

## Selected specimens examined:

NEW ZEALAND. North Island: North Auckland Land District. Without locality, *Knights n.* (H-SOL); Waipoua Forest, damp bank in forest, on rocks, 16. V. 1944, *Allison 789* (WELT 9992); Te Pahi Trig Bush, on damp clay soils, 13. III. 1976, *Bartlett 11219* (WELT M 8418). South Island: Westland Land District. Kelly's Hill, on log in upper bush level, 1100 m, I. 1943, *Martin 25* (WELT 9991, "First finding in South Island"); Kumara, on damp clay soils, 23. XII. 1978, *Bartlett 14216* (WELT M 8419).

## ACKNOWLEDGMENTS

We thank the Curators of BM, CHR, GL, and WELT for the loan of specimens, and Mr. Heinar Streimann (CBG) for information regarding *Pendulothecium punctatum*. The constructive comments which Prof. Timo Koponen (Helsinki), Prof. Daniel H. Norris (Arcata), Dr. Ryszard Ochyra (Kraków), and an anonymous referee made on the manuscript are gratefully acknowledged. The work was financially supported by the Emil Aaltonen Foundation (Tampere, Finland), the Academy of Finland, and the University of Cincinnati (Ohio, USA).

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## Ecology of a coastal lagoon to dune forest sequence, south Westland, New Zealand

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**Abstract** The vegetation and floristic patterns in and around a coastal lagoon are described from quadrat sampling and related to several environmental factors (elevation, water depth, soil organic content, and pH). A cluster analysis was used to identify 14 communities while a detrended correspondence analysis ordinated the quadrats. The ordination's Axis 1 was correlated with water depth/elevation, while Axis 2 was correlated with soil organic content and, in the opposite direction, with soil pH.

Two vegetation development sequences are proposed for the dune hollow-ridge system: one in the hollows involving stages of aquatic, bog, and forest vegetation; the second on the ridges where forest composition changes in response to increasing soil development. Rates of succession are presumably very slow.

Formal protection of the lagoon within the World Heritage area is justified because of its ecological, conservation, and scenic values; in light of diminishing natural wetlands; and the common occurrence of a vulnerable macrophyte, *Myriophyllum robustum*, in the lagoon.

**Keywords** vegetation sequence; vegetation analysis; wetland; dune forest; ecological factors; Haast Ecological District

## INTRODUCTION

The lowland outwash gravel and coastal terraces of south Westland are replete with permanent wetlands and adjoining sequences of shrubland, woodland, and forest vegetation associated with increased elevation and lower water tables (Mark & Smith 1975; Dawson 1988, fig. 68; Norton 1989). Distinctive examples of such wetland sequences, unlike any of those previously described, are associated with the series of coastal and near-coastal sand dune-hollow alternations on the South Westland coastal plain of the Paringa and Haast Ecological Districts. One example is alongside State Highway 6 in Mataketake Forest c. 3 km north of the Waita River. Here, a coastal lagoon merges with mature mixed podocarp-broadleaved dune forest via zones of sedgeland and shrubland (Fig. 1).

The aims of the study were to describe the vegetation zonation pattern and relate this to environmental parameters. The communities described by Wardle (1977) from Westland National Park, although some distance to the north, can be compared in some cases, though Wardle did not define aquatic communities, and any coastal dune forest in his area had been either disturbed or removed.

## THE STUDY AREA

The lagoon studied (Fig. 1) is between old dunes within c. 10 m elevation and 100 m distance of the coast (Fig. 2), lying in a depression bounded on the seaward side by an active dune front and on the inland side by a stabilised dune crest. Located between the Waita River and Ship Creek (Fig. 2) the lagoon forms a typical unit of the long, narrow coastal plain between the Arawata River in the south and the coastal hills north of the Waita River. As such, a detailed study of the vegetation and associated



Fig. 1 View south-west from the north-eastern end of the lagoon showing the vegetation zonation pattern. Reed beds of *Eleocharis sphacelata* stand in moderately deep open water and adjoin a zone of stunted *Leptocarpus similis* (jointed rush) which in turn merges with stunted *Leptospermum scoparium* (manuka) that increases in height with progression towards a low forest dominated by *Dacrydium cupressinum* (rimu) and *Weinmannia racemosa* (kamahi). The position from which the photo was taken is indicated in Fig. 3.

