REGENERATION CHARACTERISTICS OF A SWAMP FOREST IN NORTHWESTERN TASMANIA

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(with one table and five text-figures)

The botanical composition and regeneration characteristics are described for a *Melaleuca ericifolia-Leptospermum lanigerum* forest from northwestern Tasmania. The size classes of the two dominant species are highly correlated with tree age. Size class analysis shows that the dominants are regenerating continuously. The relationship of this forest type to rainforest and wet sclerophyll forest are discussed.
Key Words: Tasmania, swamp forest, regeneration, *Melaleuca*, *Leptospermum*

INTRODUCTION

The forests of Tasmania traditionally are treated at the formation level as either sclerophyll forest or as rainforest (e.g. Jackson 1965, Curtis 1965-66, Gilbert 1970-71). The sclerophyll forests are broken into two classes, wet and dry sclerophyll, each of which has a characteristic understorey flora. The dry sclerophyll forests are dominated by either *Eucalyptus* or *Casuarina* (Duncan & Brown 1985), whilst wet sclerophyll forests are *Eucalyptus*-dominated. The dominant species of the two sub-formations have quite different regeneration modes, with dry sclerophyll dominants being either continuous or pulse regenerators while most wet sclerophyll forests are either even-aged or contain only a few age-classes, depending on the past history of fires.

Jarman & Brown (1983) have defined cool temperate rainforest in Tasmania as those forest communities dominated by species of *Nothofagus*, *Atherosperma*, *Eucryphia*, *Athrotaxis*, *Lagarostrobos*, *Phyllocladus* or *Diselma* of at least 8 m in height. Rainforest species are defined as those species able to perpetuate themselves (either vegetatively or from seed) within forests dominated by one or more of the species listed above.

In northwestern Tasmania there are large tracts of closed swamp forest which are usually dominated by *Acacia melanoxylon* or *Melaleuca ericifolia* (Kirkpatrick & Dickinson 1984, fig. 1). These forests subsume a range of community types from almost pure *A. melanoxylon* forests through *A. melanoxylon*-Myrtaceae-*Nothofagus*(-*Phyllocladus*) dominated forests to almost pure *Lepto-*

spermum and/or *Melaleuca* forest (Anon. 1982, Jarman & Brown 1983, Jarman *et al.* 1984, R. Mesibov *pers. comm.* 1986).

Jarman & Brown (1983) considered that whilst *Leptospermum lanigerum*, *L. nitidum*, *L. scoparium* and *Melaleuca squarrosa* may be found in the rainforest canopy, they were doubtful rainforest species, and suggested that detailed studies were required to determine their status. Thus Jarman *et al.* (1984) point out that the niche occupied in rainforest by these myrtaceous species may be that of a "good" rainforest species or may instead be similar to that filled by *Eucalyptus* in the mixed forests of Gilbert (1959).

The relationships of the swamp forests to either rainforests or to sclerophyll forests have not been determined. The floristic variation they contain apparently ranges from predominantly rainforest elements to predominantly sclerophyllous and the regeneration characteristics of the non-eucalypt dominants have not been described. The aim of the present paper is to provide a floristic description of one such swamp forest and to investigate the regeneration strategies of the two forest dominants — *Leptospermum lanigerum* and *Melaleuca ericifolia.*

