

Germination of *Sophora* seeds after prolonged storage

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Abstract Germination of *Sophora* seeds 24–40 years old from New Zealand (8 species), Chile (2 species), Lord Howe Island (1 species), and Hawai'i (1 species), and of fresh seed from trees established using seeds from the same seed lots, was assessed. Germination was rapid for most seed lots, with, on average, fresh seed having high germination (77–94%) and stored seed low germination (0–40%). Exceptions to this were old *S. chrysophylla* seed, which had unusually high germination (84%), and fresh *S. longicarinata* seed, which had unusually low germination (24%). The results provide further support for the role of long-distance oceanic dispersal for the distribution of *Sophora* sect. *Edwardsia* around the Southern Hemisphere, and also suggest

that long-term seed storage could be used for the *ex situ* management of *Sophora* populations. The results also highlight some intriguing ecological correlates of germination that warrant further study.

Keywords Fabaceae; *Sophora*; *Sophora* sect. *Edwardsia*; seed storage; viability; germination; dormancy; dispersal; New Zealand flora

INTRODUCTION

Section *Edwardsia* of the shrub and small-tree genus *Sophora* (Fabaceae) is widely regarded as one of the best examples of long-distance oceanic dispersal around the Southern Hemisphere (Skottsberg 1956; Sykes & Godley 1968; Pena et al. 1993; Hurr et al. 1999). *Sophora* sect. *Edwardsia* has an essentially Pacific distribution, with closely related species present on a range of southern islands and continents (Markham & Godley 1972; Pena & Cassels 1996; Heenan et al. 2001). However, the exact relationship between and origins of the different taxa is still poorly resolved (Heenan et al. 2001). Notwithstanding this, genetic analysis has shown few differences between these taxa and has established the monophyly of section *Edwardsia* (Hurr et al. 1999; A. D. Mitchell & PBH unpubl. data).

Support for long-distance ocean dispersal of *Sophora* sect. *Edwardsia* comes from studies of their seed ecology. Seeds of some *Sophora* species appear to have good buoyancy and those floated on saltwater have been found to germinate (Guppy 1906; Sykes & Godley 1968). Seeds of New Zealand *Sophora* species have been collected from beach drift on the Kermadec Islands, 1000 km to the north-east (*S. chathamica*), and Chatham Islands, 800 km south-east (*S. microphylla*) of mainland New Zealand, and found to germinate after scarification (Sykes & Godley 1968). In both cases, the drift seed is from species that do not occur on the island group. *Sophora* seeds also remain viable for at least eight years in storage (Sykes & Godley 1968). Other legumes are also known to be tolerant of saline

conditions and capable of long-distance oceanic dispersal, while seed longevity is a more general feature of legumes (Raven & Polhill 1981; Priestley 1986). In New Zealand, seeds from *Carmichaelia* species have been observed to have good longevity, with 80% viability after 20–24 years storage for six *Carmichaelia* species (Grüner & Heenan 2001), but we are unaware of any previous comparable studies with *Sophora* species (but see Fountain et al. 2002).

The present paper reports the results of a germination trial with seeds 24–40 years old from 12 Pacific species of *Sophora*, and contrasts these with germination of fresh seed from some of the same source populations. Specifically, we wanted to know if *Sophora* seeds retained their viability after prolonged (24–40 years) storage.

MATERIALS AND METHODS

Germination trials used 62 seed lots, with at least 40 seeds each, from 12 Pacific *Sophora* species collected by or supplied to one of us (EJG) between 1961 and 1977 (Table 1; Appendix). The seeds had been collected from wild trees and were stored dry in plastic or glass vials at room temperature in the offices of EJG and then PBH in the intervening period (cf. Grüner & Heenan 2001). Additional fresh seed was collected by PBH in August 2001 from *Sophora* trees in the Landcare Research experimental gardens at Lincoln. These trees had

been established using seeds from the same original seed lots as used in this study, although fresh seed was only available for 12 seed lots from 6 *Sophora* species (Table 1). The identity of all *Sophora* seed collections was confirmed by herbarium material collected at the same time as the original seed lots, or from plants cultivated at the Landcare Research experimental gardens that originated from the wild-collected seed lots.

