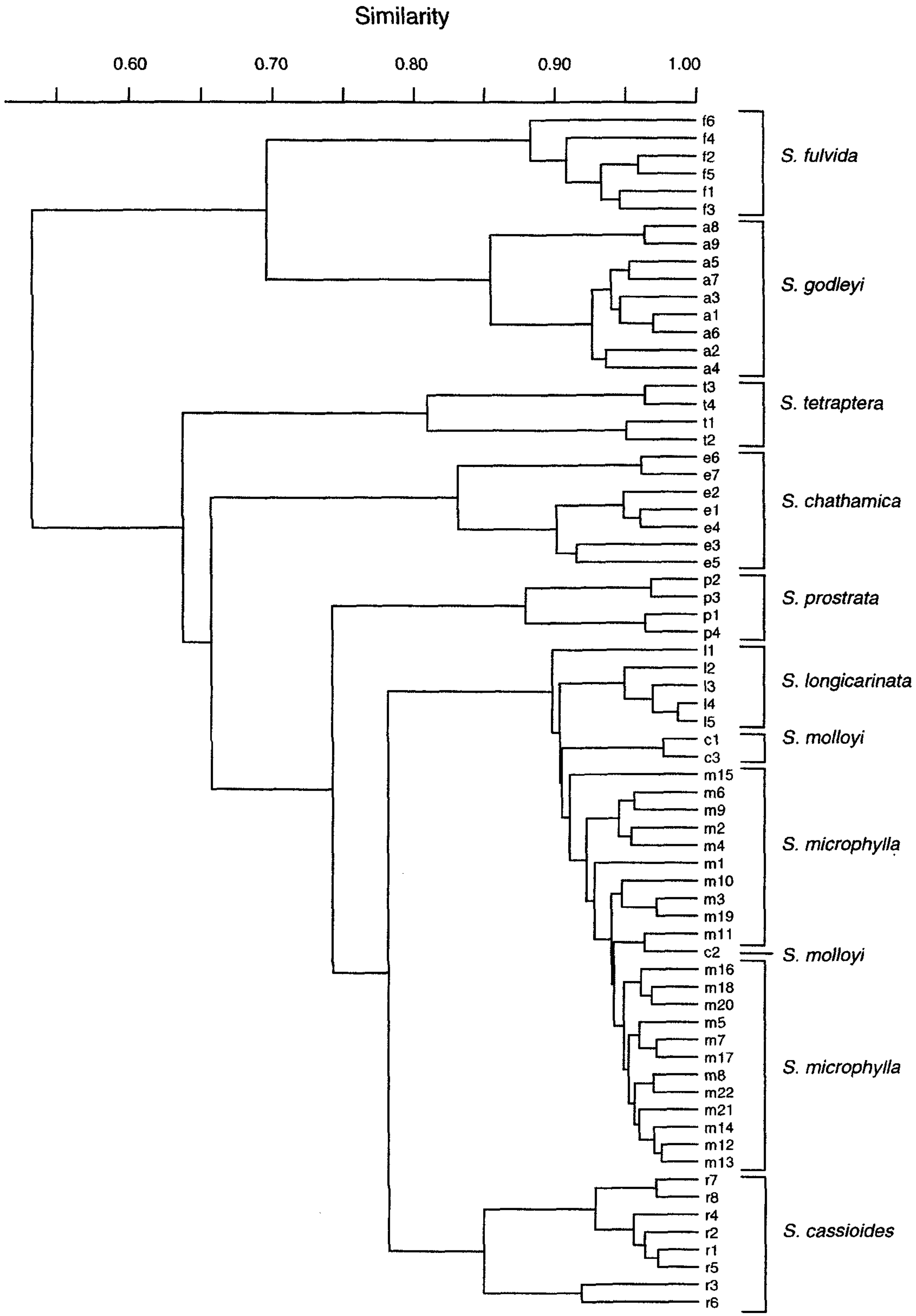
the preliminary recognition of two taxa. Subsequent field work in the North Island confirmed that there was a strong relationship between different ecological attributes and plant morphological characters and that it was appropriate to recognise these new taxa at the rank of species, these being *S. fulvida* and *S. godleyi*.

Recognition at species rank for the species accepted here is consistent with the use of that rank for other members of *Sophora* section *Edwardsia* (e.g., Philippi 1873; Cheeseman 1925; Skottsberg 1953; Allan 1961; Green 1970; St John 1985).

## RESULTS AND DISCUSSION

### Leaf characters

The species of *Sophora* accepted in this revision are sometimes difficult to recognise using only individual leaf characters (Fig. 1), but they can be distinguished by using a combination of leaf characters (Fig. 2). The leaves of *S. microphylla* sens. lat. have always been considered highly variable (e.g., Bentham in Hooker 1853; Cheeseman 1925; Godley 1979a), with difficulties often experienced in defining geographic races, let alone species. Markham & Godley (1972, fig. 1) and Godley (1979a, fig. 4, 6) illustrated leaves from a number of plants referable to *S. microphylla* sens. lat. that represent some of the variation. The variation in leaf characters can be attributed in part to the maturity of the plant from which the leaves were taken, to the number of leaflets, their size, shape, and colour, hairiness, hair type, the distance between leaflets, and petiolule length. For identification it is important to use mature leaves from the outside of the plant.


Similarity
0.60
0.70
0.80
0.90
1.00
f6
f4
f2
f5
f1
f3
a8
a9
a5
a7
a3
a1
a6
a2
a4
t3
t4
t1
t2
e6
e7
e2
e1
e4
e3
e5
p2
p3
p1
p4
l1
l2
l3
l4
l5
c1
c3
m15
m6
m9
m2
m4
m1
m10
m3
m19
m11
c2
m16
m18
m20
m5
m7
m17
m8
m22
m21
m14
m12
m13
r7
r8
r4
r2
r1
r5
r3
r6
S. fulvida
S. godleyi
S. tetraptera
S. chathamica
S. prostrata
S. longicarinata
S. molloyi
S. microphylla
S. molloyi
S. microphylla
S. cassioides

The leaves of adult plants of *S. tetraptera* and *S. prostrata* are very different from all other species (Table 2; Fig. 1, 2, 3). *S. prostrata* is easily distinguished by its short leaves and fewer leaflets. Furthermore, leaflet length and leaflet width of *S. prostrata* are smaller than *S. cassioides*, *S. chathamica*, and *S. tetraptera*, and leaflet width only slightly overlaps with *S. fulvida*, *S. godleyi*, *S. microphylla*, and *S. molloyi* (Fig. 1C, D). The petiolule length of *S. prostrata* is shorter than *S. molloyi* and *S. tetraptera*, and only slightly overlaps with those of *S. cassioides*, *S. chathamica*, and *S. longicarinata* (Fig. 1F). *S. tetraptera* is most readily distinguished by its long leaflets (Fig. 1C), and in comparison with all other species the leaflets are particularly long in relation to their width. Leaflet number is also a useful diagnostic character, separating *S. tetraptera* from all species except *S. cassioides*, *S. microphylla*, and *S. molloyi* (Fig. 1B). However, it is a combination of the 11 leaf characters that best distinguishes *S. tetraptera* from the other species (Fig. 2), with particularly useful characters including leaflet number, length, and width, hair density, and petiolule length.

*Sophora microphylla* is especially difficult to identify using only a single leaf character, as its leaf attributes are often similar to those of the other species (Fig. 1). However, the leaves of *S. microphylla* typically have a unique combination of characters, including 30–50 leaflets, and the leaflets are distant from each other, light green to green, and they have a moderate number of appressed hairs (Tables 2 and 3; Fig. 1–4).

*Sophora fulvida* and *S. godleyi* can be distinguished from the other species by a combination of characters, including more numerous leaflets, shorter petiolules, the leaflets at the distal end of the leaf are usually noticeably smaller than those at the proximal end, they are particularly hairy, and they have different hair types. *S. fulvida* has leaflets that are elliptic to elliptic-oblong, green to slightly grey-green, and it is the only species with sessile leaflets (although occasionally some leaflets have a very short petiolule up to 0.5 mm long). The leaflets of *S. godleyi* are ovate to sometimes more or less orbicular, grey to green-grey, and with a more or less distinct short petiolule. *S. godleyi* and *S. fulvida* can both be separated from *S. chathamica* and *S. tetraptera* by their smaller leaflet length and width (Fig. 2). The leaflet width of *S. fulvida* is also always less than *S. tetraptera*.

The hair types of *S. godleyi* and *S. fulvida* are particularly diagnostic (Table 2; Fig. 4). Those of *S. godleyi* are appressed, decumbent, spreading and/or patent, and are usually noticeably curly, curved, or twisted (Fig. 4). The hairs of *S. fulvida* are usually appressed, decumbent or spreading, mostly straight, sometimes twisted, but not curved or curly, and they have a rather shaggy appearance (Fig. 4). The leaf hairs of *S. cassioides*, *S. chathamica*, *S. longicarinata*, *S. microphylla*, *S. molloyi*, *S. prostrata*, and *S. tetraptera* are always appressed and straight (Fig. 4), only very rarely being slightly twisted.

*Sophora chathamica* is distinguished by having crowded and overlapping leaflets, the leaflets at the distal end of the leaf are usually smaller than those at the proximal end, and its leaflets tend to be longer and wider than all other New Zealand species except *S. tetraptera* (Table 2; Fig. 1C, D).

*Sophora molloyi* can be distinguished from all other New Zealand species except *S. microphylla* by a combination of leaf characters. Its leaf length is less than *S. godleyi* and *S. tetraptera* and greater than *S. prostrata*, leaflet number is less than *S. fulvida* and *S. godleyi* and it only slightly overlaps with *S. longicarinata*, and leaflet width is less than *S. chathamica* and *S. tetraptera* (Fig. 1A, B, D). In comparison with the other species previously included in *S. microphylla*, *S. molloyi* has a tendency to have shorter leaves and fewer and thicker leaflets, although ranges overlap (Table 2; Fig. 1A, B, E).

The general tendency is for *S. longicarinata* to have numerous and small leaflets that are distant from each other, uniform in size, dark green, glabrous or with a few appressed hairs, and with distinct petiolules (Heenan 1998a; Fig. 1B, C, D, F, G). The leaflets of *S. longicarinata* are shorter and narrower than those of *S. cassioides*, *S. chathamica*, and *S. tetraptera*, being most similar to *S. prostrata* (Fig. 1C, D). However, *S. longicarinata* differs from *S. prostrata* in its longer leaves and in having a much greater number of leaflets (Fig. 1A, B).

The Chilean and Gough Island *S. cassioides* has a slight overlap in leaflet number with *S. fulvida* and *S. godleyi*, and leaflet length overlaps slightly with *S. godleyi* and *S. tetraptera*. However, it can be distinguished by a combination of characters, including the leaflets being particularly broad in relation to their width, dark green, usually distant but

**Fig. 2** Cluster analysis of the individual *Sophora* plants using leaf measurement data. The plant codes correspond to the specimens listed in Appendix 1. Pearson cophenetic correlation coefficient = 0.9103.

**Table 2** Comparison of parameters (mean values (mm) ± SD) for plants of nine species of *Sophora* cultivated at Lincoln, Canterbury, New Zealand.

| Species | *n* | Leaf length | Leaflet number | Leaflet length | Leaflet width | Leaflet thickness | Hair density | Petiolule |
|---|---|---|---|---|---|---|---|---|
| *S. cassioides* | 8 | 94.40 ± 14.58 | 29.22 ± 5.14 | 8.60 ± 1.12 | 6.04 ± 0.89 | 0.15 ± 0.03 | 0.40 ± 1.14 | 0.50 ± 0.14 |
| *S. chathamica* | 7 | 115.68 ± 23.24 | 37.25 ± 7.49 | 11.29 ± 1.41 | 6.44 ± 0.84 | 0.14 ± 0.05 | 4.30 ± 3.20 | 0.59 ± 0.14 |
| *S. fulvida* | 6 | 97.60 ± 14.52 | 54.33 ± 7.49 | 6.45 ± 1.41 | 3.58 ± 0.63 | 0.18 ± 0.03 | 13.87 ± 3.61 | 0.11 ± 0.16 |
| *S. godleyi* | 9 | 130.29 ± 12.83 | 57.77 ± 11.23 | 5.58 ± 0.94 | 3.64 ± 0.54 | 0.14 ± 0.03 | 11.35 ± 3.23 | 0.25 ± 0.08 |
| *S. longicarinata* | 5 | 112.80 ± 18.31 | 44.96 ± 5.72 | 3.79 ± 0.66 | 2.63 ± 0.40 | 0.17 ± 0.04 | 0.28 ± 0.85 | 0.58 ± 0.14 |
| *S. microphylla* | 22 | 113.18 ± 18.19 | 35.64 ± 4.63 | 6.98 ± 1.43 | 3.90 ± 0.66 | 0.14 ± 0.03 | 3.29 ± 3.03 | 0.52 ± 0.15 |
| *S. molloyi* | 3 | 82.87 ± 5.54 | 29.0 ± 2.75 | 7.12 ± 1.23 | 3.44 ± 0.40 | 0.22 ± 0.04 | 1.77 ± 1.71 | 0.49 ± 0.09 |
| *S. prostrata* | 4 | 15.10 ± 4.46 | 9.45 ± 2.26 | 3.68 ± 0.80a | 2.03 ± 0.21 | 0.17 ± 0.04 | 0.03 ± 0.30 | 0.19 ± 0.05 |
| *S. tetraptera* | 4 | 139.70 ± 12.40 | 21.70 ± 1.63 | 29.52 ± 3.93 | 7.24 ± 0.78 | 0.14 ± 0.04 | 16.29 ± 6.00 | 0.90 ± 0.22 |

sometimes slightly crowded or overlapping, glabrous or with only a few appressed hairs (Fig. 1G), and they do not taper noticeably toward the apex.

The cluster analysis (Fig. 2) provides a graphical representation of groups formed by the overall similarity of the 11 leaf characters. Analyses of this type often suffer from distortion because the similarity relationships rarely exhibit a strictly nested hierarchical structure (de Queiroz & Good 1997). However, the cophenetic correlation provides an indication of this type of distortion (Sokal & Rohlf 1962). In this analysis the cophenetic correlation coefficient is 0.9103 which suggests a good fit between the similarity matrix and the phenogram.

The cluster analysis identified two main clusters (Fig. 2), which have a comparatively low level of similarity (c. 0.64). This separation reflects differences in leaf characters between the two groups, such as hair type and the number of leaflets. One main cluster includes all specimens of *S. fulvida* and *S. godleyi*, which form two distinct subgroups with about 0.70 similarity. Each of these subgroups contains a single species, within which all specimens merge at >0.85 similarity.

The second main cluster comprises five distinct subgroups, within which all specimens have a high level of similarity (>0.80). Four of these subgroups correspond to *S. tetraptera*, *S. chathamica*, *S. prostrata*, and the Chilean *S. cassioides*, and each of these species links in turn with the large fifth subgroup that includes *S. longicarinata*, *S. microphylla*, and *S. molloyi*.

*Sophora longicarinata*, *S. microphylla*, and *S. molloyi* have a very high level of similarity (>0.90) and are poorly separated. However, *S. longicarinata* forms a group near the base of the cluster in which four of the five specimens cluster together. Two specimens of *S. molloyi* group together, while the third (c2) is placed in the middle of the large and otherwise homogenous *S. microphylla* group. When the similarities of the individual samples are considered, *S. molloyi* specimen c2 shows its highest similarity (96%) to *S. microphylla* specimen m11, but overall its average similarity is highest to *S. molloyi* (94.0%), *S. microphylla* (92.7%), and *S. longicarinata* (91.5%). Furthermore, the other specimens of *S. molloyi* (c1, c3) have their highest similarity to each other and, significantly, their second-closest similarity to *S. molloyi* specimen c2. Therefore, the position of specimen c2 reflects a high level of similarity between *S. microphylla* and *S. molloyi* for overall leaf characters, but it may also be an artifact of the clustering techniques (de Queiroz & Good 1997).