environmental factors seemed relevant to a fuller understanding of patterns and processes in and around the lagoon. Mutch & McKellar (1975) characterise the coastal plain as having "steep-sided, dome-shaped, ice-smoothed hills and coastal swamps fronted by active and fixed sand dunes and broad gravel and sand beaches". The beach deposits are derived from marine and fluvial material of very recent origin, certainly < 5000 yr. At the northern end of the lagoon is an outcrop corresponding to the southern-most extension of a much older transgressive series of marine and alluvial deposits dating back to the Paleocene (Mutch & McKellar 1975).

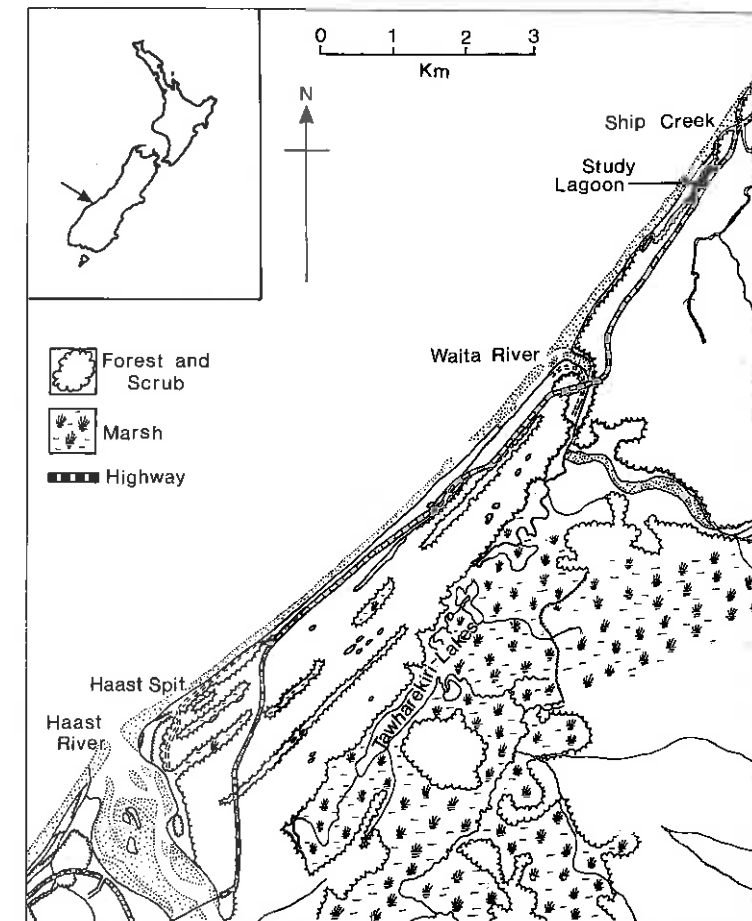
The lagoon, c. 1.5 km × 0.1 km, is elongated parallel to the shoreline with only a narrow vegetated dune separating it from the beach proper. The beach has a steep small-bouldered foreshore topped with a broad dune ridge and with a sandy backslope

colonised largely by *Desmoschoenus spiralis*\* (pingao) that is bounded by a *Phormium tenax* (New Zealand flax) tall-graminoid community which in turn grades into podocarp-broadleaved dune forest. The presence of tracks indicated occasional entry by cattle, though none were seen and there was no sign of grazing impact. The canopy plants are obviously wind-shorn with a general pattern similar to that described at Cole Creek c. 4 km northwards by Sykes & Wilson (1991). The parallel series of dune ridges and wet inter-dune hollows is particularly well developed immediately south of the Waita River.

The climate of the coastal plain area, as characterised by long-term records from Haast

\*For pteridophytes nomenclature follows Brownsey & Smith-Dodsworth (1989), for other vascular plants Connor & Edgar (1987), and references therein.

Fig. 2 Locality map showing the study lagoon and the series of parallel dune ridges and hollows south of the Waita River.