The seeds were washed in distilled water, scarified by light sanding, and then germinated on sterilised agar in covered Petri dishes in a controlled-climate room at a constant temperature of 22°C with 16 h light and 8 h dark. Seeds from each seed lot were divided into two dishes, each containing 20 seeds. Seeds were checked for germination every 2–4 days until there was no evidence of any further germination (48 days). Germination was defined by emergence of the radicle through the testa.

Germination data from the two Petri dishes were pooled for analysis, and the resultant proportion data arc-sine/square-root transformed before analysis. Analysis of variance (ANOVA), using seed lots as replicates, was used to quantify the effect of seed age (old cf. fresh) and species on germination. Regression was used to assess how well germination could be predicted by seed lot age and mean seed weight for species with 10 old seed lots. All analyses were undertaken using SAS version 8.01 (SAS Institute, Cary, N.C.).

Table 1 Summary of *Sophora* seed lots used for the study (see Appendix for full seed-lot details). NZ, New Zealand; LHI, Lord Howe Island.

Species	Origin	Old seeds				Fresh seeds		
		Sample size	Storage time (yr)	Germin. (%) ± SEM	Range	Sample size	Germin. (%) ± SEM	Range
<i>S. cassioides</i>	Chile	10	24–33	14 ± 6.5	0–60	2	84 ± 11	73–95
<i>S. chathamica</i>	NZ	10	24–37	34 ± 10.2	0–75	3	77 ± 9.4	58–87
<i>S. chrysophylla</i>	Hawai'i	5	32–40	84 ± 6.5	59–95	–	–	–
<i>S. fulvida</i>	NZ	1	38	5	5	–	–	–
<i>S. godleyi</i>	NZ	3	30–38	0	0–0	2	94 ± 1	93–95
<i>S. howinsula</i>	LHI	1	30	8	8	–	–	–
<i>S. longicarinata</i>	NZ	1	37	0	0	2	24 ± 9	15–33
<i>S. macrocarpa</i>	Chile	1	28	0	0	–	–	–
<i>S. microphylla</i>	NZ	16	24–39	40 ± 8.9	0–100	2	81 ± 12.5	68–93
<i>S. molloyi</i>	NZ	2	25–29	24 ± 19	5–43	1	85	85
<i>S. prostrata</i>	NZ	5	34–38	39 ± 17.5	0–95	–	–	–
<i>S. tetraptera</i>	NZ	7	27–35	15 ± 13.4	0–95	–	–	–

Fig. 1 Germination of fresh (—●—) and old (—○—) seeds from 12 *Sophora* species. 1, *S. cassioides*; 2, *S. chathamica*; 3, *S. chrysophylla*; 4, *S. fulvida*; 5, *S. godleyi*; 6, *S. howinsula*; 7, *S. longicarinata*; 8, *S. macrocarpa*; 9, *S. microphylla*; 10, *S. molloyi*; 11, *S. prostrata*; 12, *S. tetraptera*. Seed codes in bold are fresh seed.

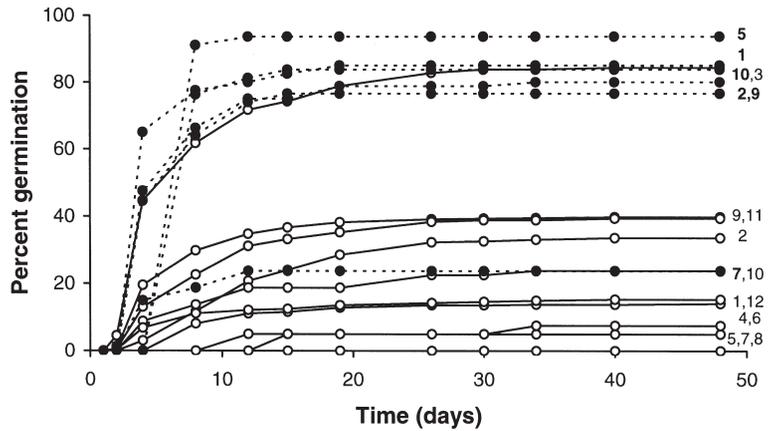


Table 2 Ordered species mean \pm SEM germination for old seed lots of eight *Sophora* species with 2 seed lots. Means followed by the same letter are not significantly different at $P < 0.05$ based on an *a posteriori* Student-Newman-Keuls test.