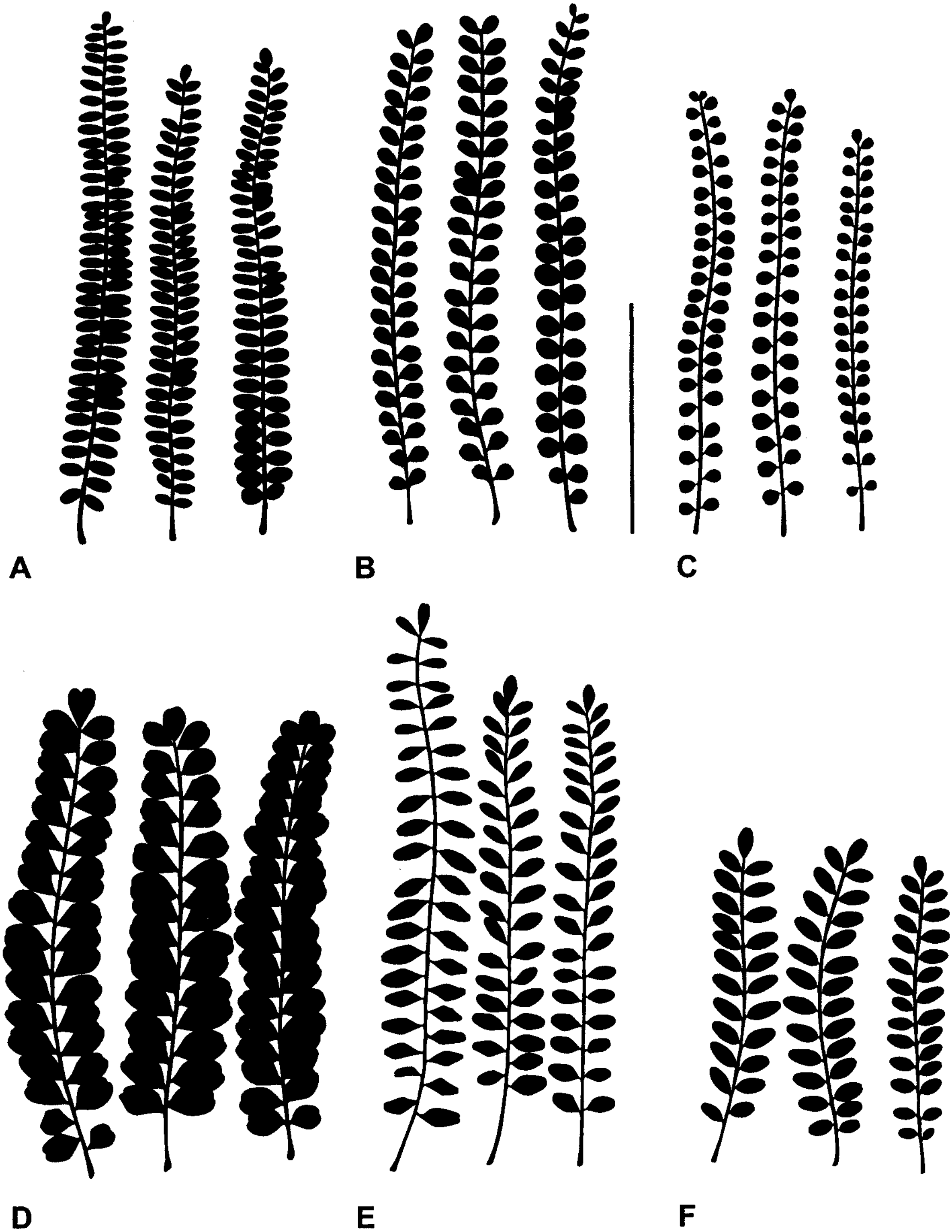



**Fig. 3** Leaf silhouettes of New Zealand indigenous species of *Sophora*. **A**, *S. fulvida*, from Whatipu; **B**, *S. godleyi*, from Taumarunui; **C**, *S. longicarinata*, from Leatham River valley; **D**, *S. chathamica*, from Chatham Island; **E**, *S. microphylla*, from Great Island, Rakaia River; **F**, *S. molloyi*, from Stephens Island. Scale bar = 5 cm. All specimens from adult plants cultivated at Lincoln, Canterbury, New Zealand.

**Table 3** Distribution of some characters in New Zealand species of *Sophora* that are allied to *S. microphylla*; based on wild-collected material.

| Character | *S. chathamica* | *S. fulvida* | *S. godleyi* | *S. longicarinata* | *S. microphylla* | *S. molloyi* |
|---|---|---|---|---|---|---|
| Growth habit | tree; juvenile growth habit absent | tree; juvenile growth habit absent | tree; juvenile growth habit absent | tree or shrub; main main stems often produced at ground level, sometimes suckering; juvenile growth habit absent | tree; juvenile growth habit present | shrub, usually broader than high; juvenile growth habit absent |
| Leaflet number | 25–55 | 61–91 | 47–75 | 35–52 | 30–50 | 23–37 |
| Leaflet size | 6.0–16.0 × 4.0–8.0 mm; distal leaflets usually smaller than proximal leaflets | 1.8–7.5 × 1.2–4.5 mm; distal leaflets usually smaller than proximal leaflets | 2.0–8.0 × 2.0–5.0 mm; distal leaflets usually smaller than proximal leaflets | 3.3–5.8 × 2.5–3.1 mm; distal and proximal leaflets similar in size | 4.5–12.5 × 2.3–5.7 mm; distal and proximal leaflets usually similar in size | 5.0–12.0 × 2.0–6.0 mm; distal and proximal leaflets similar in size |
| Leaflet shape | broadly elliptic, broadly obovate, broadly ovate, obovate to ± orbicular | elliptic to elliptic-oblong, occasionally narrowly obovate | ovate to broadly elliptic, sometimes ± orbicular | orbicular, obovate, to oblong-obovate | elliptic, broadly elliptic, obovate, to ovate, sometimes ± orbicular | elliptic, elliptic-oblong, to broadly elliptic |
| Leaf colour | light green to green | green to slightly grey-green | grey to green-grey | dark green | light green to green | dark green |
| Petiolule | present | usually absent; leaflets sessile | present | present | present | present |
| Leaf hairs | appressed, straight | appressed, decumbent, or spreading; predominantly straight or sometimes twisted | appressed, decumbent, spreading or patent; curly, curved, or twisted, but also straight | appressed, straight | appressed, straight | appressed, straight |
| Leaflet density | crowded and overlapping | often crowded and sometimes overlapping | sometimes crowded, but not overlapping | overlapping to distant | distant, not crowded or overlapping | distant, not crowded or overlapping |

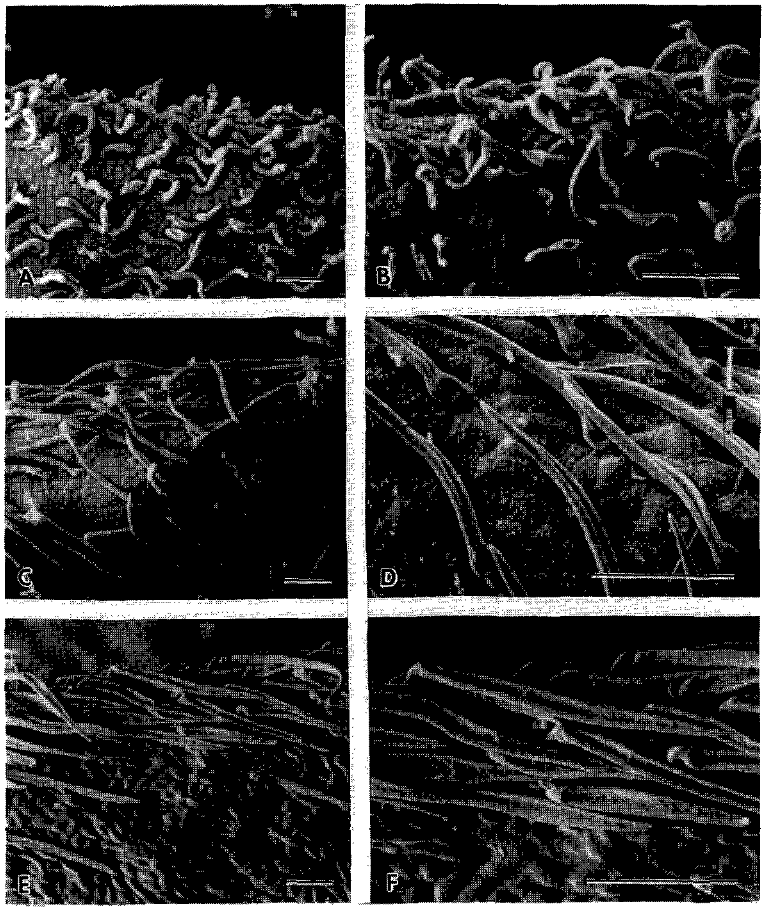



**Fig. 4** Leaf hairs. **A**, **B**, *S. godleyi*; **C**, **D**, *S. fulvida*; **E**, **F**, *S. chathamica*. Scale bars = 100 μm. The leaf hairs of *S. cassioides*, *S. longicarinata*, *S. microphylla*, *S. molloyi*, *S. prostrata*, and *S. tetraptera* are similar to *S. chathamica*.



The cluster analysis shows that, despite overlapping ranges being exhibited by most leaf characters (Fig. 1), it is possible for six species to be recognised using the combined leaf characters. The other three species, *S. longicarinata*, *S. microphylla*, and *S. molloyi*, exhibit a high degree of similarity but also have a tendency to form groups, notwithstanding the placement of the one specimen of *S. molloyi*. The close relationship of *S. longicarinata*, *S. microphylla*, and *S. molloyi* using leaf characters highlights the past difficulties of resolving variation in *S. microphylla* sens. lat. These three species are also separated by other floral and growth habit characters.

The clustering analysis result is noteworthy given that the samples were originally collected over a wide geographic area, including from throughout New Zealand, the Chatham Islands, several localities in Chile, and Gough Island (Appendix 1).

## Growth habit

The revision presented here also emphasises growth habit as providing important taxonomic characters. *S. microphylla* sens. str. differs from the other New Zealand species treated in this revision (*S. chathamica*, *S. fulvida*, *S. godleyi*, and *S. molloyi*) in being a tree with a distinct divaricate and/or strongly flexuose juvenile (sapling) phase, and by its yellow-brown to orange-brown juvenile stems. This juvenile phase lasts for varying lengths of time and attains its greatest expression in the south and south-east of the South Island where it may persist for over 20 years (Godley & Smith 1977; Godley 1979a). Adult plants of *S. microphylla* have a robust, upright, and spreading growth habit with stout trunks and branches. Some forms from Maruia (north Canterbury) and in the vicinity of Taihape (central North Island) have a distinctly weeping adult growth habit (Godley & Smith 1977; Godley 1979a).

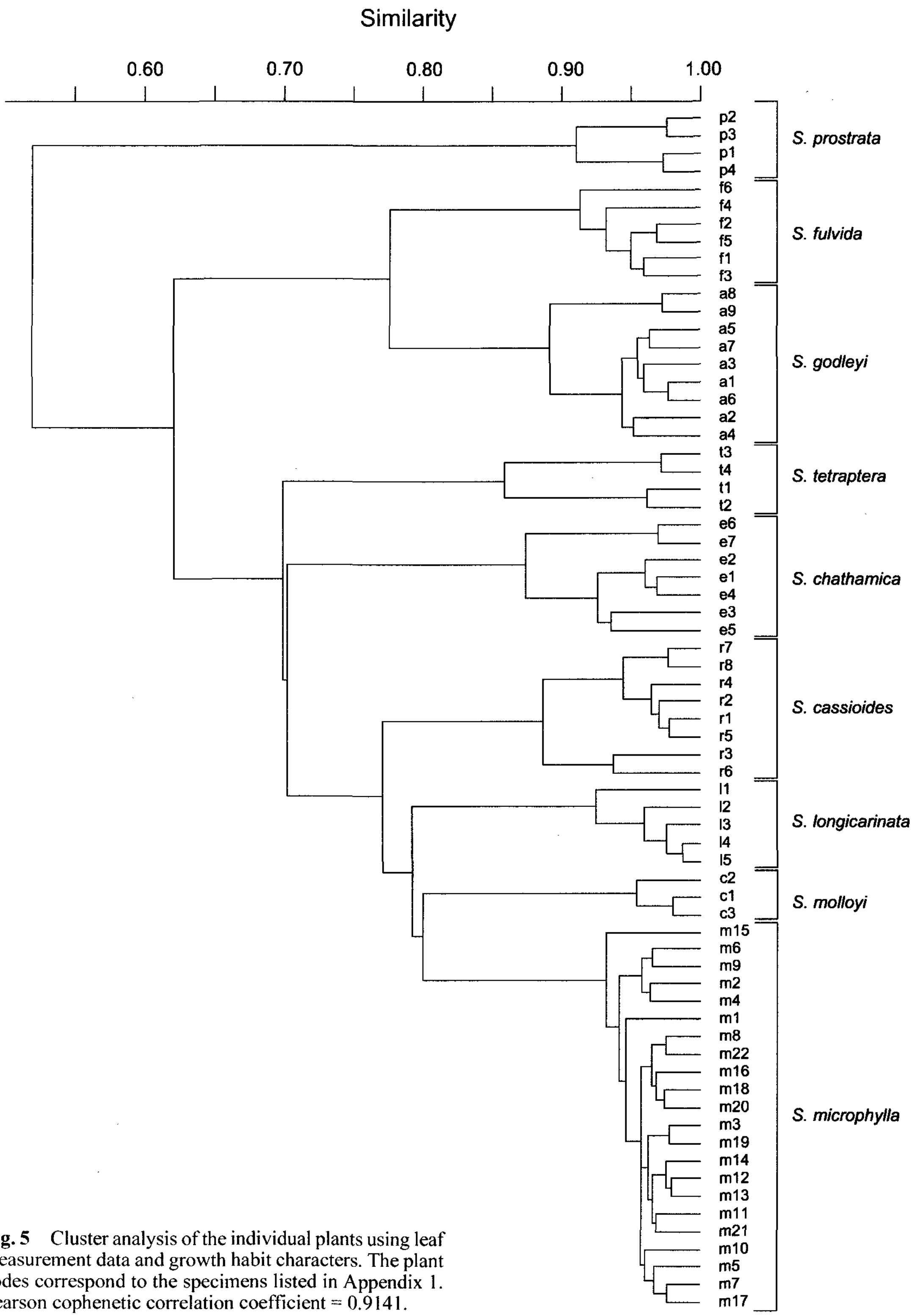



**Fig. 5** Cluster analysis of the individual plants using leaf measurement data and growth habit characters. The plant codes correspond to the specimens listed in Appendix 1. Pearson cophenetic correlation coefficient = 0.9141.

*Sophora cassioides*, *S. chathamica*, *S. fulvida*, *S. godleyi*, *S. longicarinata*, *S. molloyi*, *S. prostrata*, and *S. tetraptera* lack an obvious divaricate and/or strongly flexuose juvenile phase, and develop an adult growth form during their sapling phase of growth. The branchlets of these species are usually brown or brown-green. *S. cassioides*, *S. chathamica*, *S. fulvida*, *S. godleyi*, and *S. tetraptera* are trees with an upright and spreading growth habit, stout trunks, and main branches that develop well above ground level.

*Sophora longicarinata* forms a densely branched shrub or an upright small tree with several trunks and main branches (Heenan 1998a). It often has branches arising from and below ground level, and sometimes rhizomes are produced that extend well beyond the canopy. Shrubs up to 1.5 m high can comprise an extensive network of underground branches and rhizomatous shoots. *S. prostrata* is a shrub with strongly interlaced branchlets on the juvenile and adult, and it too can have a suckering growth habit (Godley & Smith 1977; Godley 1979a).

*Sophora molloyi* also has a shrub habit and is usually broader than high, its branchlets are not interlaced, it branches above ground level, it lacks suckers or rhizomes, and it often has decumbent and prostrate main branches and long trailing stems. Its distinctive growth habit is maintained in cultivation (Heenan 1992). The growth habit of *S. molloyi* differs from the shrub form of *S. longicarinata* in being broader and more robust, having spreading, decumbent, and prostrate main branches, and not producing underground stems or rhizomes.

The cluster analysis of the 11 leaf and 4 growth habit characters (Fig. 5) provided a greater resolution of species groups than the cluster analysis of leaf characters only (Fig. 2). The cophenetic correlation coeffiecient of 0.9141 indicates a good fit between the similarity matrix and the phenogram. In this analysis *S. prostrata* occupies an isolated position joining distantly to the remaining species, and its position has changed significantly from the cluster analysis of leaf characters (Fig. 2). The remaining specimens form two main groups (as in the first analysis), with the smaller of these containing all the specimens of *S. fulvida* and *S. godleyi*. Within this cluster the specimens from each species separate into two smaller groups, within which the specimens have about or greater than 90% similarity.