THE STUDY AREA

The study area is located on the Welcome River in the far northwest of the State. This area lies in the warm-humid climatic zone (Gentilli 1972) with a winter rainfall maximum. The swamp
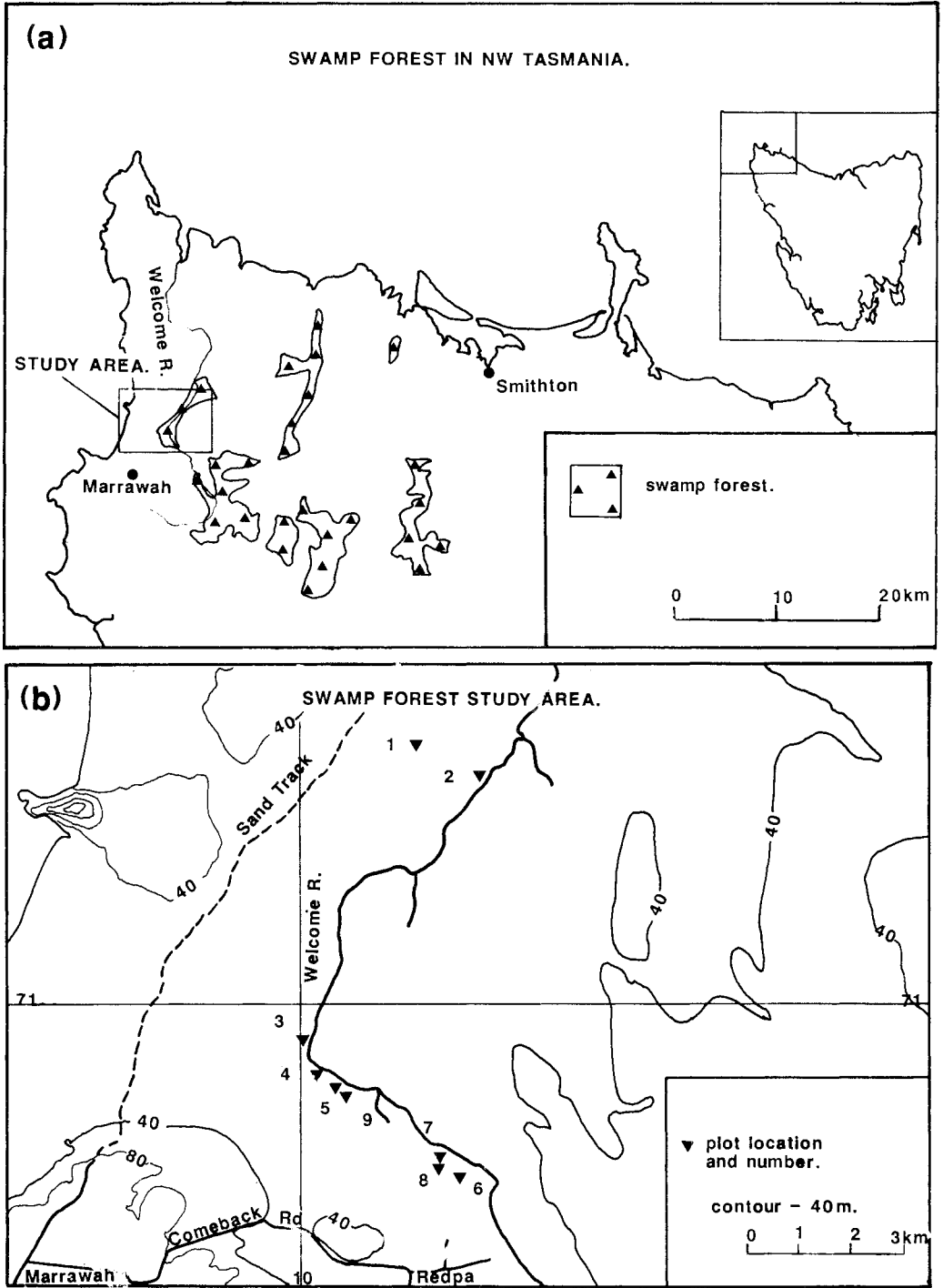
FIG.1 — (a) The occurrence of swamp forest in northwestern Tasmania (after Kirkpatrick & Dickinson 1984), and (b) the location of the study area.

forests of this area are commonly inundated in the winter months.

The topography is of a broad flat valley, the vegetation being underlain by Holocene alluvium, sand and gravel. The swamp forest in the area is dominated by *Melaleuca ericifolia* with *Leptospermum lanigerum* also being present.

METHODS

Vegetation data were collected from nine plots along the Welcome River between Redpa and Boggy Creek. Both structural and floristic data were recorded from 20 m diameter plots using the TASFORHAB system of Peters (1984). From these data a vegetation description was compiled and a generalized vegetation profile was constructed.

In the area presently being cleared to make drainage channels, 49 basal slabs of *Melaleuca ericifolia* from 10 to 460 mm diameter were collected for ageing of the trees. Nine slabs of *Leptospermum lanigerum* from 10 to 600 mm diameter were also collected. Slab diameters were determined with a diameter tape and ring counts were made on their planed tops. From these data a simple linear regression was made between age and size. Size-class analyses were undertaken from six sites. At each site, a 10 × 10 m plot was established and all individuals greater than 100 mm diameter were counted and diameters at breast height (DBH) recorded. A 5 × 5 m subplot was located in one corner of the plot and all individuals less than 100 mm diameter were counted. Size class histograms were constructed from these data.