Species	Sample size	Germin. (%) \pm SEM
<i>S. chrysophylla</i>	5	84 \pm 6.5 ^a
<i>S. microphylla</i>	16	40 \pm 8.9 ^{ab}
<i>S. prostrata</i>	5	39 \pm 17.5 ^{ab}
<i>S. chathamica</i>	10	34 \pm 10.2 ^{ab}
<i>S. molloyi</i>	2	24 \pm 19 ^{ab}
<i>S. cassioides</i>	10	14 \pm 6.5 ^b
<i>S. tetraptera</i>	7	15 \pm 13.4 ^b
<i>S. godleyi</i>	3	0 ^b

RESULTS

The onset of germination was rapid with seeds from some seed lots germinating within 2 days of the start of the trial and most seed lots having commenced germination by 8 days (Fig. 1). Most seed lots reached maximum germination by 26 days. Total germination was markedly different between fresh and old seed (Fig. 1; Table 1). Except for the two seed lots of *S. longicarinata*, all fresh seed lots showed high germination, with 58–95% of seeds germinating. In contrast, old seed had much lower overall germination (Fig. 1), although there was considerable variation among seed lots (Table 1). For all species except *S. chrysophylla*, *S. molloyi*, *S. howinsula*, and *S. fulvida* there was no germination in some or all seed lots (Table 1), while for three species, *S. microphylla*, *S. prostrata*, and *S.*

tetraptera, germination range was 0–95% or 0–100% among seed lots within species. The five *S. chrysophylla* seed lots were the exception among the old seeds, with all exhibiting high germination (59–95%).

Statistical testing was limited by the lack of replication for several species. For the four species with 2 seed lots of both fresh and old seed, *S. cassioides*, *S. chathamica*, *S. godleyi*, and *S. microphylla*, age was found to have a significant effect on germination in the ANOVA model ($F = 26.57$, $P < 0.001$), but neither species ($F = 0.33$, $P = 0.804$) nor the species*age interaction ($F = 1.27$, $P = 0.29$) was significant. However, for those species with 2 seed lots of old seed (Table 2), species was found to have a significant effect on germination ($F = 3.36$, $P = 0.005$) when the effect of species was tested for alone.

Three species, *S. microphylla*, *S. cassioides*, and *S. chathamica*, had 10 old seed lots. For these species the variance explained in the regression models using age to predict germination were low (*S. chathamica*, $R^2 = 0.358$; *S. cassioides*, $R^2 = 0.051$; *S. microphylla*, $R^2 = 0.003$), and only *S. chathamica* showed a trend of decreasing germination with increasing age (Fig. 2). However, for all three species there was a very wide range of germination values for similar-aged seed lots. For example, seed lots of *S. microphylla* aged 34–36 years old had germinations ranging from 13 to 100%, while 34-year-old seed lots of *S. chathamica* had germinations ranging from 0 to 75%. Seed weight was also a very poor predictor of germination (*S. microphylla*, $R^2 = 0.009$; *S. cassioides*, $R^2 = 0.005$; *S. chathamica*, $R^2 = 0.004$).