In the second and larger main cluster the specimens of *S. tetraptera*, *S. chathamica*, *S. cassioides*, *S. longicarinata*, and *S. molloyi* all form distinct clusters which link in turn to the cluster of *S. microphylla* specimens. The specimens in all of these small clusters show >85% similarity. A notable feature of this analysis is that the specimens of *S. molloyi*, *S. longicarinata*, and *S. microphylla* form distinct species clusters. This reflects the importance of using growth habit characters and leaf characters together for distinguishing these species.

### Floral characters

The flowers of *S. cassioides*, *S. chathamica*, *S. fulvida*, *S. godleyi*, *S. longicarinata*, *S. microphylla*, and *S. molloyi* are very similar in having five free and yellow petals, comprising one standard petal, two wing petals, and two keel petals, free filaments, and a cupulate calyx. The similar floral structure among these species reflects a successful breeding strategy, with little need for morphological differentiation. *Sophora longicarinata* is distinguished from the other species by the pedicel often being twisted (Heenan 1998a). Particularly short petals are characteristic of *S. molloyi* (range 20–30 mm). The other species have a range of (15–)30–50 mm, with some plants of *S. microphylla* from Canterbury sometimes having short petals (Godley & Smith 1977).

Flowering times of the New Zealand species of *Sophora* differ. *S. molloyi* flowers for a long period during the winter months (April–October), and the flowers are usually sparsely dispersed throughout the densely leafy canopy. The other species typically flower from August to December, although some populations or individual plants of *S. microphylla* can flower as early as May, and the flowers are usually abundantly dispersed throughout the canopy. *S. godleyi* and *S. microphylla* differ in their flowering times in the Wanganui area; *S. microphylla* flowers from August to early October, and *S. godleyi* flowers from October to December. *S. fulvida* flowers during October and November.

### Distribution, biogeography, and evolution

The species of *Sophora* recognised in this revision are New Zealand endemics, and no species is now indigenous to both New Zealand and Chile. The restriction of *S. microphylla* sens. str. to New Zealand is of significance, as its divaricate juvenile growth form is a feature that occurs in other endemic species from different genera (Cockayne 1928). The evolution of this type of growth form is generally regarded as a response to environments unsuitable for normal growth because of the high and unpredictable incidence of frost, wind, and drought in New Zealand (McGlone & Webb 1981). Such

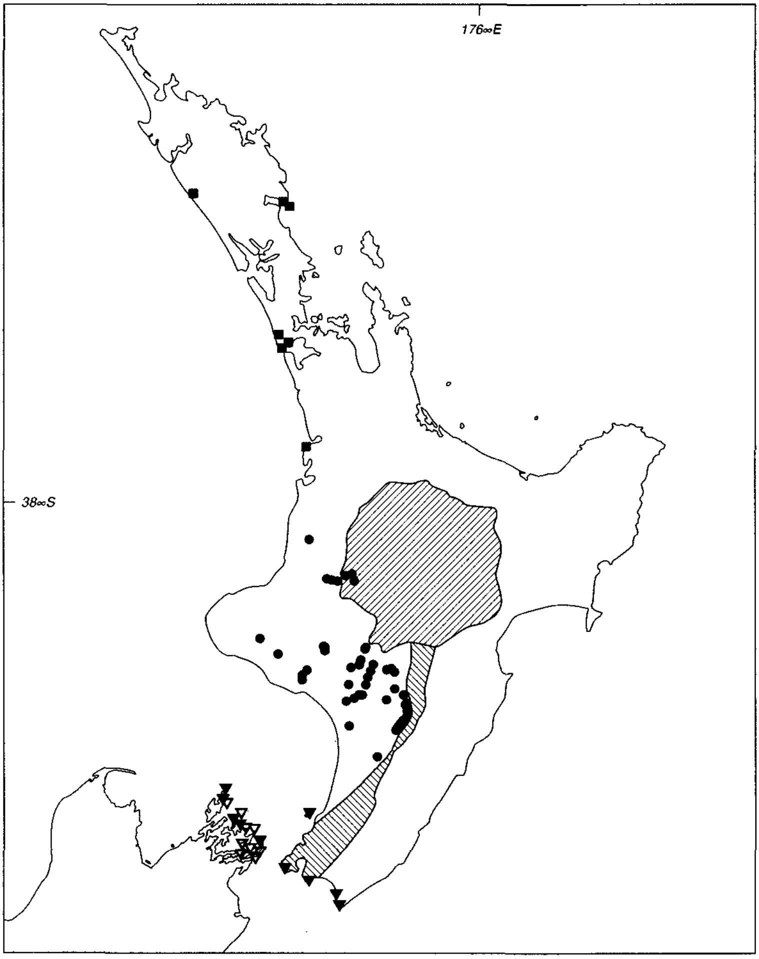



**Fig. 6** Distribution of *Sophora fulvida* ■, *S. godleyi* ●, and *S. molloyi* ▼ (herbarium vouchers); ▽ (S. Courtney pers. comm.). Greywacke of the Ruahine and Tararua ranges \\\\ (from Kingma 1962, 1967); Taupo Ignimbrite //// (from Wilson & Walker 1985).



conditions occurred from the Waikato Basin to southern South Island during the Quaternary (Brodie 1957; McIntyre & McKeller 1970; Moar 1971, 1980; McGlone et al. 1978), and were likely to have been locally common north of the Waikato Basin (M. McGlone pers. comm.).

The origin of the juvenile divaricate growth form in *S. microphylla* has been the subject of two differing hypotheses. Firstly, Cockayne (1901, 1910, 1912, 1919, 1927, 1928) suggested that the juvenile growth form arose in response to drought conditions "at the time of the glacial period" (Cockayne 1912). With this hypothesis Cockayne also regarded *S. prostrata* as a permanent juvenile form that was derived from the divaricating juvenile of *S. microphylla*. Secondly, Godley (1979a) proposed that *S. microphylla* sens. lat. may have originated from hybridisation between *S. prostrata* and *S. tetraptera*. Godley (1979a) considered that in the progeny of the natural hybrid distinct populations were formed in which various characters segregated independently. With this hypothesis the distinctive juvenile form of *S. microphylla* sens. str. would be derived from *S. prostrata*, and in species such as *S. longicarinata* the absence of a juvenile form would be obtained from *S. tetraptera* (Godley 1979a; Heenan 1998a).

The juvenile phase in *S. microphylla* is also naturally variable and persists longer in plants from southern and eastern South Island than in plants from other parts of New Zealand; perhaps this phase is more persistent in extreme climatic conditions (Godley 1975, 1979a; Godley & Smith 1977). Alternatively, the juvenile form may not be as well developed in the North Island due to gene exchange with *S. chathamica*, *S. fulvida*, *S. godleyi*, and *S. tetraptera*, species that are sympatric with *S.*

*microphylla* and which lack the divaricating juvenile growth form.

Hypotheses of the origin and evolution of species of *Sophora* through processes such as neoteny and hybridisation would best be tested by independent data sets such as those derived from DNA data.

*Sophora fulvida*, *S. godleyi*, and *S. longicarinata* are unique in sharing a number of distributional, ecological, and character similarities. Each is confined to specific base-rich substrates of relatively local distribution (i.e., volcanic rock, papa*, or marble/limestone; Fig. 6; Heenan 1998a); they predominantly occur on eroding and unstable bluffs, rock outcrops, and hillslopes; they lack a juvenile phase; and they flower when relatively young. Their lack of a juvenile growth form allows for quick growth following colonisation and establishment, and early flowering ensures reproductive success early in the life cycle. The bluff/rock outcrop habitats of *S. fulvida*, *S. godleyi*, and *S. longicarinata* are not subject to temperature inversions and excessive frost, they are dynamic habitats due to continual erosion and weathering and have high fertility soils, and they are often free of dense vegetation. These three species are similar in having small and numerous leaflets, characteristics that may reflect either a common ancestor or convergence due to similar ecological conditions. In contrast, *S. tetraptera*, which also lacks a juvenile growth form, has large leaflets and is commonly associated with lowland temperate/maritime forest amongst *Pseudopanax arboreus*†, *Pittosporum tenuifolium*, and *Griselinia littoralis*. Its large leaves may give it a competitive advantage in sites that are moderately well vegetated. However, it will sometimes grow on open, severely eroding or disturbed sites such as on the Volcanic Plateau ignimbrites.

The restriction of *S. godleyi* to Pleistocene limestone, sandstone, and siltstone to the west of the greywacke of the Ruahine Range (Fig. 6) is of particular interest, as parent materials of a similar lithology occur to the east of the Ruahine Range in the Wairarapa and Hawke's Bay areas (Kingma 1962, 1967). This suggests that *S. godleyi* may have evolved after the uplift of the Ruahine Range during the Pleistocene (Beu et al. 1981) or late Pliocene (Browne 1978). Alternatively, it may have evolved prior to this and been more widespread, but its current distribution is now constrained by other environmental gradients.

Another factor limiting the distribution of *S. godleyi* may be the effects of the Taupo eruption at 1850 yr B.P. (Wilson et al. 1980; Sparks et al. 1995). The northern and north-eastern distributional limits of *S. godleyi* correspond with the approximate extent of the Taupo ignimbrite (Wilson & Walker 1985; Froggatt & Lowe 1990; Fig. 6). The only minor exceptions to this are near Taumaranui where *S. godleyi* is within the ignimbrite zone (Fig. 6). At these sites *S. godleyi* was collected from river or roadside papa banks which underlie the ignimbrite and have been exposed by erosion. The ignimbrite flows from the Taupo eruption have covered a large area of papa, which previously extended across the central North Island toward East Cape and south into the Wairarapa. Throughout much of the area covered by the ignimbrite the original forest was destroyed (Wilmshurst & McGlone 1996), and *S. godleyi* may have been displaced because of its preference for base-rich papa.

Other species that are endemic to papa and within the distributional range of *S. godleyi* are *Anaphalioides subrigida*, *Brachyglottis turneri*, and *Corybas papa*, while *Corybas orbiculatus* and *C. iridescens*, though not truly endemic to these calcareous rocks, seem to be more common on them than elsewhere (Molloy & Irwin 1996; St George et al. 1996). *S. godleyi* along with *Selliera rotundifolia* (Heenan 1997), *Mazus novaezeelandiae* subsp. *novaezeelandiae* (Heenan 1998b), and *Olearia gardneri* (Heads 1998) are newly recognised taxa endemic to the lower North Island floristic gap, an area previously noted for having few endemic species (Cockayne 1928; McGlone 1985; Rogers 1989).

*Sophora chathamica* is like *S. microphylla* in being more of a generalist in its habitat requirements than *S. fulvida*, *S. godleyi*, and *S. longicarinata*. It is most common in coastal/lowland sites, and the southern limit of the northern populations (Fig. 7) corresponds to approximately latitude 39°S, a

* The term "papa" is Maori for earth (Williams 1985). In the North Island of New Zealand papa is frequently used as a vernacular for a range of usually calcareous Tertiary marine siltstones and mudstones widespread throughout Taranaki and central and south-eastern North Island (Gage 1980). These rocks, although highly fertile, are extremely susceptible to slumping and slipping because of their unusually high content of smectite clays (Gage 1980).

† Nomenclature of plants other than *Sophora* follows Allan (1961), Breitwieser & Ward (1997), Brownsey & Smith-Dodsworth (1989), Connor & Edgar (1987), Edgar & Connor (2000), and Moore & Edgar (1980).

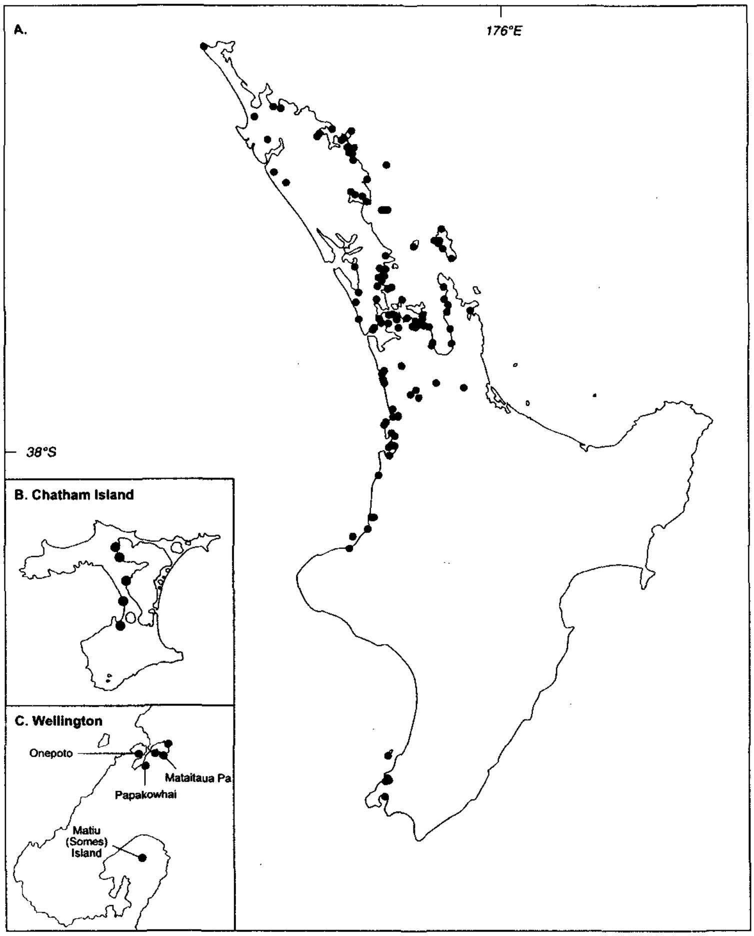



**Fig. 7** Distribution of *Sophora chathamica* in New Zealand. **A**, North Island; **B**, Chatham Island; **C**, Wellington area enlarged.



common biogeographic boundary (Wardle 1963; McGlone 1985). The disjunct distribution of *S. chathamica* from the central North Island to Wellington (Fig. 7) may be of biogeographic significance as the area it is absent from corresponds to the lower North Island floristic gap (Cockayne 1928; McGlone 1985; Rogers 1989).

An alternative explanation for the gap in the distribution may be that the Wellington occurrences of *S. chathamica* are not natural, but rather are the result of deliberate Maori plantings. The distribution of the species in the Wellington Region (e.g., Kapiti Island, Porirua, Papakowhai, Paremata, and Matiu/Somes Island) corresponds with the location of settlements and pa sites (Department of Lands & Survey 1976; Fig. 7) occupied by hapu of Ngati Toa, Ngati Raukawa, Ngati Tama, and Ngati Mutunga iwi (tribal groups) (Burns 1980; Park 1995). This confederation of western Waikato and Taranaki tribes invaded and displaced the local Wellington Maori in a series of protracted wars which lasted until the 1820s. The Ngati Raukawa have traditions that they deliberately planted kowhai (*Sophora* spp.) from their former Waikato tribal territory to the Wellington region, as a medicinal and an ornamental plant (H. Rauweru pers. comm.). Based on this information, and the spiritual and medicinal significance of species of *Sophora* to Maori people, we cannot discount the possibility of *S. chathamica* being deliberately introduced to the Wellington area from the Waikato. It has also been suggested to us that *S. chathamica* may not have naturally occurred on the Chatham Islands, perhaps having been taken there by Maori (B. P. J. Molloy pers. comm.).

Trans-oceanic long-distance dispersal of seed is an important factor in the biogeographic and evolutionary history of species of *Sophora* sect. *Edwardsia* (e.g., Hurr et al. 1999). The recognition that the Chilean and Gough Island *S. cassioides* is distinct from the New Zealand species of *Sophora* is significant as it invalidates the argument for a recent (e.g., late Holocene) trans-pacific distribution for *S. microphylla* (e.g., Guppy 1906; Wace & Dickson 1965; Sykes & Godley 1968; Markham & Godley 1972; Hurr et al. 1999). However, it is still likely that *S. cassioides* is derived from an ancestor that dispersed from New Zealand to South America, as the predominant direction of the ocean current circulation patterns is from New Zealand to localities further east (e.g., Fleming 1962, p. 94; Sykes & Godley 1968).