The size distributions were then modelled against the power function $y = y_o x^{-b}$ and the negative exponential $y = y_o e^{-bx}$, where y is the number of individuals in size class x, y_o is the initial population size and b is mortality. The power function is appropriate to forest stands in which there is continuous regeneration with a mortality that decreases with increasing age, whilst the negative exponential reflects constant mortality (Hett & Loucks 1976). These models were tested for the four plots of *Melaleuca ericifolia* for which data were available in at least five size classes.

As a further check on the regeneration mode of the two species, increment counts were made from rings near the centre and at the outside of stem slabs. These measurements were made to determine whether there was any indication that episodic release from suppression of more or less even-aged stems was giving rise to apparent continual regeneration.

Nomenclature follows Curtis (1963, 1967), Curtis & Morris (1975), Willis (1970), and Jones & Clemesha (1981).

RESULTS

Vegetation

The vegetation of the area is dominated by a closed canopy of *Melaleuca ericifolia* with *Acacia melanoxylon* and *Leptospermum lanigerum* as sub-dominants. The canopy also contains occasional individual trees of *Eucalyptus ovata* and *E. obliqua* on better-drained sites. The understorey is dominated by *Melaleuca ericifolia* with *Coprosma quadrifida*, *Drimys lanceolata*, *Leptospermum lanigerum* and occasionally *Pomaderris apetala*, again on better drained sites. The ground layer contains *Gahnia grandis* and *Lepidosperma elatius* together with the ferns *Polystichum proliferum*, *Blechnum nudum* and *Dicksonia antarctica*. Epiphytic ferns, including *Microsorium diversifolium*, *Hymenophyllum peltatum*, *Ctenopteris heterophylla* and *Grammitis billardieri* were occasionally present. A generalized vegetation profile is shown in figure 2. At the time of sampling (June) the free water surface was at or above ground level in most of the area traversed.

Regeneration Modes of the Dominant Species

A highly significant correlation was found between diameter and age for both *Melaleuca ericifolia* and *Leptospermum lanigerum* (figs 3 and 4). Thus size of stem provides a reasonable means of estimating age. Examination of the incremental growth of individual stems indicated that considerable suppression of individuals was occurring through the stand, but there was no indication that the initial regeneration resulted from a single disturbance event, nor that the release of individuals was tied to some broad scale disturbance such as fire or windthrow. Thus size class analysis can be used to describe adequately the population dynamics of those samples for which data are available. In all of the plots, there were large numbers of seedlings and saplings (individuals less than 100 mm diameter) found under closed canopies (fig. 5). In plots 1, 2, 3 and 5, size class distributions fitted the power function model (table 1).

DISCUSSION

The occurrence of large numbers of seedlings and saplings scattered through the forest suggests