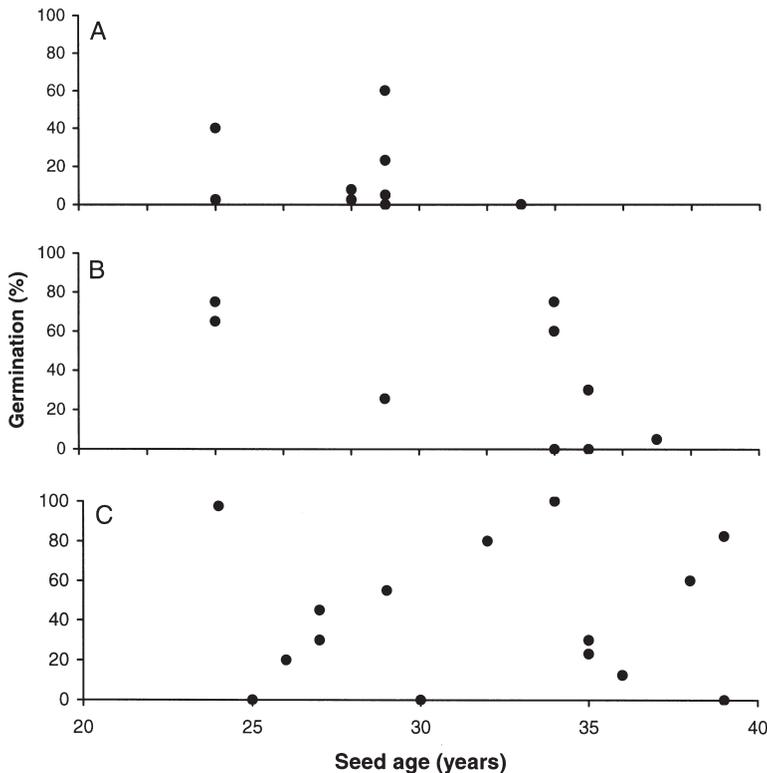


Fig. 2 Relationship between germination and seed lot age for the three *Sophora* species with 10 old seed lots with regression lines fitted. **A**, *S. cassioides*; **B**, *S. chathamica*; **C**, *S. microphylla*.

DISCUSSION

The considerable longevity of legume seeds is well established (Priestley 1986) and the results of the present study show that *Sophora* species fit this pattern. For example, 34- and 39-year-old seed lots of *S. microphylla* had 100% and 83% germination, respectively, while the oldest seed lot studied here (40 years, *S. chrysophylla*) had 90% germination. Grüner & Heenan (2001) also found high levels of viability in *Carmichaelia* seeds 20–24 years old, with up to 100% germination in one 24-year-old seed lot, although they did not have any seeds older than 24 years.

While seed longevity in our study was high, the results presented are for seeds that had been stored dry at room temperature. It is likely that seeds stored under field conditions (e.g., in soil) may not have retained viability for as long, as moist field conditions would have resulted in degradation of the testa over this time. For example, Williams et al. (1996) found a significant reduction in the germination of *Carmichaelia muritai* seed in Marlborough to c. 10% after 2 years burial. In contrast, seeds of *C. hollowayi*

buried for 6 years in skeletal limestone soils at Awahokomo, Otago, remained intact and germinated after scarification of the testa (PBH unpubl. data). Almost all surviving seeds of the exotic legume *Ulex europaeus* remained viable after 10 years burial in soil at three different sites, although the absolute number of seeds that survived showed significant declines with time (Hill et al. 2001). *Sophora microphylla* seeds have been recorded from soil seed banks in Canterbury (Partridge 1989; Webb 1993), suggesting that seeds can survive in the soil for some time, but no data have been published on the age of these buried seeds. Field studies with buried seeds are required to link the results obtained in the present study with natural seed storage patterns.

The very high germination of fresh *Sophora* seed recorded here is consistent with the results of other germination studies with *Sophora* species (Webb 1993) and with other legume species (Williams et al. 1996; Grüner & Heenan 2001; Hill et al. 2001). The only requirement for rapid and high germination of fresh seed in these species is the need for appropriate scarification (Fountain & Outred 1991). In our study, scarification was achieved by lightly

sanding the testa, as scarification of *Sophora* seed in the wild appears to involve abrasion from sand and rock (Webb 1993).