*Sophora cassioides* is similar to *S. chathamica* in lacking a juvenile growth habit and in some of its leaf characters (e.g., large leaflets) (Fig. 1, 5). Seeds of *S. chathamica* and *S. microphylla* are known to float from the main New Zealand islands to outlying islands. Indeed, *Sophora* seeds collected from beaches on the Kermadec Islands (Sykes & Godley 1968; E. J. Godley pers. comm.) and the Chatham Islands (B. P. J. Molloy pers. comm.; PJdL pers. obs.) have proven to be *S. chathamica* and *S. microphylla* sens. str. (e.g., sample m22, Fig. 2), respectively, when germinated and grown on. It is not improbable that the seeds of either of these species could have floated from New Zealand to Chile during, for example, the early Quaternary, and that the influences of different environmental gradients and reproductive isolation have resulted in the evolution of new morphological and genetic characteristics. Unfortunately, the relationships of species in *Sophora* sect. *Edwardsia* are poorly resolved, and there is no phylogenetic study that includes all species (e.g., Peña et al. 1993; Peña & Cassels 1996; Hurr et al. 1999). Therefore, the closest relatives of *S. cassioides* are not known.

## Hybridism

Many of the difficulties in identifying species of *Sophora* in New Zealand can be attributed to putative hybrids. Fieldwork throughout the North Island verifies that the widespread *S. microphylla* hybridises with *S. chathamica*, *S. fulvida*, *S. godleyi*, and *S. tetraptera*, as do *S. longicarinata* (PBH pers. obs.) and *S. prostrata* in the South Island (Cockayne 1923; Cockayne & Allan 1934). *S. tetraptera* hybridises with *S. molloyi* and, possibly, *S. godleyi*. $F_1$ plants can generally be detected at most sites due to being intermediate in a number of morphological characters. Backcross and $F_2$ hybrids are probably also relatively common at some sites as there is often a continuum in variation between the putative parental species.

Interspecific gene exchange has probably always been quite common throughout the history of *Sophora* in New Zealand: when two or more species occur in the same general area, pollinating birds could easily pollinate trees of the different species by flying between them. However, in a natural ecosystem each species' edaphic and habitat requirements are rather specific, and this has probably prevented hybrid plants from being particularly common. Furthermore, natural habitats that could be suitable for hybrid plants have perhaps been uncommon. In the North Island, in particular, it is possible that gene exchange has occurred more extensively over the last 1000 years due to the breakdown of species' ecological requirements that has resulted from modification of the vegetation by Maori and European settlers. Such phenomena are considered to have also influenced species' distributions and opportunities for gene exchange in *Chionochloa* (Molloy et al. 1963; Connor 1967).

The effect of habitat disturbance by man is unknown, but these influences may be significant for two reasons. Firstly, species that were formerly separated by their different habitat requirements may be brought together. In this situation interspecific hybridisation may occur more readily due to the closer proximity of the two species. Secondly, new and novel habitats may be favoured by hybrid plants which were previously unable to compete with either parental species in their preferred habitats.

Different flowering times are likely to provide some reproductive isolation, although if the end of flowering for one species corresponds with the onset of flowering in another, there is potential for interspecific hybridisation. For example, *S. microphylla* flowers from August to October when it occurs in the distributional range of *S. godleyi*, which flowers from October to December.

### Sophora chathamica × S. microphylla

As was noted by Cockayne & Allan (1934), *S. chathamica* and *S. microphylla* often grow together in Northland, Auckland, and the western Waikato, and hybrids frequently occur between the two species. These hybrids are sometimes difficult to detect because the juvenile form is often similar to *S. microphylla* in being moderately divaricating or flexuose. However, as with *S. chathamica*, the transition from young to adult plants is often rapid (1–2 years), and the intermediate-phase branches are more curved and drooping. The hybrids frequently lack the upright shoots that are typical of young *S. chathamica*.

The leaves on young plants of *S. chathamica* and *S. microphylla*, and their hybrids, are not readily distinguishable from each other as the leaflets in all cases are few, round, and widely spaced. Hybrids are most readily distinguished by their adult foliage. In the leaves emerging from the leaf-bud in hybrid plants the apical leaflets are often crowded and overlapping (e.g., AK 237042, AK 237043), but as they mature they become less crowded and more distant from each other. In mature leaves the leaflets are frequently elliptic (e.g., AK 237022), in some respects resembling those of the hybrids between *S. microphylla* and *S. tetraptera*. However, the *S. microphylla* attributes are often evident, and include a greater tendency for spacing between leaflets, a green rather than light-green colour, fewer hairs, and the trees are distinctly taller, with the branches often weeping.

Sophora fulvida × S. chathamica

*Sophora chathamica* and *S. fulvida* hybrids occur at several localities in the Waitakere Ranges and Whangarei Heads. In the Waitakere Ranges there appear to be complex patterns of hybridism between *S. chathamica*, which usually occurs around forest margins, and *S. fulvida*, which is predominantly on volcanic rock outcrops. For example, at Mill Bay and Armour Bay, *S. chathamica* (CHR 513371, 513378) was present, as were *S. chathamica* × *S. fulvida* hybrids (CHR 513379, 513381), but *S. fulvida* was absent. However, *S. fulvida* is present at nearby Cornwallis Bay (CHR 512963), and it is possible that pollen was taken from these plants to the nearby *S. chathamica* by nectar-feeding birds. Alternatively, *S. fulvida* may have once occurred at Mill Bay and Armour Bay. At Huia and Whatipu the distributions of *S. chathamica* and *S. fulvida* overlap and hybrids are present. The situation at Whatipu is particularly interesting as *S. chathamica* (CHR 513385) grows on alluvial substrates near Whatipu Stream, and *S. fulvida* (CHR 513387) is on nearby rubble slopes and the disturbed margins of Whatipu Road. At this site several adult hybrid trees were present near the roadside (CHR 513388), as were seedlings and saplings of both parental species, and possibly hybrids, on the roadside bank.

The *S. fulvida* × *S. chathamica* hybrids are usually intermediate between the two parental species. The leaves are generally mid-sized and moderately pubescent. On some hybrid plants the new leaves are very much like *S. fulvida* in that the leaflets are crowded and smaller. In the field there are often plants that do not look like typical *S. fulvida* or *S. chathamica* (e.g., CHR 513374), but these are not as intermediate as would be expected with $F_1$ hybrids. These may be $F_2$ or backcross hybrids.

Sophora godleyi × S. microphylla

*Sophora microphylla* occurs throughout the range of *S. godleyi*. It is sometimes present in only small numbers (e.g., 3–4 plants) among much larger populations of *S. godleyi*, but at other sites it is often at least as common as *S. godleyi*. Where *S. microphylla* and *S. godleyi* are both relatively common there is often almost a continuum of variation between the two species, and backcrosses, $F_2$, and subsequent hybrid generations are almost certainly present. Where *S. microphylla* is present in small numbers, hybrids between it and *S. godleyi* are absent or scarce, but when present they are usually intermediate between the putative parents and therefore are most likely $F_1$ hybrids.

Sophora godleyi × S. tetraptera

Some wild collections of *Sophora* from the Manawatu and Rangitikei rivers approach *S. godleyi*, but they are not typical. It is possible that these plants are the result of hybridisation with *S. tetraptera*. For example, near Mangaweka, Rangitikei River, a population includes three or four plants of *S. godleyi* (e.g., CHR 517187), and other plants that have a rather variable assemblage of leaf sizes and shapes (e.g., CHR 517186, 517188–517190). The latter plants are most probably hybrids with *S. tetraptera*, but this species is not currently known from the site.

Another example occurs near Palmerston North where *S. godleyi* (CHR 855, CHR 177875) and *S. tetraptera* (CHR 33497) occur together along with possible hybrids (CHR 21232, CHR 33496). A collection from Vinegar Hill, Rangitikei River, has large and few leaflets (e.g., CHR 107822), approaching the size of those of *S. tetraptera*, but the hairs are appressed, spreading, ascending, and often twisted as in *S. godleyi*. However, these specimens have larger leaves and a greater number of appressed hairs than is typical of *S. godleyi*, and are probably hybrids between *S. godleyi* and *S. tetraptera*.

Sophora microphylla × S. tetraptera

Hybrids between *S. microphylla* and *S. tetraptera* often occur where these two species grow together in Hawke's Bay and southern Wellington. The hybrids lack the strongly divaricate juvenile form of *S. microphylla*, but are more flexuose than juvenile *S. tetraptera*. The leaves of the hybrids are intermediate in a number of characters between those of *S. microphylla* and *S. tetraptera* (CHR 182739–182741). The leaflets are fewer in number, larger, and hairier than those of *S. microphylla*, and greater in number, smaller, and less hairy than those of *S. tetraptera*. The leaflets are usually lanceolate to narrowly elliptic and 10–15 mm long.

### Sophora molloyi × S. tetraptera

The southern limit for *S. tetraptera* is near Cape Palliser, Cook Strait. At one site along the Cape Palliser Road (NZMS 260 S28/947652) it grows with *S. molloyi*. Here *S. tetraptera* is represented by about five trees on a hillslope, and a population of several hundred *S. molloyi* occurs on a steep, dry, wind-swept, rock and shingle face. An alluvial fan below the cliff face is dominated by *Kunzea ericoides*, but there also occur three plants of *S. tetraptera*, about 10 plants of *S. molloyi*, and several dozen putative hybrids between the two species.

The hybrid plants exhibit a variety of forms, but they generally differ from the parental species in their upright and spreading habit (lacking the heavily branched and shrubby habit of *S. molloyi*), slightly folded leaflets (flat in *S. tetraptera*, subconduplicate in *S. molloyi*), variable leaflet size and colour (grey-green in *S. tetraptera*, green in *S. molloyi*), and they were flowering heavily and more or less deciduous at flowering time (similar to *S. tetraptera*). It is likely that either $F_2$ or perhaps backcross plants were present, as some plants had leaflets of intermediate size and were flowering heavily like *S. tetraptera*, but they were similar to *S. molloyi* in having a shrubby habit, subconduplicate dark green leaflets, and being evergreen at flowering time. A few plants were similar to *S. tetraptera* in being tree-like, but like *S. molloyi* they had dark green leaves and were moderately leafy at flowering time.

## Conclusions

Based on the above information on leaf, flower, and growth habit characteristics, hybridisation, habitat preferences, and distribution, *S. microphylla* is circumscribed to include only those plants with distant leaflets, a moderate number of appressed leaf hairs, and a distinct divaricating and/or strongly flexuose juvenile phase. *S. microphylla* var. *fulvida* is shown to have a unique set of morphological characters and specific habitat preferences. This evidence supports the recognition of *S. microphylla* var. *fulvida* at species rank, and a new combination is therefore provided below. Other plants previously included within *S. microphylla* have different leaf attributes and lack a juvenile phase, and these are placed in the reinstated *S. chathamica*. The study also provides evidence for segregating two new species of *Sophora* from *S. microphylla*. One of these is from the Wanganui/Rangitikei area and the other the Cook Strait district. We name and describe these below.



## TAXONOMIC TREATMENT

***Sophora*** L., *Sp. Pl.*: 373 (1753)

### Key to the New Zealand species (see also Table 1)

This key is only for New Zealand species of *Sophora*, and does not include hybrid material. If the key does not work, the plant material should be checked to see if it is of hybrid origin.

*1* Shrub, branches at or near ground level and usually slender .......... *2*
Tree, branches well above ground level and usually thick .......... *5*

*2* Branchlets not interlaced, usually grey to grey-brown glabrous to sparsely hairy .......... *3*
Branchlets interlaced, usually yellow-brown to orange-brown, sparsely to moderately hairy .......... *4*

*3* Shrub usually wider than high; main branches spreading to decumbent, sometimes prostrate, underground branches and rhizomes absent; leaves with 23–37 leaflets; leaflets 5.0–12.0 × 2.0–6.0 mm, elliptic, elliptic oblong, to broadly elliptic, sparsely hairy; Kapiti Island, islands in Cook Strait, southern headlands of North Island, dry and exposed windy bluffs .......... ***5. S. molloyi***
Shrub usually of similar width and height; main branches upright to spreading, underground branches and rhizomes usually present, often with numerous branches near the base; leaves with 35–52 leaflets; leaflets 3.3–5.8 × 2.5–3.1 mm, orbicular, obovate, to oblong-obovate, usually more or less glabrous; northern Nelson, western Marlborough, marble and limestone rock outcrops .......... ***S. longicarinata***

*4* Branchlets interlaced on juvenile and adult; leaves < 3 cm long, leaflet pairs 1–5, usually glabrous; standard petal orange; pods lacking wings; seeds dark brown; eastern South Island, dry grey scrub communities ........ ***S. prostrata***
Branchlets interlaced in juvenile only; leaves > 3 cm, leaflet pairs > 6, sparsely to moderately hairy; flowers usually absent, if present standard petal yellow; pods usually absent, if present winged; seeds yellow or yellow-brown; North and South islands, terraces and hillslopes ........ **4. *S. microphylla***

*5* Ovary and leaves with hairs spreading, curved and/or twisted; leaflets densely hairy ........ *6*
Ovary and leaves with hairs appressed, straight; leaflets not densely hairy, or if densely hairy greater than 15 mm long ........ *7*

*6* Leaves with 61–91 leaflets; leaflets elliptic to elliptic-oblong, occasionally narrowly obovate, usually sessile; leaflet hairs appressed, decumbent, or spreading, predominantly straight and sometimes twisted; northern North Island, andesitic and basaltic volcanic rock outcrops ........ **2. *S. fulvida***
Leaves with 47–75 leaflets; leaflets ovate, broadly elliptic, to sometimes more or less orbicular, with a more or less distinct petiolule; leaflet hairs appressed, decumbent, spreading, or patent, predominantly curly, curved, or twisted; central North Island, siltstone, sandstone, and mudstone (papa) ........ **3. *S. godleyi***

*7* Leaves with less than 23 leaflets; leaflets more than 18 mm long, three times longer than wide, narrowly elliptic to elliptic-oblong, densely hairy; eastern North Island, terraces and hillslopes ........ ***S. tetraptera***
Leaves with more than 24 leaflets; leaflets less than 16 mm long, length usually less than twice their width, elliptic, broadly elliptic, obovate, broadly obovate, ovate, broadly ovate, oblong to more or less orbicular, glabrous or moderately hairy ........ *8*

*8* Juvenile growth habit present, leaflets 4.5–12.5 × 2.3–5.7 mm; distal and proximal leaflets usually similar in size, distant, not crowded or overlapping, elliptic, broadly elliptic, obovate to ovate, sometimes more or less orbicular, usually moderately hairy; North and South islands, terraces and hill country ........ **4. *S. microphylla***
Juvenile growth habit absent; leaflets 6.0–16.0 × 4.0–8.0 mm, distal leaflets usually smaller than proximal leaflets, crowded and overlapping, broadly elliptic, broadly obovate, broadly ovate, obovate to more or less orbicular, moderately hairy; North Island and Chatham Islands, coastal and lowland hill country ........ **1. *S. chathamica***
Juvenile growth habit absent; leaflets 3.3–5.8 × 2.5–3.1 mm, distal and proximal leaflets similar in size, overlapping to distant, orbicular, obovate, to oblong-obovate, usually more or less glabrous; northern Nelson, western Marlborough, marble and limestone rock outcrops ........ ***S. longicarinata***



**1. *Sophora chathamica*** Cockayne, *Trans. & Proc. New Zealand Inst. 34*: 270/319 (1902)
coastal kowhai

≡ *Sophora microphylla* var. *chathamica* (Cockayne) Yakovlev, *Trudy Leningradskii Khimiko – Farmatsevticheskii Instit 21*: 57 (1967).

LECTOTYPE (here designated, Fig. 8): WELT 19447, Coll. *L. Cockayne*, Feb. 1901. No. 7404. Growing on the limestone, Te Whanga Lagoon, Chatham Island. Herbarium of L. Cockayne. Sophora tetraptera Mill. var. chathamica Cockayne var. nov. ined. Perhaps a distinct species. Annotated: "Type specimen, L.C., 16 xii 31". Isolectotype: AK 4973.