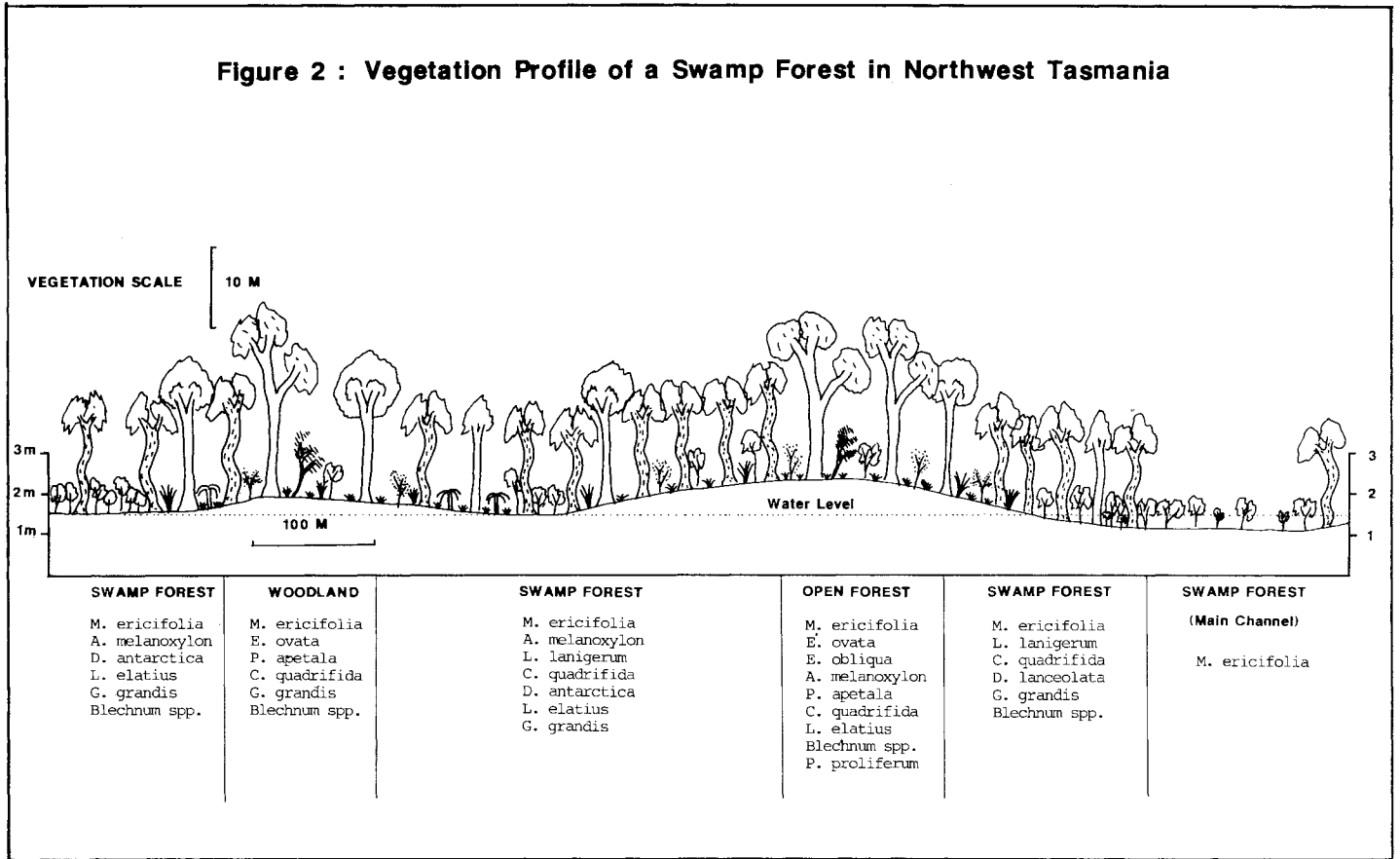**Figure 2 : Vegetation Profile of a Swamp Forest in Northwest Tasmania**

SWAMP FOREST	WOODLAND	SWAMP FOREST	OPEN FOREST	SWAMP FOREST	SWAMP FOREST
M. ericifolia	M. ericifolia	M. ericifolia	M. ericifolia	M. ericifolia	(Main Channel)
A. melanoxylon	E. ovata	A. melanoxylon	E. ovata	L. lanigerum	
D. antarctica	P. apetala	L. lanigerum	E. obliqua	C. quadrifida	M. ericifolia
L. elatius	C. quadrifida	C. quadrifida	A. melanoxylon	D. lanceolata	
G. grandis	G. grandis	D. antarctica	P. apetala	G. grandis	
Blechnum spp.	Blechnum spp.	L. elatius	C. quadrifida	Blechnum spp.	
		G. grandis	L. elatius		
			Blechnum spp.		
			P. proliferum		

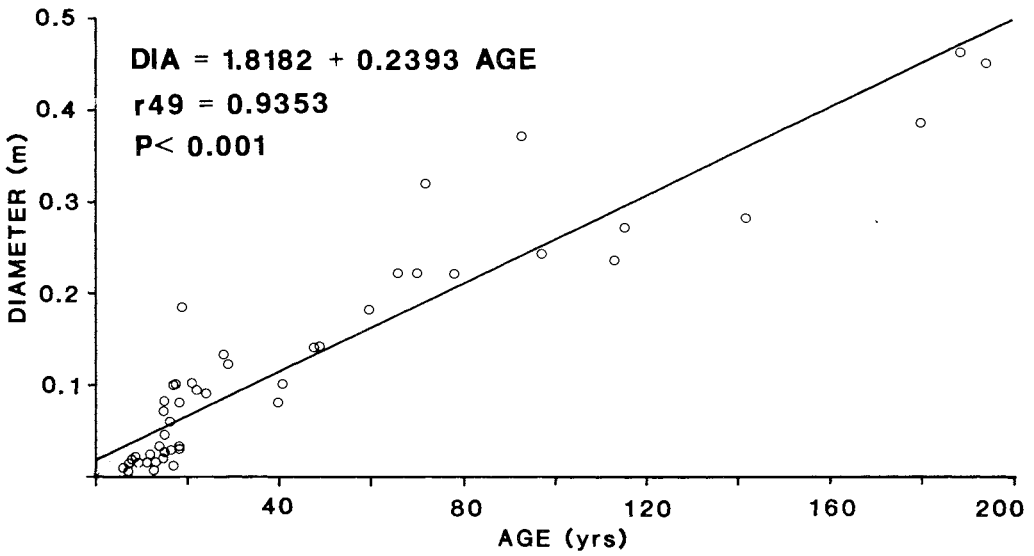**DIA = 1.8182 + 0.2393 AGE**
r49 = 0.9353
P< 0.001