While the average viability of old seeds was lower than for fresh seed, the variability in germination among old seed lots of individual species was considerable, with similar-aged seed lots ranging from no or very low germination to very high or complete germination. Grüner & Heenan (2001) also observed high variation in seed viability amongst similar-aged old seed lots. One explanation for this variability is that there was variability in the maturity of different seed lots at the time of collection. *S. microphylla* (Webb 1993), and probably other *Sophora* species, sheds seeds over a protracted period of time. For *S. microphylla* seed shed occurs in autumn soon after the seeds mature, but a second period of seed shed occurs during the following spring and summer. In Canterbury, where Webb (1993) studied *S. microphylla*, this was attributed to seasonally strong winds. However, the persistence of seed on trees for many months after seed maturity is a general feature of New Zealand *Sophora* species and means that field collections may be of relatively “old” fresh seed.

There was considerable variability in the viability of old seeds among the New Zealand *Sophora* species that may correlate with aspects of their ecology and general morphology. Three species in particular, *S. fulvida*, *S. godleyi*, and *S. longicarinata*, had no or very low germination of old seeds compared with higher average germination among most other species. These three species are ecologically similar, occurring on eroding or unstable bluffs, rock outcrops, or hill slopes. They are also similar morphologically, lacking a divaricating juvenile phase and flowering when young, and may be derived from a common ancestor (Heenan et al. 2001). A soil seed bank is likely to be of limited value in such dynamic habitats, where rapid growth and early flowering are likely to be more important for the persistence of these species. However, the limited amount of data we have on seed viability for old seed lots from these species does not allow for a more detailed analysis of this relationship. Grüner & Heenan (2001) also found links between growth habit/ecology and seed viability in *Carmichaelia*, where longer-lived tree species had reduced seed viability after prolonged storage compared with the short-lived shrub species. The results of these studies suggest that a more detailed assessment of the life-history of *Sophora* species might yield some useful insights into the ecology of woody species in unstable dynamic habitats.

Two species, *S. chrysophylla* and *S. longicarinata*, showed quite different germination patterns to the other species. *S. chrysophylla* had unusually high germination among all five old (32–40 years) seed lots, ranging from 59 to 95%. It is, however, unclear why germination is so high in this Hawaiian species. In contrast, *S. longicarinata* exhibited unusually low germination among young seeds and no germination of old seeds. While the result for fresh seeds is based on only two seed lots, it is so different from the other results obtained here (*S. longicarinata* 15–33% cf. other *Sophora* species 58–95% germination) and in other studies of *Sophora* germination (Webb 1993) that it warrants comment. The fresh seed was collected by one of us (PBH) and, based on considerable experience in germinating and growing *Sophora* plants, was not considered to be unusual in comparison with other collections of fresh seed that have shown high germination. Several reasons can be proposed to explain this pattern. *S. longicarinata* is unusual among the New Zealand *Sophora* species in occurring on limestone and marble rocks with particularly high levels of calcium carbonate (Heenan 1998), and it may be that some aspect of substrate chemistry is important in germination. Alternatively, *S. longicarinata* may be of hybrid origin and poor seed viability may be a result of this (Heenan 1998). Reduced viability of fresh seed may also be related to pollination; self-pollination may have been much higher in the cultivated plants from which seed was sourced, although fresh seed from other *Sophora* species germinated here also came from cultivated plants. A final possibility relates to the biology of naturally uncommon species. For example, Hodgson (1986) showed that a greater proportion of rare species than common species produced non-viable seed, while fewer rare species than common species were capable of “immediate” germination, in the Sheffield study area. While these are fascinating possibilities, considerably more research is required to test if any of them actually account for the observed low viability of *S. longicarinata* seed.

The results of this study have clearly shown that seeds from several *Sophora* species stored for 24–40 years under dry conditions retain considerable viability. As well as providing further support for the role of long-distance oceanic dispersal for the distribution of *Sophora* sect. *Edwardsia* around the Southern Hemisphere, these results also suggest that long-term seed storage could be used for the *ex situ* management of *Sophora* populations if necessary. This study has also highlighted some intriguing

ecological correlates of germination that warrant further study. Perhaps most significantly, this study has highlighted the incredible value of long-term seed collections for better understanding species biology. Many of the seed lots used in this study still have substantial numbers of seeds remaining, and testing of their viability in the future will add considerably to our knowledge of long-term seed viability patterns.