DESCRIPTION (Fig. 3, 4): Moderate to large tree up to 20 m high, with 1 main trunk or several prominent main branches; main branches spreading to upright. Divaricating and/or strongly flexuose juvenile branchlets usually absent, or very weakly flexuose; branchlets densely pubescent, becoming glabrous with age; hairs appressed, straight. Seedlings and juveniles moderately to densely leafy, leaves with increasing numbers of leaflets. Leaflets on juveniles 4.4–9.0 × 4.4–7.5 mm, ± orbicular to very broadly obovate, crowded, usually overlapping. Leaves on adults up to 15 cm long, imparipinnate, petioles and rachis channelled above, leaflets 25–55. Leaflets on adults 6.0–16.0 × 4.0–8.0 mm, broadly elliptic, broadly obovate, broadly ovate, obovate to ± orbicular, distal leaflets usually smaller than proximal leaflets, usually crowded and overlapping, adaxial surface light green to green, dull, abaxial surface lighter than adaxial surface and slightly concave; apices retuse to obtuse; bases obtuse; petiolules 0.3–0.5 mm long, distinct; petioles,

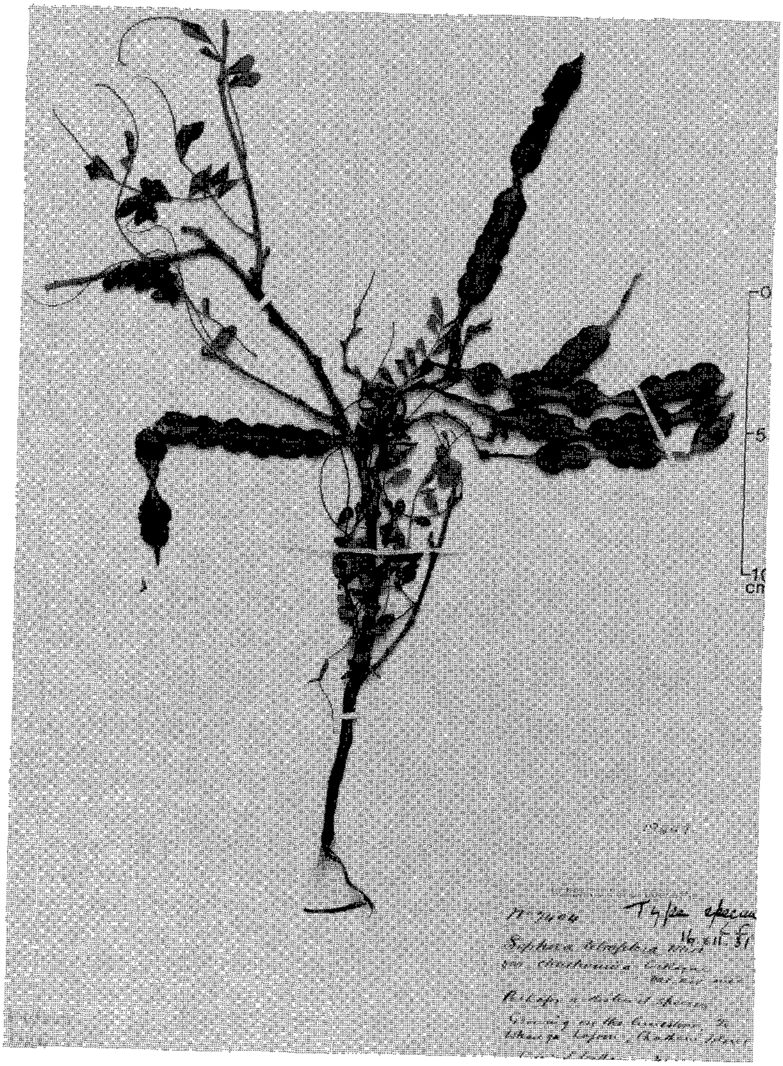


**Fig. 8** Lectotype of *Sophora chathamica.*



rachides, petiolules, and leaflets usually pubescent, hairs up to 0.4 mm long, appressed, straight. Inflorescences racemose, with up to 11 flowers; peduncle and rachis 15–45 mm long; pedicels up to 25 mm long, each subtended by a bract; bract 2–3 mm long; peduncles, rachides, pedicels, bracts, and calyces moderately to densely pubescent, hairs brown to yellow-brown, appressed. Calyx 8–10 × 10–13 mm, cupulate, rim shallowly lobed, with deeper notch adjacent to standard. Corolla yellow; keel petal blade 29–43 × 9–11 mm, wing petal blade 25–42 × 9–11 mm, standard petal blade 25–34 × 20–25 mm; petals with distinct claws, 4–6 mm long. Stipe 3.5–7.0 mm long, glabrous to sparsely pubescent. Ovary 17–27 mm long, densely pubescent; hairs up to 0.5 mm long, off-white to light brown, appressed, straight. Style 10–13 mm long, glabrous to sparsely pubescent. Filaments 27–35 mm long. Anthers 2.0–3.5 × 0.8–1.5 mm. Fruit 50–180 mm long, 4-winged, brown, sparsely to moderately pubescent, with up to 12 seeds. Seeds 5.5–8.0 × 4.0–5.0 mm, oblong, elliptic to ± orbicular, yellow to light yellow-brown. FL Aug–Nov; FT Oct–Sep. Chromosome number $n = 9$ or $2n = 18$ (Hair & Beuzenberg 1966; CHR 102308, 102309, 102310, 102311).

REPRESENTATIVE SPECIMENS: NORTHLAND: Kaitaia, ?*R. H. Matthews*, Aug 1897, AK 103321; Taipa, *R. C. Cooper*, 10 Jan 1950, AK 123982; Whangaruru Peninsula, Bland Bay, *L. J. Forester*, 12 Aug 1997, AK 233995; Kerikeri, *R. C. Cooper*, 2 Dec 1949, AK 35825; Whangarei, Helena Bay, *R. C. Cooper*, 21 Oct 1961, AK 126169; Whangaruru Harbour, *L. J. Forester*, 12 Aug 1997, AK 233995; Aorangi Island, *E. K. Cameron 8501 & P. J. de Lange*, 8 Aug 1996, AK 228841; Whatupuke Island, *B. S. Parris*, 7 Feb 1968, AK 123082. AUCKLAND: Auckland, *T. Kirk*, Sep 1871, AK 11351; Remuera, Herb. *T. Kirk*, Oct 1865, WELT 19439; Broadwood, *E. J. Godley*, 23 Nov 1961, CHR 185888; Mahurangi Heads, *E. J. Godley*, 20 Nov 1961, CHR 185878; Waitakere Ra., *W. R. B. O[liver]*, 16 Jan 1937, WELT 14018 right-hand specimen; Orakei Basin, *R. O. Gardner 4366*, 7 Oct 1984, AK 174337; Waiwera River, *P. B. Heenan & P. J. de Lange*, 26 Aug 1998, CHR 517103; Warkworth, *P. B. Heenan & P. J. de Lange*, 26 Aug 1998, CHR 517110; Maunganui Island, *P. B. Heenan & P. J. de Lange*, 26 Aug 1998, CHR 517111; Little Barrier Island, *F. Shakespear*, 1900–1902, AK 127498; Rakino Island, *R. O. Gardner 4366*, 7 Oct 1984, AK 168434; Rangitoto Island, Islington Bay, *R. O. Gardner 5244*, 18 Jul 1987, AK 178668; Great Barrier Island, Port Fitzroy, *R. C. Cooper*, 28 Aug 1962, AK 91954. WAIKATO: Port Waikato-Waikaretu Rd, *P. J. de Lange 3554 & R. O. Gardner*, 2 Sep 1998, AK 237027; Raglan Harbour, Ponganui Inlet, *P. J. de Lange 3559 & R. O. Gardner*, 2 Sep 1998, AK 237028; Raglan Harbour, Te Akau Wharf, *P. J. de Lange 3558 & R. O. Gardner*, 2 Sep 1998, AK 237026; Kawhia Harbour, Te Arero Point, *P. J. de Lange 3571 & L. Collins*, 17 Sep 1998, AK 237024; Mokau River, *P. J. de Lange 3568 & L. Collins*, 17 Sep 1998, AK 237025. COROMANDEL PENINSULA: Long Bay, Coromandel, *R. C. Cooper*, 18 Feb 1966, AK 126485; Papa Aroha, *R. Cooper*, 18 Feb 1966, AK 106574. TARANAKI: Taranaki, Tongaporutu River, *P. J. de Lange 3570 & G. M. Crowcroft*, 20 Sep 1998, AK 237023. WELLINGTON: Porirua Harbour, *T. Kirk*, 27 Sep 1883, WELT 19371; Porirua City, Papakowhai, *P. B. Heenan & P. J. de Lange*, 21 Oct 1998, CHR 517665. CHATHAM ISLANDS: Te Whanga Lagoon, *K. P. Olsen*, 31 Jan 1978, AK 150425; Waitangi Village, *P. J. de Lange CH1 & G. M. Crowcroft*, 20 Feb 1996, AK 227144; Te Whanga Lagoon, *P. J. de Lange CH37 & G. M. Crowcroft*, 22 Feb 1996, AK 227163.

DISTRIBUTION (Fig. 7): *S. chathamica* occurs in mainly coastal and lowland sites in Northland, Auckland, Coromandel Peninsula, Waikato, northern Taranaki, Wellington, and on the Poor Knights Islands, Hen & Chickens Islands, Little Barrier Island, Great Barrier Island, and Chatham Island. Cockayne (1902) reported *S. chathamica* on Pitt Island and South East Island, but there are no representative herbarium vouchers and it is currently not known from there (G. Taylor & P. Dilks pers. comm.). *S. chathamica* may have also occurred in Nelson, as a cultivated specimen from Treadwell's garden in the Hutt Valley, Wellington, is labelled "originally from Nelson" (WELT 47998, *B. C. Aston*). No other collections of *S. chathamica* are known from Nelson, and it is most probable that this collection was from a cultivated plant.

HABITATS: *S. chathamica* is restricted to coastal sites on limestone, igneous rock outcrops/cliffs, alluvium, stream banks, the margins of mangrove swamp, and hill slopes. It is frequently associated with mixed podocarp/hardwood forest and coastal scrub. On the Hauraki Gulf islands it usually occurs in association with base-rich igneous rocks, or on the richly manured soils associated with petrel colonies (e.g., Poor Knights Islands). In the Chatham Islands it is mainly coastal and occurs on limestone and basalt bluffs chiefly on the western margin of Te Whanga Lagoon (Cockayne 1902).

ETYMOLOGY: The specific epithet *chathamica* refers to the locality from which the species was originally collected.

**2. *Sophora fulvida*** (Allan) Heenan & de Lange, comb. and stat. nov. Waitakere kowhai

≡ *Sophora microphylla* var. *fulvida* Allan, *Fl. N. Z. I*: 370/976 (1961).

HOLOTYPE (Fig. 9): Anawhata, *L. B. Moore*, CHR 8205! Isotype: CHR 8206!

DESCRIPTION (Fig. 3, 4): Small to moderate tree, up to 10 m high, with 1 main trunk or several prominent main branches; main branches upright to spreading. Divaricating and/or strongly flexuose juvenile branchlets absent; branchlets densely pubescent, becoming glabrous with age; hairs appressed, decumbent, or spreading, predominantly straight or sometimes twisted. Seedlings and juveniles moderately to densely leafy, leaves with increasing numbers of leaflets. Leaflets on juveniles 4.0–6.6 × 2.0–3.0 mm, elliptic, elliptic-oblong to narrowly obovate, ± glabrous, to sparsely, and then moderately pubescent, crowded, often overlapping. Leaves on adults up to 14 cm long, imparipinnate, petioles and rachides channelled above, leaflets 61–91. Leaflets on adults 1.8–7.5 × 1.2–4.5 mm, elliptic to elliptic-oblong, occasionally narrowly obovate, sometimes ± orbicular, distal leaflets usually smaller than proximal leaflets, often crowded and sometimes

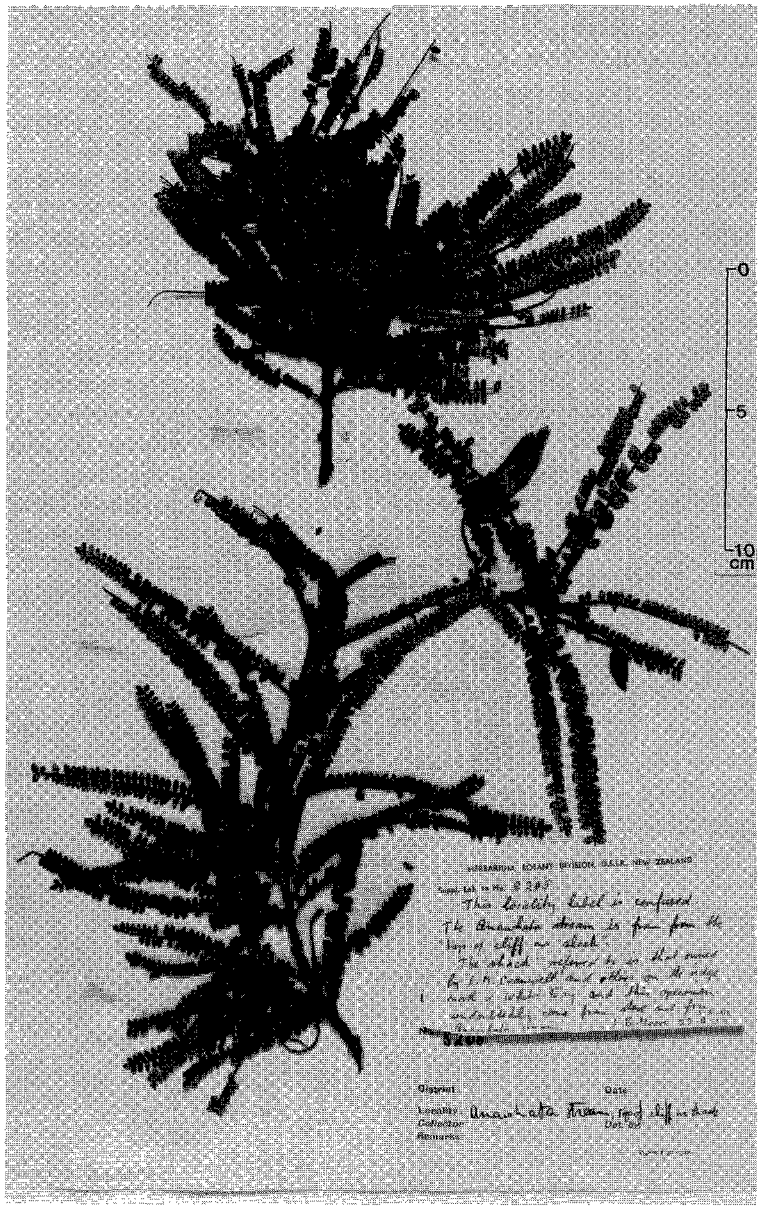



**Fig. 9** Holotype of *Sophora fulvida.*



overlapping, adaxial surface dull green, green, to slightly grey-green, abaxial surface lighter than adaxial surface and slightly concave; apices retuse, obtuse to subacute; bases obtuse; sessile, or occasionally with petiolules up to 0.3 mm long on leaflets > 6 mm long; margin often thickened on abaxial surface; petioles, rachides, petiolules, and leaflets usually ± pubescent or villous, hairs 0.2–0.6 mm long, appressed, decumbent, or spreading, predominantly straight or sometimes twisted. Inflorescences racemose, with up to 7 flowers; peduncle and rachis 14–35 mm long; pedicels up to 20 mm long, each subtended by a bract; bracts 2–3 mm long; peduncles, rachides, pedicels, bracts, and calyces moderately to densely pubescent, hairs brown, appressed, decumbent, or spreading. Calyx 10–13 × 8–15 mm, cupulate, rim shallowly lobed, with deeper notch adjacent to standard. Corolla yellow; keel petal blade 31–40 × 9–14 mm, wing petal blade 25–40 × 7–12 mm, standard petal blade

23–35 × 11–18 mm; petals with distinct claws, 4.0–6.5 mm long. Stipe 7–9 mm long, glabrous to sparsely pubescent. Ovary 15–21 mm long, densely pubescent; hairs 0.4–0.7 mm long, off-white to light brown, appressed, decumbent, or spreading, straight or sometimes twisted. Style 6–12 mm long, glabrous to sparsely pubescent. Stigma fringed with short hairs. Filaments 25–35 mm long. Anthers 1.8–2.0 × 0.9–1.0 mm. Fruit 60–190 mm long, 4-winged, brown, sparsely to moderately pubescent, with up to 11 seeds. Seeds 5.0–7.5 × 4.0–5.2 mm, oblong, yellow to yellow-brown. FL Oct–Nov; FT Jan–May. Chromosome number $n = 9$ (Hair & Beuzenberg 1966; CHR 200325).