FIG.3 — Regression of diameter on age for Melaleuca ericifolia.

that *Melaleuca ericifolia* is capable of continuous regeneration in an essentially closed-canopy forest. This observation is confirmed by the age and size class analyses and the fit to the power function. However, although there is a highly significant correlation of size and age, it is apparent from the increment counts that growth rates are variable

DIA = −7.5155 + 0.6105 AGE
r9 = 0.9353
P< 0.001
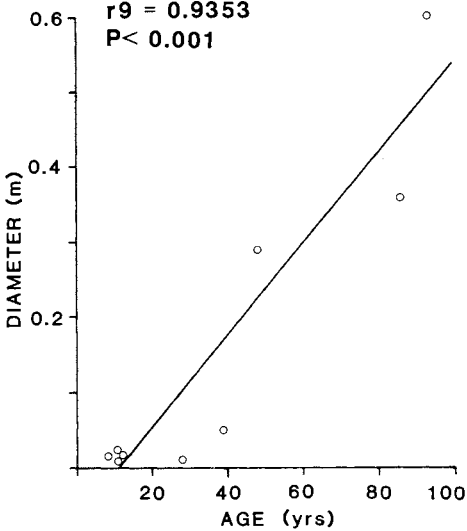
FIG.4 — Regression of diameter on age for Leptospermum lanigerum.

and that suppression can occur for periods in excess of 20 years. Further analyses of the pattern
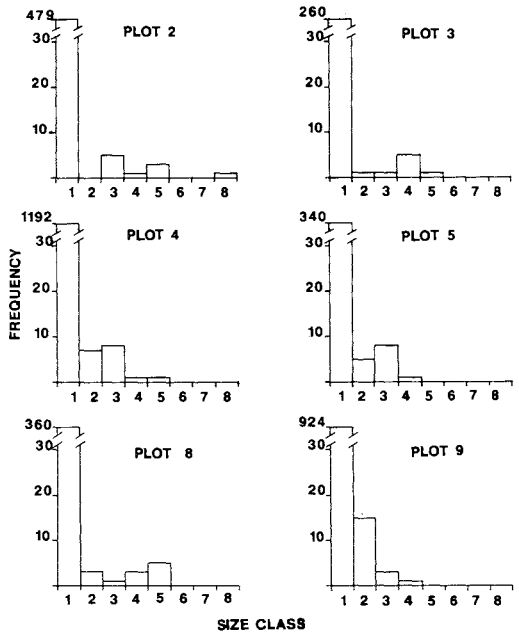

FIG.5 — Frequency-size class distributions for Melaleuca ericifolia *from six sample plots. Stems grouped into 100 mm size classes.*

TABLE 1

Size class (x) and frequency (y) relationships for four samples taken within the *Melaleuca ericifolia* swamp forest. (a) Exponential function, (b) Power function.

Sample no.	Relationship		r	P
1	(a)	ln(y+1) = 38.411-0.513x	-0.608	
	(b)	ln(y+1) = 20.796-1.277ln x	-0.633	<0.05
2	(a)	ln(y+1) = 88.269-0.864x	-0.648	
	(b)	ln(y+1) = 67.997-2.347ln x	-0.762	<0.05
3	(a)	ln(y+1) = 897.823-1.417x	-0.850	<0.05
	(b)	ln(y+1) = 488.947-3.720ln x	-0.920	<0.01
4	(a)	ln(y+1) = 111.756-0.848x-	0.634	
	(b)	ln(y+1) = 108.400-2.566ln x	-0.783	<0.05

of occurrence of seedlings in relation to tree death and canopy gaps would be necessary to determine absolutely whether the observed release from suppression is light (cf. Duncan 1981, Ogden 1985, Read & Hill 1985) or moisture-related (cf. Bowman & Kirkpatrick 1986). However, regenerating seedlings and saplings of *Leptospermum lanigerum* were always present in higher numbers than *Melaleuca ericifolia* under canopy gaps and adjacent to forest edges.