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Appendix I *Sophora* seed lots used in this study. Seed lots for which fresh seed was available are indicated by *.

Code	Species	Collection location	Collector	Date collected	Storage time (yr)
M2	<i>S. microphylla</i>	Howard Junction, Buller River	E. J. Godley	Mar 1972	29
M8	<i>S. microphylla</i>	Waitangiroti River, Westland	E. J. Godley	Oct 1971	30
M13	<i>S. microphylla</i>	Northburn, Dunstan Mountains	K. F. O'Connor	Sep 1974	27
M16	<i>S. microphylla</i>	Redcliffe Stream, Rakaia River	E. J. Godley & D. H. Smith	Jan 1977	24
M20	<i>S. microphylla</i>	Waitangiroti River, Westland	E. J. Godley	Oct 1971	30
M22	<i>S. microphylla</i>	Waitangiroti River, Westland	E. J. Godley	Oct 1975	26
M63	<i>S. microphylla</i>	Kakahu River, near Geraldine	E. J. Godley	Jul 1974	27
M67	<i>S. microphylla</i>	Ohau	E. J. Godley	1966	35*
M76	<i>S. microphylla</i>	Junction of Wairau & Leatham rivers	E. J. Godley	Jul 1966	35
M83	<i>S. microphylla</i>	Palmerston, Otago	E. J. Godley	Jul 1967	34
M92	<i>S. microphylla</i>	The Snout, Picton	J. B. Irwin	Nov 1965	36
M99	<i>S. microphylla</i>	Pukaki	G. I. Collett	May 1969	32
M104	<i>S. microphylla</i>	Rakaia	E. J. Godley	Jul 1963	38
M108	<i>S. microphylla</i>	Diamond Harbour	A. J. Healy	Apr 1962	39
M144	<i>S. microphylla</i>	Hen Island	I. A. E. Atkinson	1962	39*
M148	<i>S. microphylla</i>	Cronndum, Inangahua River	E. J. Godley	Mar 1972	29
P1	<i>S. prostrata</i>	Willow Stream, Awatere	E. J. Godley	1966	35
P5	<i>S. prostrata</i>	Wither Hills, Blenheim	E. J. Godley	1967	34
P6	<i>S. prostrata</i>	Seddon	E. J. Godley	1967	34
P9	<i>S. prostrata</i>	The Kowhais, Canterbury	E. J. Godley	Aug 1966	35
P14	<i>S. prostrata</i>	Lake Tekapo	A. W. Anderson	1963	38
M95	<i>S. godleyi</i>	Ohingaiti	E. J. Godley	Feb 1971	30*
M58	<i>S. godleyi</i>	Kitchener Park, Fielding	E. J. Godley	Aug 1967	34*
M109	<i>S. godleyi</i>	Taumarunui, Echo Bank Rd	E. J. Godley	Jun 1963	38
M24	<i>S. molloyi</i>	Stephens Island, Cook Strait	M. J. Meads	May 1976	25*
M65	<i>S. aff. molloyi</i>	Haulashore Island, Nelson	M. J. A. Bulfin	Dec 1972	29
M166	<i>S. longicarinata</i>	Takaka Hill	D. R. Given	Aug 1964	37*
–	<i>S. longicarinata</i>	Cultivated tree <i>ex</i> Takaka Hill ¹	P. B. Heenan	Sep 2001	
M165	<i>S. fulvida</i>	Lion Rock, Piha	I. R. Fryer	Apr 1963	38
M94	<i>S. chathamica</i>	Port Fitzroy, Great Barrier Island	E. J. Godley & R. S. Cooper	Feb 1964	37*
M110	<i>S. chathamica</i>	Wilson Bay, Coromandel Peninsula	I. A. E. Atkinson	Apr 1972	29
M137	<i>S. chathamica</i>	Cape Reinga (plant A)	G. C. Kelly	Apr 1967	34
M138	<i>S. chathamica</i>	Cape Reinga (plant B)	G. C. Kelly	Apr 1967	34
M70	<i>S. chathamica</i>	Parekura Bay	E. J. Godley	Oct 1966	35
M71	<i>S. chathamica</i>	Parekura Bay	E. J. Godley	Oct 1966	35
M27	<i>S. chathamica</i>	Makomako, Aotea Harbour	P. Devlin	Dec 1967	34
M29	<i>S. chathamica</i>	Makomako, Aotea Harbour	P. Devlin	Dec 1967	34
M124	<i>S. chathamica</i>	Cultivated <i>ex</i> Chatham Islands (tree 2)	D. H. Smith	Oct 1977	24*
M125	<i>S. chathamica</i>	Cultivated <i>ex</i> Chatham Islands (tree 3)	D. H. Smith	Oct 1977	24*
T1	<i>S. tetraptera</i>	Big Hill Stream, W. of Hastings	E. J. Godley	Jul 1974	27
T2	<i>S. tetraptera</i>	Big Hill Stream, W. of Hastings	E. J. Godley	Jul 1974	27
T3	<i>S. tetraptera</i>	Makaretu River, Hawke's Bay	E. J. Godley	Jul 1974	27
T7	<i>S. tetraptera</i>	Motu River, Bay of Plenty	E. J. Godley	Jul 1972	29
T10	<i>S. tetraptera</i>	Motu River, Bay of Plenty	E. J. Godley	Jul 1972	29
T12	<i>S. tetraptera</i>	Te Kahika Stream, Havelock North	N. Elder	1966	35
T13	<i>S. tetraptera</i>	Moawhango	E. J. Godley	1967	34