(4 m a.s.l.), on the coast 15 km to the south-west, is perhumid mesothermal (Garnier 1951) with high, evenly distributed rainfall (3455 mm annual mean; 178 rain days per year) and relatively mild temperatures (mean annual air temperature 11.3°C) with only slight diurnal and seasonal fluctuations (New Zealand Meteorological Service 1983). Air frosts (at 1.3 m) occur on average only 7.5 days a year between May and October while ground frosts occur on c. 55 days annually. Despite the high rainfall and numerous raindays, sunshine duration is relatively high: 1853 hours annually or 44% of the possible total. Fog and snow are both uncommon (6.6 and 0.8 days annually).

## METHODS

### Vegetation and site sampling

Five transects were randomised across the short axis of the lagoon (Fig. 3), extending from the road verge on the east and including at least the low forest on the

western (coastal) side. These criteria resulted in transects 160–200 m long. Quadrats (1 m × 1 m) were located on a restricted random basis in a 20 m wide belt, the total number of quadrats being 322. The presence/absence of all terrestrial and aquatic vascular plant species was recorded for each quadrat. (The quadrat size was chosen to minimise the problem of a quadrat overlapping zones where the vegetation gradient was steep; quadrats contained up to 10 species, even in the mature forest.) Canopy height was estimated above ground or water level each 5 m along the centreline of each transect, while measurements of ground elevation or water depth (with level or a weighted line) were made in each quadrat.

A soil sample (0–10 cm) was removed from the centre of each terrestrial quadrat (Table 1) and analysed in duplicate for colour (using Munsell standard soil colours), pH (after 1:1 by volume dilution with distilled water), and organic matter (igniting oven-dried samples at 700°C for 2 h). From our knowledge of the soils we do not believe

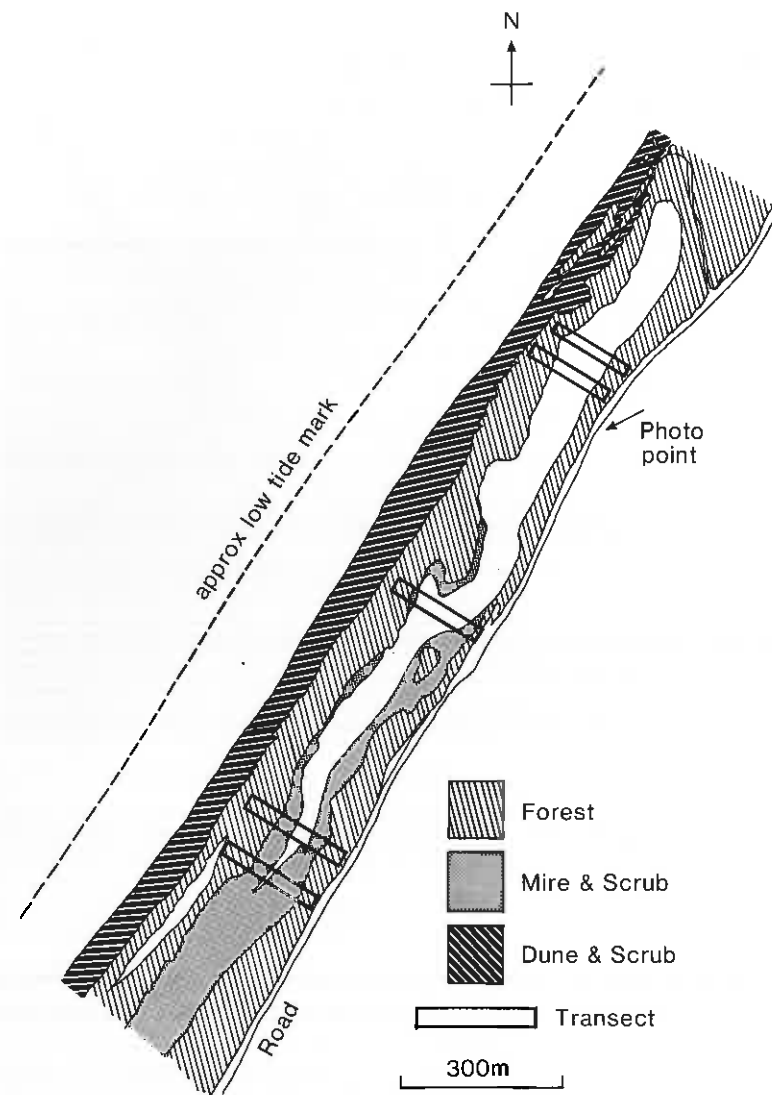


Fig. 3 Positions of the transects (numbered from north to south – see Fig. 6), and the photograph point for Fig. 1.

that charcoal or colloid-bound water represent a significant problem in organic matter determination. (We did not take soil samples from aquatic quadrats because of the total number of quadrats involved and because we considered that water regime, not soil characters, would be the over-riding environmental factor.) Vegetation, water level, and soil sampling was carried out in April and May, 1984.