REPRESENTATIVE SPECIMENS: NORTHLAND: Maunganui Bluff, *A. E. Esler & A. G. Dobbins*, 23 Feb 1977, AK 219545; Maunganui Bluff, *R. C. Cooper*, 9 Jun 1966, AK 219545; Ocean Beach, Whangarei Heads, *T. W. Mellor*, Jan 1956, WELT 14118; high hill above Manaia Gardens, *T. W. Mellor*, Jan 1957, WELT 64913; Mt Manaia, *P. B. Heenan*, 27 Aug 1997, CHR 513392; Bream Head, *P. B. Heenan*, 27 Aug 1997, CHR 513396. AUCKLAND: Piha, *R. C. Cooper*, 18 Oct 1967, AK 127438; Anawhata, *E. K. Cameron 7991*, 10 Dec 1994, AK 221393; Whatipu, *P. B. Heenan & P. J. de Lange*, 26 Aug 1997, CHR 513387; Little Huia, *P. B. Heenan & P. J. de Lange*, 26 Aug 1997, CHR 513375. WAIKATO: near Te Papanui-iti Point, Mt Karioi, *P. J. de Lange 3623*, 20 Jul 1998, AK 236322.

DISTRIBUTION (Fig. 6): *S. fulvida* occurs in Northland, Auckland, and Waikato. In Auckland it occurs at numerous sites throughout the Waitakere Ranges, and in Northland on Maunganui Bluff, Bream Head, and near Mt Manaia. The southern limit is near Mt Karioi (Waikato), at the southern entrance to Raglan Harbour.

HABITATS: *S. fulvida* grows on base-rich volcanic submarine basalts, basalts, andesites, and both andesitic and basaltic breccia (Thompson 1961; Schofield 1967; Hayward 1983). In the Waitakere Ranges *S. fulvida* predominantly occurs on rock outcrops protruding from the dense mixed conifer/hardwood forest, although plants are now sometimes seen along disturbed road verges (e.g., on parts of Whatipu Road and Mt Donald McLean Road). At Bream Head *S. fulvida* usually occurs among rock rubble or on rock outcrops among mixed podocarp/hardwood forest.

ETYMOLOGY: The specific epithet *fulvida* refers to the colour of the leaf hairs in the original collection from Anawhata.



**3. *Sophora godleyi*** Heenan & de Lange, sp. nov.
Godley's kowhai; papa kowhai

DIAGNOSIS: A *S. microphylla* ramificatione juvenili non divaricata, foliis cinereis et foliolis pluris late ellipticis vel orbiculatis pilis eorum appressis vel effusis arcuatis torsivisque, et in habitatione in arenosaxo, limosaxo et calcareo substrato differt.

Differs from *S. microphylla* in lacking a divaricating juvenile growth form, having grey leaves, the leaflets being more numerous, broadly elliptic to more or less orbicular, and the leaf hairs being appressed, spreading or ascending, and curved or twisted. Grows on sandstone, mudstone, and other calcareous substrates.

HOLOTYPUS (Fig. 10): New Zealand, Rangitikei, Horopito Stream, Pohangina Valley East Rd, *P. J. de Lange & P. B. Heenan*, 20 Oct 1998, CHR 517648; Isotypi: AK, BISH, BM, BRI, CHR, CANU, HO, K, LE, NZFRI, OTA, P, SGO, WAIK, WELT, WELTU.

DESCRIPTION (Fig. 3, 4): Small to large tree, often up to 25 m high, with 1 main trunk or several prominent main branches; main branches upright to spreading. Divaricating and/or strongly flexuose juvenile branchlets absent; branchlets densely pubescent, becoming glabrous with age; hairs appressed, spreading or patent, predominantly curly, curved, or twisted, also straight. Seedlings and juveniles moderately to densely leafy, leaves with increasing numbers of leaflets. Leaflets on juveniles 6.0–9.0 × 3.5–6.0 mm, ovate, ± orbicular to elliptic, glabrous to sparsely pubescent, becoming moderately pubescent, not crowded or overlapping. Leaves on adults up to 17 cm long, imparipinnate, petioles and rachides channelled above, leaflets 47–75. Leaflets on adults 2.0–8.0 × 2.0–5.0 mm, ovate to broadly elliptic, sometimes ± orbicular, distal leaflets usually smaller than proximal leaflets, sometimes crowded but not overlapping, adaxial surface grey to green-grey, abaxial surface lighter than adaxial surface and often concave; apices usually retuse to sometimes rounded; bases obtuse; petiolules up to 2 mm long, often only up to 0.5 mm long on leaflets < 3 mm long; petioles, rachides, petiolules, and leaflets usually pilose, sometimes villous, hairs 0.2–0.6 mm long, appressed, decumbent, spreading or patent, predominantly curly, curved, or twisted, but also straight. Inflorescences racemose, with up to 7 flowers; peduncle and rachis 20–40 mm long; pedicels up to 20 mm long, each subtended by a bract; bracts 1.5–3.5 mm long; peduncles, rachides, pedicels, bracts, and calyces moderately to densely pubescent;

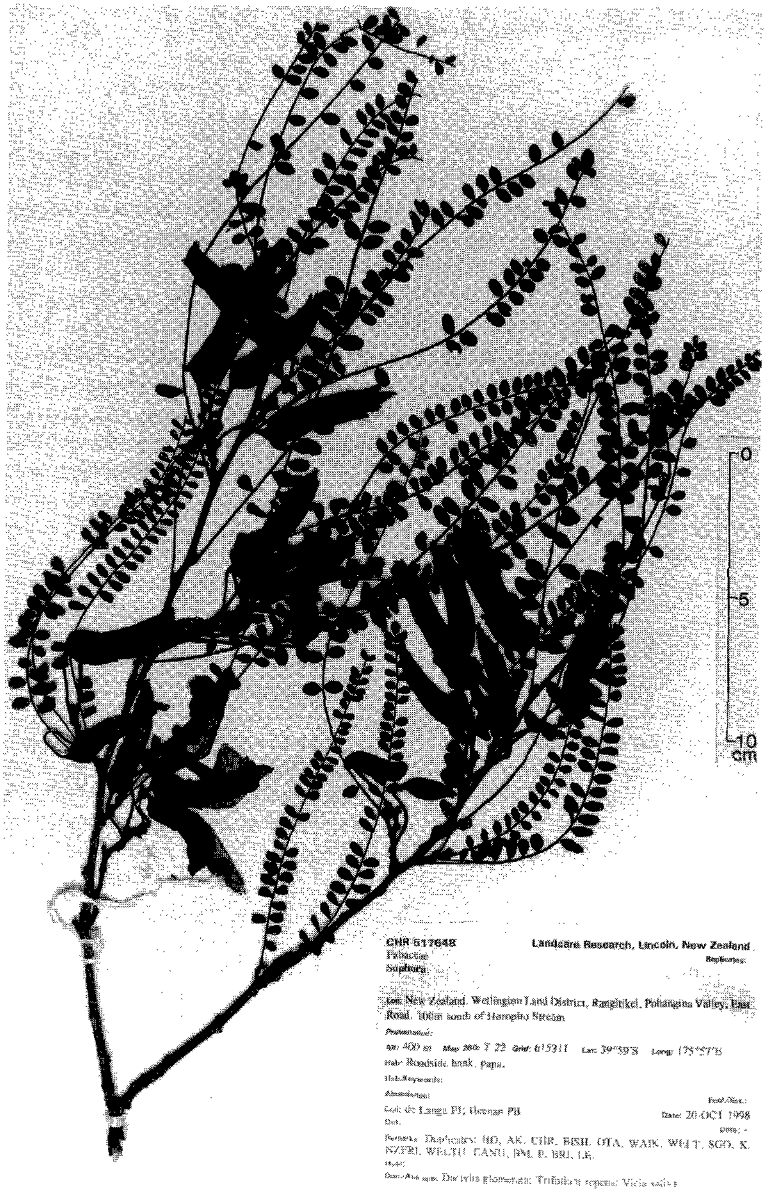



**Fig. 10** Holotype of *Sophora godleyi*.

hairs brown, appressed, decumbent, spreading, or patent. Calyx 9–13 × 10–16 mm, cupulate, rim shallowly lobed, with deeper notch adjacent to standard. Corolla yellow; keel petal blade 34–50 × 9–14 mm, wing petal blade 25–48 × 6–9 mm, standard petal blade 20–35 × 11–21 mm; petals with distinct claws, 5.0–6.5 mm long. Stipe 6–11 mm long, ± glabrous. Ovary 17–23 mm long, densely pubescent; hairs 0.4–0.7 mm long, off-white to light brown, appressed, spreading or patent, straight, curved, or twisted. Style 12–14 mm long, exerted beyond anthers, glabrous or with a few twisted hairs. Stigma fringed with short hairs. Filaments 25–40 mm long; anthers 1.8–2.0 × 0.9–1.0 mm. Fruit 60–120 mm long, 4-winged, brown, sparsely to moderately pubescent, with up to 11 seeds. Seeds 5–8 × 4–5 mm, oblong, yellow to yellow-brown. FL Oct–Dec; FT Jan–May.

REPRESENTATIVE SPECIMENS: TARANAKI: Mokauiti Stream, near Aria, *P. J. de Lange 4391*, 11

Aug 2000, AK 250570; Aukopae, near Taumarunui, *V. D. Zotov*, 16 Jul 1929, CHR 3234; Otunui, *M. F. Merrett*, 28 Oct 1996, WAIK 15875; upper Patea River, *E. J. Godley*, 25 Oct 1967, CHR 182750–182752; Rotorangi, Patea River, *P. A. Suisted*, 17 May 1998, CHR 491134/516537; Tangarakau Gorge Scenic Reserve, *P. J. de Lange*, 31 Jul 2000, CHR 536480. WELLINGTON: *W. Colenso 2319*, [no date], WELT 23904; Wanganui River, *J. H. MacMahon*, 15 Dec 1935, WELT 19613; Taumarunui, *E. J. Godley*, 16 Jun 1963, CHR 145213; lower Waitotara River, *E. J. Godley*, 25 Oct 1967, CHR 182768; Waitotara Valley Road, *P. B. Heenan*, 22 Aug 1998, CHR 517155; Pipiriki, *D. Petrie*, Feb 1923, WELT 14112; south of Pipiriki, *P. J. de Lange 3521*, 2 Sep 1997, CHR 515519; Whangaehu River, *R. K. Ward*, 29 Mar 1937, WAIK 9825; Mangawhero River Road, *P. B. Heenan*, 28 Aug 1998, CHR 515571; Turakina Valley Road, *P. B. Heenan*, 21 Aug 1998, CHR 517140; east of Kauangaroa, *P. Heenan*, 21 Aug 1998, CHR 517153; Taihape, *W. R. B. Oliver*, 31 Jan 1954, WELT 64593; Taihape, *P. B. Heenan*, 21 Aug 1998, CHR 517191; Mangaweka, *P. B. Heenan*, 20 Aug 1998, CHR 517187; Pohangina River valley, *P. B. Heenan*, 20 Aug 1998, CHR 517172; Pohangina Valley East Road, *P. B. Heenan & P. J. de Lange*, 20 Oct 1998, CHR 517785; Fielding, Kitchener park, *L. M. Cranwell*, 26 Jun 1932, AK 103430/103434; Palmerston North, *V. D. Zotov*, 5 Jan 1929, CHR 855; Manawatu River, *A. J. Healy*, 1 Jul 1938, CHR 33496.



DISTRIBUTION (Fig. 6): *S. godleyi* is restricted to the North Island where it occurs in eastern and southern Taranaki, King Country, Wanganui, Rangitikei, and Manawatu. *S. godleyi* is particularly abundant in the middle and upper parts of the catchments of the Pohangina, Oroua, Rangitikei, Turakina, Whanganui, and Mangawhero rivers, and is present at several sites along the Patea and Waitotara rivers and near Palmerston North.

*Sophora godleyi* is sympatric with *S. microphylla* thoughout its range. The two species have been collected together from the Pohangina River (CHR 517178, 517183), Oroua River (CHR 517184, 517185), Hautapu River (CHR 517138, 517139), Turakina River (CHR 517144, 517145), and Waitotara River (CHR 517157, 517158). *S. godleyi* is also partially sympatric with *S. tetraptera* as the distributions of the two species overlap near Palmerston North and Mangaweka.

A single collection of *S. godleyi* is labelled as coming from Dannevirke (*Colenso*, WELT 23905, right-hand specimen), to the east of the Ruahine Mountains. During October 1998 we unsuccessfully searched for *S. godleyi* in the south-eastern North Island, in the vicinity of the Colenso collecting localities of Norsewood and Dannevirke (Bagnall & Petersen 1948), and throughout the Wairarapa, south to Cook Strait. Only *S. microphylla* and *S. tetraptera* occur in this area. It is most likely that the Colenso specimen of *S. godleyi* has been inadvertently mixed with a collection of *S. microphylla* from Dannevirke. Another collection of *S. godleyi*, in Herb T. Kirk from the "Banks of the Wilberforce Canterbury D^r^ von Haast March 1879" (WELT 19460), is also likely to have been mislabelled.

HABITATS: *S. godleyi* usually occurs on limestone and papa rock (i.e., calcareous mudstones, siltstones, and sandstones) of marine origin (Lensen et al. 1959; Kingma 1962; Hay 1967), and on alluvium derived from these parent materials. It has also been collected from old sand dunes in the vicinity of Bulls and Lake Alice.

ETYMOLOGY: The specific epithet *godleyi* honours E. J. Godley, Director (1958–1980) of Botany Division, DSIR, who has undertaken studies of *Sophora* in New Zealand (e.g., Sykes & Godley 1968; Godley 1975, 1979a, 1985, 1989; Godley & Smith 1977). It also acknowledges his important contribution to the present study through the extensive collection of *Sophora* he established at Lincoln, Canterbury, New Zealand, during the late 1950s and 1960s.

ILLUSTRATION: Eagle (1982, fig. 75) as *S. microphylla*, from a cultivated plant originally from Wanganui.

**4. *Sophora microphylla*** Aiton, *Hort. Kew. 2*: 43 (1789) small-leaved kowhai

≡ *Edwardsia microphylla* (Aiton) Salisb., *Trans. Linn. Soc. Lond. 9*: 299 (1808).

≡ *Edwardsia grandiflora* var. *microphylla* (Aiton) Hook.f., *Fl. N.Z. 1*: 52 (1852).

≡ *Sophora tetraptera* var. *microphylla* (Aiton) Hook.f., *Handb. N.Zeal. fl.*: 53 (1864).

LECTOTYPE (*fide* Heenan 1998a): *Sophora microphylla*, 1769–70, "Nova Zelandia, prope Opuragi, Totara-nui – Sir J. Banks & Dr Solander (1769)" (on back of sheet), bottom leafy piece with three mature fruit, BM (photocopy seen).