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Appendix I *continued*

Code	Species	Collection location	Collector	Date collected	Storage time (yr)
M130	<i>S. cassioides</i>	Cultivated <i>ex</i> Gough Island (tree 16)	D. H. Smith	Oct 1977	24*
M131	<i>S. cassioides</i>	Cultivated <i>ex</i> Chile (tree 9)	D. H. Smith	Oct 1977	24*
M152	<i>S. cassioides</i>	Gough Island	N. M. Wace	May 1968	33
M154	<i>S. cassioides</i>	Arauco, Chile	F. Schlegel	Feb 1973	28
M155	<i>S. cassioides</i>	Arauco, Chile	F. Schlegel	Feb 1973	28
M156	<i>S. cassioides</i>	Rio Negro, Chile	M. H. Bannister	Dec 1972	29
M157	<i>S. cassioides</i>	Rio Negro, Chile	M. H. Bannister	Dec 1972	29
M158	<i>S. cassioides</i>	Volcan Llaima, Chile	M. H. Bannister	Oct 1972	29
M159	<i>S. cassioides</i>	Cauquenes, Chile	H. Schmidt	Oct 1972	29
M160	<i>S. cassioides</i>	Cultivated, <i>ex</i> Centro Forestal, Frutillar, Chile	M. H. Bannister	Dec 1972	29
MC2	<i>S. macrocarpa</i>	Malleco, Chile	F. Schlegel	Feb 1973	28
C1	<i>S. chrysophylla</i>	Mauna Kea, Hawai'i	I. A. E. Atkinson	Mar 1969	32
C3	<i>S. chrysophylla</i>	Mauna Kea, Hawai'i	I. A. E. Atkinson	Mar 1969	32
C4a	<i>S. chrysophylla</i>	Mauna Kea, Hawai'i	I. A. E. Atkinson	Mar 1969	32
C6	<i>S. chrysophylla</i>	Pohakuloa, Hawai'i	C. A. Fleming	Sep 1961	40
C8	<i>S. chrysophylla</i>	Mauna Kea, Hawai'i	P. Wardle	1964	37
2054	<i>S. howinsula</i>	Transit Hill, Lord Howe Island	P. S. Green	Sep 1971	30

¹The tree that this seed was collected from did not come from the old seed lot used in this study (M166) but was included to provide a second *S. longicarinata* fresh seed lot.