Three water samples were taken in the centre of the lagoon, and three at its north end, and analysed for pH, conductivity, and chlorinity.

#### Analyses of data

The presence/absence data were ordinated with Detrended Correspondence Analysis (Hill & Gauch

1980). Flexible sorting strategy ( $\beta = -0.25$ ) with the complement of the Simple matching coefficient was used to produce a Cluster Analysis (Clifford & Stephenson 1975), the dendrogram truncated at the level of 8 groups (designated "types") and also at the finer level of 14 subgroups ("communities"). This seemed to be the minimum number of communities that adequately described the ecological gradient. Scores for the first two axes of the ordination were used as dependent variables in simple regressions on elevation, soil pH, and soil organic content. Soil colour was compared with the vegetation types obtained from the Cluster Analysis using  $\chi^2$  tests. The other environmental parameters were assessed against the vegetation types by Analysis of Variance.

Table 1 The major species and their frequency in the vegetation groupings. Life forms in the study area according to Raunkaer (Braun-Blanquet 1932), for the first 7 categories according to the height above ground (/water) of the resting buds in winter: Ps (Mesophanaerophyte) 8–30m, Pc (Microphanaerophyte) 2–8m, Pn (Nanophanaerophyte) 0.25–2m, Ch (Chamaephyte) 1–25cm, H (Hemicryptophyte) 0, Cr (Cryptophyte) <0, E epiphyte, L liane.

Species	Life form	Total no. of Occurrences	Plant community													
			A <sub>1</sub>	A <sub>2</sub>	A <sub>3</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	C <sub>1</sub>	C <sub>2</sub>	D <sub>1</sub>	D <sub>2</sub>	E	F	G	H
<b>Ferns and fern allies</b>																
<i>Asplenium bulbiferum</i>	H	22	7			30	8	19								
<i>Asplenium flaccidum</i>	E	45	4	18		44	42	26								
<i>Blechnum capense*</i>	H	86	59	74	73	21	19									
<i>Blechnum discolor</i>	Pn	22	37	5		23										
<i>Blechnum procerum</i>	H	27	70	10	7	2	4	4								
<i>Ctenopteris heterophylla</i>	E	22	37	3	27	14				5						
<i>Dicksonia squarrosa</i>	Pc	95	26	26	13	74	65	100								
<i>Gleichenia dicarpa</i>	H	18	4	13						15	57		7			
<i>Grammitis billardieri</i>	E	16	19	5		14	4	7								
<i>Hymenophyllum demissum</i>	E	39	48	23	40											
<i>Hymenophyllum dilatatum</i>	E	15	4			30	4									
<i>Hymenophyllum ferrugineum</i>	E	7		3		14										
<i>Hymenophyllum multifidum</i>	E	22	15	5	40	2	4	7	30							
<i>Hymenophyllum rarum</i>	E	7		3		14										
<i>Hymenophyllum revolutum</i>	E	10	4	3		14										
<i>Hymenophyllum sanguinolentum</i>	E	49	52	15	7	30	46	7								
<i>Lastreopsis hispida</i>	H	6		3		2		15								
<i>Phymatosorus diversifolius</i>	Ch	46	26	23	13	33	42	7								
<i>Pyrrosia eleagnifolia</i>	E	24		3	7	21	46	4								
<i>Rumohra adiantiformis</i>	E	34	4	5		53	4	26								
<i>Tmesipteris tannensis</i>	E	9	7	13		5										
<i>Trichomanes reniforme</i>	E	50	48	33		49		11								
<b>Conifers</b>																
<i>Dacrycarpus dacrydioides</i>	Ps	53		13	47	35	46	26	20				10			
<i>Dacrydium cupressinum</i>	Ps	62	74	54		19	31	4	15	7						
<i>Lagarostrobos colensoi</i>	Pn	51	74	18	53	2	31	4	5				13			
<i>Phyllocladus alpinus</i>	Pc	6	15	3					5							
<i>Prumnopitys ferruginea</i>	Ps	24	15	8		3	8	4								
<i>Podocarpus hallii</i>	Ps	20	11	3	7	12	8	30								
<b>Dicotyledons</b>																
<i>Ascarina lucida</i>	Pc	20		21		19	4	11								
<i>Carpodetus serratus</i>	Pc	8		3			23	4								
<i>Coprosma ciliata</i>	Pn	22	19	26	13	2	8	4	5							
<i>Coprosma colensoi</i>	Pc	14	37	3			4	7								
<i>Coprosma foetidissima</i>	Pc	31	63	15		19										
<i>Coprosma lucida</i>	Pc	29	19	23	13	21	8	4	5							
<i>Coprosma propinqua</i>	Pc	37	4	13	87	9	35	11	10							
<i>Coprosma rhamnoides</i>	Pc	64	67	8	7	49	54	26								
<i>Coprosma rotundifolia</i>	Pc	25				20	5	58	19							
<i>Coprosma aff. intertexta</i>	Pc	12								50	14					
<i>Coprosma cf. parviflora</i>	Pc	10	4	15			4	4	5							
<i>Elaeocarpus hookerianus</i>	Ps	5		3	7			3	5							
<i>Griselinia littoralis</i>	Pc	13		10	13	5	4	4	5		3					
<i>Hedycarya arborea</i>	Pc	50		3	7	44	69	41								
<i>Hydrocotyle sp.</i>	H	6		3	27										7	
<i>Leptospermum scoparium</i>	Pc	26		23	27					90	64					
<i>Melicytus ramiflorus</i>	Pc	13			6	7	27	7								
<i>Metrosideros diffusa</i>	Pl	149	81	82	20	93	96	100								
<i>Metrosideros fulgens</i>	Pl	26	26	26	21	27										
<i>Muehlenbeckia australis</i>	Pl	19		18	27	5	8	11	5							