The goodness-of-fit to the power function model suggests that highest mortality occurs in the smaller size classes, but once stems are larger than about 100-200 mm DBH, there is a high probability that they will grow through to old age (i.e. in excess of 200 years). Less data are available for *Leptospermum lanigerum*, but it also appears to have a linear size-age relationship.

The oldest trees in this forest are approximately 200 years old. The age to senescence of *Melaleuca ericifolia* (and of *Leptospermum lanigerum*) is unknown but species of both *Melaleuca* and *Leptospermum* are found as codominants in rainforests (e.g. Jarman & Crowden 1978, Jarman *et al.* 1984), some of which are known to be at least 300 years old (e.g. Brown & Podger 1982). Elsewhere in the northwestern region, these species occur in swamp forests together with *Nothofagus*, *Phyllocladus* and such rainforest understorey shrub species as *Trochocarpa cunninghamii* and *Anopterus glandulosus* (Anon. 1982), and the whole of the region is climatically suited to the growth of rainforest (Jackson 1965).

Thus there may be a seral and/or successional relationship in which these relatively young Myrtaceae-dominated forests are eventually replaced by forests containing the more usual rain-forest dominants. However there is no evidence in the present case of colonization by any rainforest species *sensu* Jarman & Brown (1983) (see appendix). An alternative interpretation is that the *Melaleuca* (and/or *Acacia melanoxylon*) swamp forests represent a deflected climax vegetation, whose occurrence is related to the poor drainage and longevity of seasonal inundation. Further work is necessary to determine whether *Melaleuca/ Leptospermum* are able to grow in periodically anoxic conditions which may limit the growth of *Nothofagus* and *Phyllocladus*. Until such work is undertaken, it is not possible to determine whether *Melaleuca ericifolia* or *Leptospermum lanigerum* in these swamp forests are behaving as "good" rainforest species (cf. Jarman *et al.* 1984).

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APPENDIX

Check-list of vascular plants found in the *Melaleuca ericifolia* swampforest.

PTERIDOPHYTA

Aspidiaceae
Polystichum proliferum

Blechnaceae
Blechnum nudum
Blechnum wattsii

Dennstaedtiaceae
Histiopteris incisa
Hypolepis rugosula

Dicksoniaceae
Dicksonia antarctica

Grammitidaceae
Ctenopteris heterophylla
Grammitis billardieri

Hymenophyllaceae
Hymenophyllum peltatum
Hymenophyllum sp.

Polypodiaceae
Microsorium diversifolium

ANGIOSPERMAE: DICOTYLEDONEAE

Apiaceae
Hydrocotyle javanica

Apocynaceae
Parsonsia straminea

Asteraceae
Cirsium sp.
Helichrysum dendroideum
Senecio sp.

Brassicaceae
Brassica sp.
Cardamine heterophylla

Elaeocarpaceae
Aristotelia peduncularis

Mimosaceae
Acacia melanoxylon

Myrtaceae
Eucalyptus obliqua
E. ovata
Leptospermum lanigerum
Melaleuca ericifolia
M. squarrosa

Onagraceae
Epilobium hirtigerum

Oxalidaceae
Oxalis corniculata

Pittosporaceae
Billardiera longiflora

Polygonaceae
Muehlenbeckia gunnii

Ranunculaceae
Clematis aristata
Ranunculus sp.

Rhamnaceae
Pomaderris apetala

Rosaceae
Acaena novae-zelandiae

Rubiaceae
Coprosma quadrifida

Thymelaeaceae
Pimelea drupacea

Winteraceae
Drimys lanceolata

ANGIOSPERMAE: MONOCOTYLEDONEAE

Cyperaceae
Carex appressa
Gahnia grandis
Lepidosperma elatius
Schoenus maschalinus
Scirpus fluitans

Juncaceae
Juncus effusus