DESCRIPTION (Fig. 3): Moderate to large tree up to 25 m high, with 1 main trunk or several prominent main branches; branches weeping, spreading and ascending. Divaricating and/or strongly flexuose juvenile branchlets present; branchlets often strongly interlaced, yellow-brown to orange-brown, glabrous to sparsely pubescent, becoming increasingly pubescent during the transition to adult branchlets; hairs appressed, straight. Seedlings and juveniles sparsely to moderately leafy, leaves with increasing numbers of leaflets. Leaflets on juveniles 3.0–5.8 × 2.3–4.9 mm, broadly obovate to orbicular, ± glabrous to sparsely pubescent, distant, not crowded or overlapping. Leaves on adults up to 15 cm long, imparipinnate, petioles and rachides channelled above, leaflets 30–50. Leaflets on adults 4.5–12.5 × 2.3–5.7 mm, elliptic, broadly elliptic, obovate to ovate, sometimes ± orbicular, distal and proximal leaflets usually similar in size, not crowded or overlapping, distant, adaxial and abaxial surfaces ± planar, adaxial surface light green to green, abaxial surface light green; apices retuse to rounded; bases cuneate to obtuse; petiolules 0.4–1.1 mm long, distinct; petioles, rachides, petiolules, and leaflets sparsely to moderately pubescent, hairs 0.2–1.0 mm long, appressed, straight. Inflorescences racemose, with up to 7 flowers; peduncle and rachis 10–25 mm long; pedicels up to 16 mm long, each subtended by a bract; bracts 1.8–3.4 mm long; peduncles, rachides, pedicels, bracts, and calyces moderately to densely pubescent, hairs brown to yellow-brown, usually appressed but sometimes weakly spreading. Calyx 5–11 × 7–10 mm, cupulate, rim shallowly lobed, with deeper notch adjacent to standard. Corolla yellow; keel petal blade 18–50 × 7–13 mm, wing petal blade 18–50 × 6–11 mm, standard petal blade 20–35 × 14–25 mm; petals with distinct claws, 4.0–8.0 mm long. Stipe 7–10 mm long, glabrous to moderately pubescent. Ovary 8–17 mm long, densely pubescent; hairs up to 0.5 mm long, off-white to light brown, appressed to spreading, straight. Style 10–15 mm long, glabrous to sparsely pubescent. Stigma glabrous or fringed with few short hairs. Filaments 20–35 mm long. Anthers 2.0–2.5 × 1.0–1.3 mm. Fruit 50–200 mm long, 4-winged, brown, sparsely to moderately pubescent, with up to 12 seeds. Seeds 5.5–8.5 × 4.0–5.5 mm, oblong, elliptic to ± orbicular, yellow to light yellow-brown. FL (May–)Aug–Oct; FT Oct–May. Chromosome number $2n = 18$ (Hair & Beuzenberg 1966; CHR 102312).

REPRESENTATIVE SPECIMENS: NORTH ISLAND: NORTHLAND: Whangarei, *H. Carse*, 11 Sep 1897, CHR 296608; Kaitaia, ?*R. H. Matthews*, Aug 1897, AK 71104; Puketi Forest, Waipapa River, *P. J. Bellingham*, 27 Sep 1984, AK 169759; Kowhai Lake, South Head, Kaipara, *E. K. Cameron 8894*, 21 Oct 1997, AK 234513; Taranga (Hen) Island, *A. E. Wright 2279*, 25 Aug 1977, AK 142723. AUCKLAND: Waitakere Ranges, Bethells Beach, *P. Hynes*, 16 Sep 1961, AK 71104; Huia, *P. B. Heenan & P. J. de Lange*, 18 Jun 1997, CHR 512957; Henderson Creek, Henderson, *R. O. Gardner 4380*, 14 Oct 1984, AK 168433; Coromandel Peninsula, *A. E. Esler 3517*, 10 Oct 1971, CHR 225537; Titirangi, *H. Carse*, 6 Sep 1922, CHR 296634; Whirinaki River, *E. J. Godley*, 28 Jun 1978, CHR 325568. WAIKATO: Aotea Harbour, *P. Hynes*, 15 May 1963, AK 93151. GISBORNE: Poverty Bay, Ngatapa, *W. R. Sykes 575/72*, 2 Oct 1972, CHR 231778. WELLINGTON: Wainuioru, Ngatapa Bush, *P. J. de Lange 2180 & T. Silbery*, 29 Aug 1993, AK 220656; Tongariro, Papakai, *E. J. Godley*, 23 Oct 1967, CHR 182765; Moawhango, *E. J. Godley*, 20 Oct 1967, CHR 182759; Wairarapa, *A. P. Druce*, Jan 1966, CHR 158943/158944; Carterton, *B. H. Macmillan 70/242*, 14 Nov 1970, CHR 215249; Tararua Range, *A. P. Druce*, Jan 1970, CHR 209613/209614. SOUTH ISLAND: NELSON: D'Urville Island, Greville Harbour, *W. R. B. O[liver]*, 9 Feb 1943, WELT 14116; Heaphy River, *E. J. Godley*, 17 Jan 1962, CHR 185865; Westport, *D. R. Given 9613 & B. P. J. Molloy*, 30 Sep 1976, CHR 355884; Buller River, *M. J. A. Simpson 3155*, 30 Oct 1961, CHR 146464. WESTLAND: Inangahua, *W. R. B. Oliver*, 25 Dec 1947, WELT 14088; Barrytown flats, *P. J. de Lange 979*, 31 Sep 1991, AK 203235; Waitangiroto River, *E. J. Godley*, 7 Oct 1971, CHR 191446; Okarito Lagoon, *P. Wardle*, 30 May 1964, CHR 117500; Mahers Swamp, *P. J. de Lange 979*, 31 Aug 1991, CHR 473566. MARLBOROUGH: Oaro, *B. B. Given*, 24 Jul 1976, CHR 285432; Leatham River, *P. B. Heenan 104/95*, 29 Nov 1995, CHR 506486. CANTERBURY: Akaroa, *W. R. B. Oliver*, 13 Mar 1948, WELT 14084; Rakaia village, *L. Cockayne 9175*, 1 Nov 1905, WELT 19563; Waiau, *E. J. Godley*, 15 Sep 1977, CHR 285481; Banks Peninsula, Okains Bay, *B. P. J. Molloy*, 20 May 1974, CHR 191304. OTAGO: Lake Wakatipu, *P. N. Johnson 847*, 27 Jul 1989, CHR 463698; Waikouaiti, *E. J. Godley*, 15 Oct 1976, CHR 285426; Roxburgh, *A. J. Healy 62/304*, 7 Sep 1962, CHR 127231. SOUTHLAND: George Sound, *R. Mason*, Apr 1949, CHR 65612; Naigara River, *R. J. Clarke*, 9 Apr 1966, CHR 167174; Lake Hauroko, *E. J. Godley*, 1 Mar 1970, CHR 194440–194443.

DISTRIBUTION (Fig. 11): *S. microphylla* occurs throughout the North Island and South Island. It is relatively uncommon in parts of the North Island where it is sympatric with *S. godleyi*, *S. chathamica*,

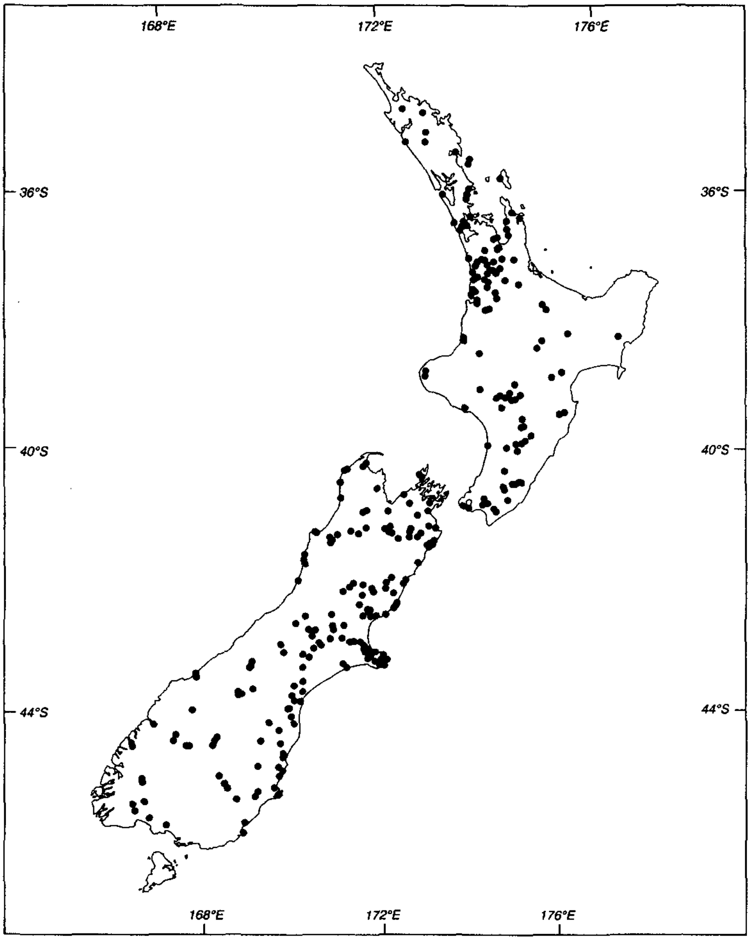



**Fig. 11** Distribution of *Sophora microphylla.*



and *S. tetraptera.* It is absent from northern Hawke's Bay and East Cape, the northern part of the range of *S. tetraptera*, but is sympatric with this species from southern Hawke's Bay to Cook Strait. Field observations in Northland and Auckland indicate that *S. microphylla* is predominantly an inland species, perhaps having been replaced in coastal sites by *S. chathamica.*

HABITATS: *S. microphylla* occurs in a number of habitats. It most commonly grows on alluvial river terraces, dunes, flood plains, lake margins, and on hill slopes among loose and rubbly rock. At these sites it usually grows with grey scrub communities and mixed podocarp/hardwood forests.

ETYMOLOGY: The specific epithet *microphylla* refers to the size of the leaflets, which are small when compared with those of *S. tetraptera.*

**5. *Sophora molloyi*** Heenan & de Lange, sp. nov.
Cook Strait kowhai

DIAGNOSIS: A *S. microphylla* differt ramificatione juvenili non divaricata, facie compacta fruticosa saepe decumbenti, foliis atroventribus subanthesi noncaducis et interea floribus plerumque sparsim dispositis, et in habitatione in scopulis expositis.

Differs from *S. microphylla* in lacking a divaricating juvenile growth form, having a shrubby, often decumbent, and compact growth habit, dark green leaves, the leaves persistent at flowering time, and with the flowers usually sparsely scattered through the canopy. Grows on exposed, windy, and dry rock bluffs and cliffs.

HOLOTYPUS (Fig. 12): New Zealand, Wellington, Ngawihi, vicinity of Cape Palliser, *P. J. de Lange & P. B. Heenan*, 21 Oct 1998, CHR 517661; Isotypi: AK, BISH, CHR, K, LE, NSW, SGO, WELT.

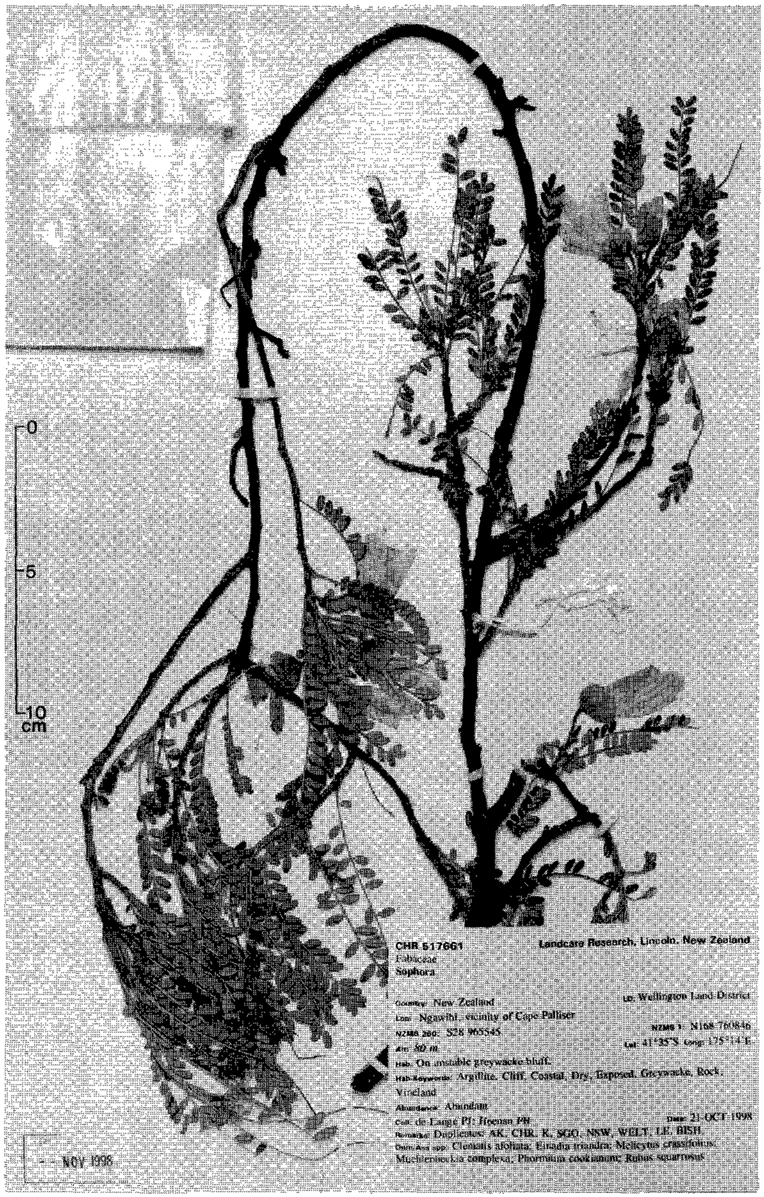



**Fig. 12** Holotype of *Sophora molloyi.*

DESCRIPTION (Fig. 3): Bushy, spreading to decumbent shrub, up to 3 m high, with several prostrate, decumbent and/or spreading main branches arising at or near ground level. Divaricating and/or flexuose juvenile branchlets absent; branchlets prostrate, decumbent to spreading, moderately to densely pubescent, becoming glabrous with age; hairs appressed, straight. Seedlings and juveniles moderately to densely leafy, leaves with increasing numbers of leaflets. Leaflets of juveniles 2.5–3.5 × 2.0–2.5 mm, rotund to broadly elliptic, sparsely to moderately hairy, not crowded or overlapping. Leaves on adults up to 10 cm long, imparipinnate, subconduplicate, petioles and rachides channelled above, leaflets 23–37. Leaflets on adults 5.0–12.0 × 2.0–6.0 mm, elliptic, elliptic oblong, to broadly elliptic, distal and proximal leaflets similar in size, not crowded or overlapping, distant, adaxial surface dark green, abaxial surface light green; apices round to slightly retuse; bases obtuse; petiolules 0.4–0.5 mm long; petioles, rachides, petiolules, and leaflets usually pubescent, hairs c. 0.2 mm long, appressed, straight. Inflorescences racemose, with up to 5 flowers, flowers usually hidden among foliage; peduncles and rachides 10–20 mm long; pedicels up to 15 mm long, each subtended by a bract; bracts 1–2 mm long; peduncles, rachides, pedicels, bracts, and calyces moderately to densely pubescent, hairs brown, appressed. Calyx 9–12 × 10–16 mm, cupulate, rim shallowly lobed, with deeper notch adjacent to standard. Corolla yellow; keel petal blade 26–30 × 7.5–11 mm; wing petal blade 25–30 × 6.5–8.5 mm; standard petal blade 20–23 × 18–21 mm; petals with distinct claws, 4.5–7.5 mm long. Stipe 5–7 mm long, glabrous to sparsely pubescent. Ovary 18–20 mm long, densely pubescent; hairs 0.2–0.4 mm long, off-white to light brown, appressed. Style 11–12 mm long, glabrous to sparsely pubescent. Stigma fringed with short hairs. Filaments 24–30 mm long. Anthers 1.7–2.1 × 0.8–0.9 mm. Fruit 50–100 mm long, 4-winged, brown, sparsely to moderately pubescent, with up to 9 seeds. Seeds 4.3–8.8 × 3.0–4.0 mm, oblong, light brown to yellow. FL Apr–Oct; FT Jun–May.

REPRESENTATIVE SPECIMENS: WELLINGTON: Cape Palliser, Ngawihi, *P. J. Brownsey & P. J. de Lange*, 20 Sep 1991, WELT 79240; Cape Palliser, Ngawihi, *P. J. de Lange 1052 & P. J. Brownsey*, 20 Sep 1991, WELT 79120; Cape Palliser, Ngawihi, *P. B. Heenan & P. J. de Lange*, 21 Oct 1998, CHR 517662/517663/517797; Humenga Farm Station, Cape Palliser Road, *P. B. Heenan & P. J. de Lange*, 21 Oct 1998, CHR 517664; Cape Terawhiti, *P. J. de Lange 3624*, 23 Oct 1998, AK 236324; cultivated ex Cape Turakirae, *P. J. de Lange 3562*, 3 Sep 1998, AK 237021. COOK STRAIT: Stephens Island, *P. H. Raven & T. Engelhorn*, 20 Sep 1969, CHR 199551/199575; Stephens Island, *G. Walls*, 30 Jul 1976, CHR 285430; Stephens Island, *B. H. Macmillan 68/146*, 15 Feb 1968, CHR 188730. KAPITI ISLAND: Western Cliffs, Onepoto Bay, *P. J. de Lange 3622 & J. W. D. Sawyer*, 27 Nov 1998, AK 236319; Western Cliffs, 1300 m north of Tuteremoana Trig, *P. J. de Lange 3621 & J. Neul*, 27 Nov 1998, AK 236321.