(continued)

Table 1 (continued)

	Life form	Total no. of Occurrences	Plant community															
			A <sub>1</sub>	A <sub>2</sub>	A <sub>3</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	C <sub>1</sub>	C <sub>2</sub>	D <sub>1</sub>	D <sub>2</sub>	E	F	G	H		
<i>Myriophyllum pedunculatum</i>	Cr	5								15								
<i>Myriophyllum robustum</i>	Cr	46			7					30							100	44
<i>Myrsine australis</i>	Pc	19	15	5		12	19	11	5									
<i>Myrsine divaricata</i>	Pc	40	37	18	40	21	15	4	5									
<i>Neomyrtus pedunculata</i>	Pc	51	52	33	13	23	46											
<i>Nertera depressa</i>	Ch	16	15	8	13	2	15	4	5									
<i>Nertera scapanioides</i>	Ch	5								10	21							
<i>Nertera cf. dichondrifolia</i>	Ch	47	63	15		26	50											
<i>Parsonsia heterophylla</i>	Pl	23	4		7	5	38	33										
<i>Pseudopanax colensoi</i>	Pc	11	11	8		12												
<i>Pseudopanax crassifolius</i>	Pc	27	11	15	7	12	35	7	5									
<i>Pseudowintera colorata</i>	Pc	6				5	4	11										
<i>Rubus australis</i>	Pl	9			3	5												
<i>Weinmannia racemosa</i>	Ps	144	93	87	27	95	46		15							13	100	
Unidentified aquatic weed	Cr	13			13													
<b>Monocotyledons</b>																		
<i>Astelia grandis</i>	H	9	7		5	15			5									
<i>Baumea tenax</i>	H	121	4	15					100	100	100	100					100	
<i>Carex virgata</i>	H	8			27	2	4		5									
<i>Centrolepis ciliata</i>	H	7							5	14		29						
<i>Earina autumnalis</i>	E	7	4	13			4											
<i>Eleocharis sphacelata</i>	Cr	71												7	100	100	91	86
<i>Freycinetia baueriana</i> †	Pl	53	4	87	13	33	4	4										
<i>Gahnia xanthocarpa</i>	H	49	74	15	53	23	8		15									
<i>Lepidosperma australe</i>	H	15							5	100								
<i>Leptocarpus similis</i>	H	25							45	29	3	86						
<i>Luzuriaga parviflora</i>	E	5	19															
<i>Microlaena avenacea</i>	H	8				7	15	4										
<i>Phormium tenax</i>	H	12	3	27			4		30									
<i>Potamogeton cheesemanii</i>	Cr	8			13									43		9	3	
<i>Ripogonum scandens</i>	Pl	46	4	5	13	53	50	19										
<i>Uncinia ?angustifolia</i>	H	20	41	6	5	5	8											
<i>Uncinia ?uncinata</i>	H	18	3	7	19	19	11											

\*sensu Allan (1961)

†ssp. *banksii*

The Teddybear (Wilson 1975) multivariate package was used for both the regressions and analysis of variance.

## RESULTS AND INTERPRETATION

The vegetation types and communities derived from Cluster Analysis (Fig. 4, Table 1) are confirmed by the ordination diagram (Fig. 5). The types are described in sequence. Comparisons with Wardle's (1977) communities are made only when there were comparable communities in his area.

### Type A: podocarp - *Weinmannia* forest

Community A<sub>1</sub>: *Dacrydium* - *Lagarostrobos* - *Weinmannia* forest

*Dacrydium cupressinum* (rimu) and *Lagarostrobos colensoi* (silver pine) along with *Weinmannia racemosa* (kamahi), form a low forest c. 9 m tall, of relatively uniform diameter trees. A shrub layer of *Coprosma foetidissima*, *C. rhamnoides*, and *Neomyrtus pedunculata* is associated with a herb layer in which *Gahnia xanthocarpa*, *Blechnum capense* (sensu Allan 1961), *B. procerum*, and *B. discolor* (crown fern) are all conspicuous. Beneath these is a ground cover of a fine-leaved *Uncinia ?angustifolia*, *Nertera cf. dichondrifolia*, *Luzuriaga parviflora* (lantern berry), *Trichomanes reniforme* (kidney fern) and *Hymenophyllum demissum*, with *H. sanguinolentum* a common epiphyte on podocarp trunks. Lianes of *Metrosideros diffusa* are present on most trees with the larger leaved *M. fulgens* less frequent.

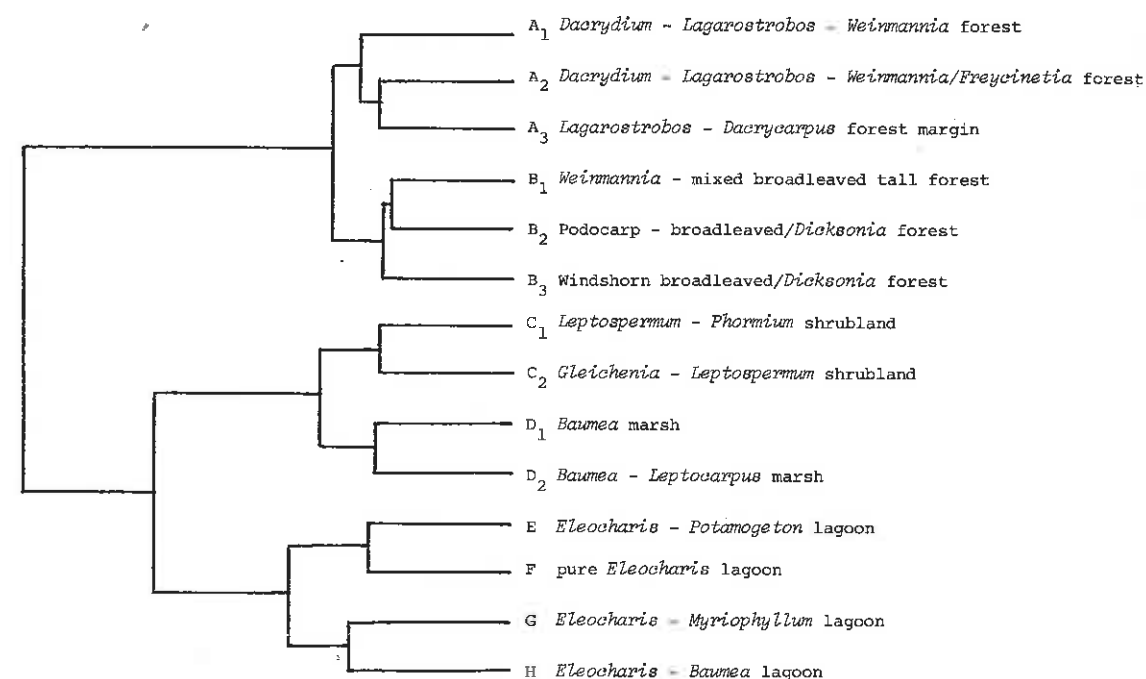
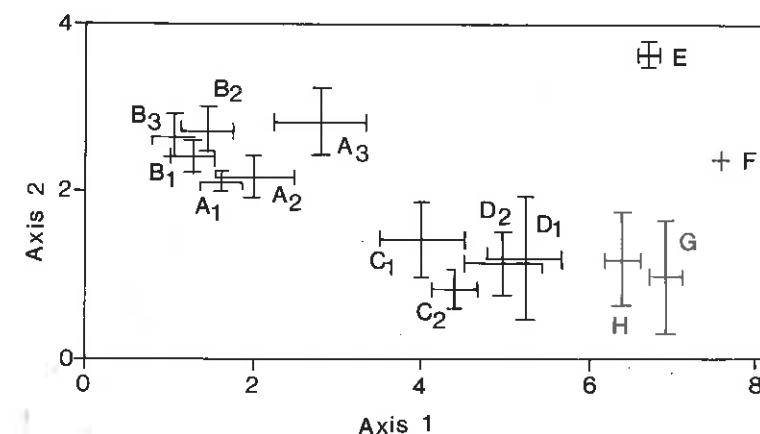