DISTRIBUTION (Fig. 6): *S. molloyi* grows in the vicinity of Cook Strait, occurring on Stephens Island, Rangitoto Islands, Chetwode Islands, Titi Island, Arapara Island, Kapiti Island (Atkinson & Bell 1973; Walls 1979, 1981, 1982, 1986; Ogle 1983), and several headlands along the southern Wellington coast, e.g., Cape Palliser and Turakirae Head.

Throughout its range *S. molloyi* is sympatric with *S. microphylla*, *S. chathamica*, and *S. tetraptera*. At one site near Cape Palliser there were putative hybrids with *S. tetraptera*.

HABITATS: *S. molloyi* is a low scrambling coastal shrub with specific site requirements. Favoured habitats include cliff, talus, and active alluvial fans, in extremely exposed locations, where drought, salt burn, and severe wind damage are significant constraints on plant growth and diversity. Common associates of *S. molloyi* include *Phormium cookianum* subsp. *hookeri*; the vines and lianoid scramblers *Clematis afoliata*, *Convolvulus verecundus* subsp. *waitaha*, *Scandia geniculata*, and *Einadia allanii*; the "hot rock" ferns (sensu Brownsey & Lovis 1990) *Asplenium flabellifolium*, *Cheilanthes distans*, *C. sieberi* subsp. *sieberi*, *Pellaea calidirupium*, and *Pleurosorus rutifolia*; the grasses *Rytidosperma petrosum*, *Trisetum antarcticum*, and *T. arduanum*; a wood rush *Luzula banksiana* var. *banksiana*; and the herbs *Crassula multicaulis* and *C. sieberiana*. Although other woody plants are generally sparse, co-dominants with *S. molloyi* may include *Brachyglottis greyi*, *Ozothamnus leptophyllus*, *Olearia solandri*, *Coprosma crassifolia*, and *C. propinqua* var. *latiuscula*, occasional *Muehlenbeckia astonii*, with *Kunzea ericoides* becoming dominant on the more stabilised alluvial fans near Cape Palliser. It is not uncommon for *S. molloyi* to be the sole dominant shrub species on lichen-covered or otherwise bare rock. In these situations plants are often covered in the orange lichen, *Teloschistes flavicans*. A notable exception to these floral assemblages is Kapiti Island, where *S. molloyi* often grows intermeshed with windshorn *Olearia paniculata*, *Myoporum laetum*, and *Hebe stricta* var. *macroura* along the western cliff tops.

ETYMOLOGY: The specific epithet *molloyi* honours our friend and colleague, B. P. J. Molloy, who has made a significant contribution to conservation, ecology, and taxonomy in New Zealand, and who has frequently provided PBH and PJdL with encouragement, support, and wise counsel.

## CONSERVATION STATUS

The most worrying aspect of the conservation of the New Zealand species of *Sophora* is not the individual species requirements but the serious damage being inflicted on the wild gene pools through planting for revegetation and horticultural purposes (Godley 1972). In our assessment, many plants cultivated as

"*Sophora microphylla*" consist of a diverse assemblage of the species discussed here, their hybrids, and, to a lesser extent, *S. tetraptera* and *S. longicarinata*. Many local authority and residential plantings using this horticultural resource are inadvertently mixing species distributions, and as these plantings mature the risk of hybridism with natural populations of the different species of *Sophora* increases. Furthermore, historic Maori plantings of *Sophora*, such as those suggested for *S. chathamica*, and other more recent amenity plantings, make it difficult to determine species' natural distributions. The value of using local genetic plant material for such plantings cannot be overstated.

### *Sophora chathamica*

In mainland New Zealand, *S. chathamica* seems to be adequately protected only in the northern part of its range. It is especially abundant from Auckland and Coromandel, and is also present on many of the islands in the Hauraki Gulf and on the larger inner gulf islands. Many of these islands are nature reserves managed by the New Zealand Department of Conservation. Along the west coast to the south of Auckland *S. chathamica* is locally scattered from Port Waikato to the Tongaporutu River (Taranaki), being most common around the Port Waikato, Raglan, Aotea, and Kawhia harbours. Few of these occurrences, with the notable exception of the southern Kawhia Harbour, are on adequately protected land, and many sites consist of mature trees in heavily modified forest remnants or in browsed paddocks. Recruitment is often poor or lacking, and some sites are threatened by quarrying. At some of these sites trees persist only for cultural reasons, being valued for their flowers, as a nectar source for apiarists, and because to Maori they are an important source of medicine (rongoa). Indeed, many trees or stands of trees are revered as sacred (tapu), such that their indiscriminant felling is considered a serious breach of tapu (R. Takiari and H. Rauweru pers. comm.).

The Wellington occurrences of *S. chathamica* are inadequately protected. The majority of these populations occur on public roadsides or on private residential land. A few trees are protected within several scenic reserves skirting the Porirua Harbour, most notably the Pauatahanui Inlet. On Matiu/Somes Island, in Wellington Harbour, two trees persist amongst boxthorn (*Lycium ferocissimum*). On Rekohu/Chatham Island few trees of *S. chathamica* are protected, and most owe their existence to their inaccessibility on the limestone bluffs that skirt the western margin of Te Whanga lagoon. Although we are not certain that the Wellington and Chatham Island occurrences are natural, we advocate direct intervention in these areas to prevent any further decline of the species.

### *Sophora fulvida*

*Sophora fulvida* is a naturally uncommon, range-restricted endemic (sensu de Lange & Norton 1998) that occurs locally throughout the Waitakere Ranges, on Maunganui Bluff, and at Mt Manaia and Bream Head. At these locations there is a range of seedlings, juveniles, and adults. At Mt Karioi it is known from only a few individuals. It is notable that all of the sites at which *S. fulvida* occurs are protected, either as scenic reserves, or, in the case of the Waitakere Ranges, as a Regional Park (de Lange 1996). Furthermore, as these locations contain other nationally significant flora and fauna, browsing animals and, to a lesser extent, weeds are routinely controlled (T. Lovegrove & D. McKenzie pers. comm.). In the Waitakere Ranges, the pampas grasses (*Cortaderia jubata* and *C. selloana*) are becoming more common in the open bluff and rock land habitat favoured by *S. fulvida*. However, *S. fulvida* can usually regenerate adequately under its own canopy and it is only in very dense stands of pampas grasses that it may be excluded.

### *Sophora godleyi*

*Sophora godleyi* is a common tree of riversides, gorges, cliffs, and roadside banks within the Wanganui/Rangitikei papa hill country. With the exception of its northern and western limits, we do not consider *S. godleyi* warrants any level of conservation concern. However, in the western and northwestern parts of its range, to the west of Taumarunui and in the Patea and Waitotara districts, *S. godleyi* appears less secure, often occurring as isolated trees or stands of trees within riverside paddocks. To prevent further losses in these areas, and to ensure that a representative sample of the species' former range is secured, we advocate that some measures are undertaken to protect existing populations. Some sites in the western part of its range will be included within the Whanganui National Park and associated reserves.

### *Sophora microphylla*

We do not consider *S. microphylla* to be nationally threatened, yet our fieldwork indicates that this species is often represented in some regions only by mature trees within browsed riparian or pastoral sites. Recruitment at the majority of these sites is lacking, and we suspect that if this situation continues *S. microphylla* will become extirpated in many locations within several centuries.

### *Sophora molloyi*

*Sophora molloyi* is restricted to the islands and headlands bordering the Cook Strait district (as defined by Harris 1990). The consideration of *S. molloyi* as a possible threatened species (Given 1990, as *S. microphylla* var. "Cook Strait") arose from it being traditionally regarded as a Stephens Island endemic, and that as a low sprawling cliff species, often intermeshed amongst associated vegetation, an accurate assessment of the numbers of plants was difficult.

The remoteness of the primarily insular habitat occupied by *S. molloyi* does preclude a thorough conservation assessment. However, based on our field inspections at Cape Palliser, Turakirae Head, Cape Terawhiti, and Kapiti Island, anecdotal accounts (M. Avis & D. Newman pers. comm.) of the species' abundance on Stephens Island, and records of other occurrences in the northern Marlborough Sounds (Atkinson & Bell 1973; Walls 1979, 1981, 1982, 1986; Ogle 1983), *S. molloyi* does not seem under serious threat. Indeed, *S. molloyi* is often locally abundant on wind-swept and unstable cliff and talus slope habitats. At most sites seedlings, saplings, and adult plants were present. The cliff habitat of the species precludes it from most active forms of threat except fire and browsing animals (especially feral and domestic goats), both serious problems along stretches of the south Wellington coast (Ogle 1988). Management of these threats will require ongoing education of landowners and public.

Statutory protection of the majority of *S. molloyi* populations is afforded through the provision of Nature, Scientific, and Scenic Reserves, although the Cape Palliser and Cape Terawhiti populations are on private land either farmed or used for eco-tourism horse treks and farm home-stays. As the majority of *S. molloyi* populations are on remote, inaccessible, island reserves, it would be difficult to justify a high-risk assessment to this species on the basis of any possible short-term threats to the mainland populations. Accordingly, we view *S. molloyi* as a Naturally Uncommon, Range Restricted Species (sensu de Lange & Norton 1998).



## ACKNOWLEDGMENTS

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**Appendix 1** Samples of species of *Sophora* used for statistical analyses.

| Species | Sample | Collection Locality | Voucher |
|---|---|---|---|
| *S. cassioides* | r1 | Frutillar, Chile | CHR 529899 |
| *S. cassioides* | r2 | Frutillar, Chile | CHR 529900 |
| *S. cassioides* | r3 | Gough Island, Atlantic Ocean | CHR 529901 |
| *S. cassioides* | r4 | Chepu River, Chile | CHR 529902 |
| *S. cassioides* | r5 | Chepu River, Chile | CHR 529903 |
| *S. cassioides* | r6 | Chepu River, Chile | CHR 529904 |
| *S. cassioides* | r7 | Ocean Beach, Chepu, Chile | CHR 529905 |
| *S. cassioides* | r8 | Ocean Beach, Chepu, Chile | CHR 529906 |
| *S. chathamica* | e1 | Bay of Islands, Northland, NZ | CHR 529907 |
| *S. chathamica* | e2 | Whangarei, Northland, NZ | CHR 529908 |
| *S. chathamica* | e3 | Chatham Island, NZ | CHR 529909 |
| *S. chathamica* | e4 | Manakau Heads, Auckland, NZ | CHR 529910 |
| *S. chathamica* | e5 | Te Whanga Lagoon, Chatham Island, NZ | CHR 529911 |
| *S. chathamica* | e6 | Paremata, Wellington, NZ | CHR 529912 |
| *S. chathamica* | e7 | Te Whanga Lagoon, Chatham Island, NZ | CHR 529913 |
| *S. fulvida* | f1 | Whatipu, Auckland, NZ | CHR 529914 |
| *S. fulvida* | f2 | Whatipu, Auckland, NZ | CHR 529915 |
| *S. fulvida* | f3 | Whatipu, Auckland, NZ | CHR 529916 |
| *S. fulvida* | f4 | Whatipu, Auckland, NZ | CHR 529917 |
| *S. fulvida* | f5 | Whatipu, Auckland, NZ | CHR 529918 |
| *S. fulvida* | f6 | Piha, Auckland, NZ | CHR 529919 |
| *S. godleyi* | a1 | Taumarunui, King Country, NZ | CHR 515548 |
| *S. godleyi* | a2 | Pohangina, Wellington, NZ | CHR 529920 |
| *S. godleyi* | a3 | Pohangina, Wellington, NZ | CHR 529921 |
| *S. godleyi* | a4 | Taumarunui, King Country, NZ | CHR 529922 |
| *S. godleyi* | a5 | Pipiriki, Wanganui, NZ | CHR 515551 |
| *S. godleyi* | a6 | Waitotara, Wanganui, NZ | CHR 515550 |
| *S. godleyi* | a7 | Waitotara, Wanganui, NZ | CHR 529923 |
| *S. godleyi* | a8 | Taihape, Wellington, NZ | CHR 515554 |
| *S. godleyi* | a9 | Ohingaiti, Wellington, NZ | CHR 515553 |
| *S. longicarinata* | l1 | Takaka Hill, Nelson, NZ | CHR 529924 |
| *S. longicarinata* | l2 | Takaka, Nelson, NZ | CHR 529925 |
| *S. longicarinata* | l3 | Takaka, Nelson, NZ | CHR 529926 |
| *S. longicarinata* | l4 | Takaka, Nelson, NZ | CHR 529927 |
| *S. longicarinata* | l5 | Takaka, Nelson, NZ | CHR 529928 |
| *S. microphylla* | m1 | Taihape, Wellington, NZ | CHR 529929 |
| *S. microphylla* | m2 | Rakaia Gorge, Canterbury, NZ | CHR 529930 |
| *S. microphylla* | m3 | Hundalee Hills, Canterbury, NZ | CHR 529931 |
| *S. microphylla* | m4 | Rakaia Gorge, Canterbury, NZ | CHR 529932 |
| *S. microphylla* | m5 | Haast, Westland, NZ | CHR 529933 |
| *S. microphylla* | m6 | Roxburgh, Otago, NZ | CHR 529934 |
| *S. microphylla* | m7 | Haast, Westland, NZ | CHR 529935 |
| *S. microphylla* | m8 | Heaphy River, Nelson, NZ | CHR 529936 |
| *S. microphylla* | m9 | Pareora, Canterbury, NZ | CHR 529937 |
| *S. microphylla* | m10 | Heaphy River, Nelson, NZ | CHR 529938 |
| *S. microphylla* | m11 | Banks Peninsula, Canterbury, NZ | CHR 529939 |
| *S. microphylla* | m12 | Dunedin, Otago, NZ | CHR 529940 |
| *S. microphylla* | m13 | Woodside Creek, Marlborough, NZ | CHR 529941 |
| *S. microphylla* | m14 | Wairau River, Marlborough, NZ | CHR 529942 |
| *S. microphylla* | m15 | Taumarina, Marlborough, NZ | CHR 529943 |
| *S. microphylla* | m16 | Waiouru, Wellington, NZ | CHR 529944 |
| *S. microphylla* | m17 | Warkworth, Auckland, NZ | CHR 529945 |
| *S. microphylla* | m18 | Wairarapa, Wellington, NZ | CHR 529946 |
| *S. microphylla* | m19 | Murchison, Nelson, NZ | CHR 529947 |
| *S. microphylla* | m20 | Hapuku, Marlborough, NZ | CHR 529948 |
| *S. microphylla* | m21 | Maruia, Canterbury, NZ | CHR 529949 |

| Species | Sample | Collection Locality | Voucher |
|---|---|---|---|
| *S. microphylla* | m22 | seed ex beach, Chatham Island, NZ | CHR 529950 |
| *S. molloyi* | c1 | Stephens Island, Cook Strait, NZ | CHR 529951 |
| *S. molloyi* | c2 | Turakirae Head, Wellington, NZ | AK 237021 |
| *S. molloyi* | c3 | Stephens Island, Cook Strait, NZ | CHR 529953 |
| *S. prostrata* | p1 | Waitohi River, Canterbury, NZ | CHR 529954 |
| *S. prostrata* | p2 | Waitohi River, Canterbury, NZ | CHR 529955 |
| *S. prostrata* | p3 | Waiau River, Canterbury, NZ | CHR 529956 |
| *S. prostrata* | p4 | Waiau River, Canterbury, NZ | CHR 529957 |
| *S. tetraptera* | t1 | Frasertown, Hawke's Bay, NZ | CHR 529958 |
| *S. tetraptera* | t2 | Frasertown, Hawke's Bay, NZ | CHR 529190 |
| *S. tetraptera* | t3 | Frasertown, Hawke's Bay, NZ | CHR 529191 |
| *S. tetraptera* | t4 | Frasertown, Hawke's Bay, NZ | CHR 529192 |