Fig. 4 Results of the normal Cluster Analysis showing the 14 vegetation types recognised.

Fig. 5 Two-dimensional ordination showing the position (with standard deviation) of each of the 14 vegetation types (notation as in Fig. 4).



This community corresponds generally to the "Type B3e forest (rimu/kamahi-quintinia)" that Wardle (1977) described in Westland National Park, to the north of our study area, except that the latter is beyond the southern limit of *Quintinia acutifolia*. It occupies the better drained sites several metres above water level on the eastern side of the lagoon. Community A<sub>2</sub>: *Dacrydium* - *Lagarostrobos* - *Weinmannia* / *Freycinetia* forest

This community is characterised by vigorous development of *Freycinetia baueriana* ssp. *banksii* (kiekie) which forms a tangled mass beneath the canopy of *Dacrydium cupressinum* and *Weinmannia racemosa*. *Lagarostrobos colensoi* is less prevalent than in community A<sub>1</sub>. The *F. baueriana* virtually excludes shrubs and small-trees and the ground is only sparsely vegetated, being inundated with water during frequent heavy rain. *Blechnum procerum* is the only near-constant herb.

Stands occupy the small terrace adjacent to the lagoon and close to its water level. Largely restricted to the lagoon's eastern side, they are exposed to onshore winds and are windshorn. The canopy is usually somewhat lower than in community A<sub>1</sub>.

**Community A<sub>3</sub>: *Lagarostrobos* - *Dacrycarpus* forest margin**

Restricted to the forest edge on both sides of the lagoon, this community is characterised by immature *Lagarostrobos colensoi* and saplings of *Dacrycarpus dacrydioides* (kahikatea). *Weinmannia racemosa* is less common than in other types and *Dacrydium cupressinum* is absent. It corresponds to Wardle's (1977) type B1 forest (open kahikatea forest transitional to swamps). Shrubs are common, especially *Coprosma propinqua* and *Myrsine divaricata*, while the large herbs *Gahnia xanthocarpa* and *Blechnum procerum* are also conspicuous. *Leptospermum scoparium* (manuka) occurs near the margin of the lagoon together with *Carex virgata* and occasional *Phormium tenax*. Ground cover varies with the amount of free water; *Hymenophyllum demissum* is usually present but *Nertera* cf. *dichondrifolia* is rarely so. The more light-demanding *H. multifidum* replaces *H. sanguinolentum* of the A<sub>1</sub> community as the most frequent epiphyte.

**Type B: *Hedycarya* - *Weinmannia* / *Dicksonia* forest**

**Community B<sub>1</sub>: *Weinmannia* - mixed broadleaved tall forest**

*Weinmannia racemosa* is the main canopy dominant at c. 8 m in this community, with only sparse podocarps - *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*. Subcanopy species include *Dicksonia squarrosa* and the broadleaved *Ascarina lucida*, *Hedycarya arborea* (pigeonwood), and *Coprosma lucida*. *Coprosma rhamnoides*, *C. foetidissima*, *Myrsine divaricata*, and *Neomyrtus pedunculata* predominate among the shrubs with occasional *Freycinetia baueriana* and *Gahnia xanthocarpa* in the herb layer. *Rumohra adiantiformis* and *Trichomanes reniforme* are common ground ferns while *Asplenium flaccidum* and several filmy ferns (*Hymenophyllum* spp.) are epiphytic. Lianes of *Metrosideros diffusa* and *Ripogonum scandens* (supplejack) are abundant.

This community occupies the sloping banks on the lagoon's eastern side that are better drained than the flatter terraces above and below it, or as taller dune forest on the coastal side of the lagoon.

**Community B<sub>2</sub>: podocarp - broadleaved / *Dicksonia* forest**

This community differs from the B<sub>1</sub> community in

its dominant species rather than its physiognomy. *Hedycarya arborea* is common in the canopy, *Weinmannia racemosa* is less common, and *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, and *Lagarostrobos colensoi* are all of minor but consistent occurrence. *Dicksonia squarrosa* is again common in the subcanopy stratum but *Carpodetus serratus* and *Melicytus ramiflorus* may occur as canopy or subcanopy species. Shrubs of *Coprosma rotundifolia* are characteristic with less of *C. rhamnoides*, *C. propinqua*, or *Neomyrtus pedunculata*. *Hymenophyllum sanguinolentum* is common as an epiphyte with *Phymatosorus diversifolius* and *Pyrrosia eleagnifolia* as climbers. Other ferns found in the B<sub>1</sub> community are largely absent. Ground cover is composed of *Nertera* cf. *dichondrifolia* with occasional *Microlaena avenacea* (bush rice grass) and *Uncinia* spp. Lianes (*Ripogonum scandens*, *Metrosideros diffusa*, and less *Parsonsia heterophylla*) are again abundant.

This community is restricted to the lagoon's coastal side in the forest zone least exposed to salt-laden winds and sufficiently elevated to avoid waterlogged soils.

**Community B<sub>3</sub>: windshorn broadleaved / *Dicksonia* forest**

This community, occurring near the foreshore margin of the coastal forest, is depressed and sculptured by salt-spray. It includes the podocarps *Podocarpus hallii* (thin-barked totara) and *Dacrycarpus dacrydioides* as well as *Hedycarya arborea*. *Weinmannia racemosa* is absent. *Dicksonia squarrosa* alone forms the sub-canopy layer with the shrub species of *Coprosma* listed for the B<sub>2</sub> community much less common. *Lastreopsis hispida* is a common ground fern while other ferns are more minor than in communities B<sub>1</sub> and B<sub>2</sub>. Lianes of *Muehlenbeckia australis*, *Lycopodium volubile*, *Ripogonum scandens*, and *Parsonsia heterophylla* are frequent. This community is relatively poor floristically, perhaps due to occasional grazing by cattle.

**Type C: *Leptospermum* shrubland**

**Community C<sub>1</sub>: *Leptospermum* - *Phormium* shrubland**

A 2 m tall *Leptospermum scoparium* shrubland with occasional co-dominant *Phormium tenax* and two common graminoid subdominants, *Baumea tenax* and *Leptocarpus similis* (jointed rush), plus *Coprosma* cf. *intertexta*, is located alongside and grades into the margin of forest community A<sub>3</sub>. This

shrubland contains occasional seedlings (< 30 cm) of *Weinmannia racemosa*, *Dacrydium cupressinum*, and *Dacrycarpus dacrydioides*.

**Community C<sub>2</sub>: *Gleichenia* - *Leptospermum* shrubland.**

Beyond the *Leptospermum* - *Phormium* shrubland, *L. scoparium* becomes more sporadic and smaller (c. 1 m) and is commonly associated with *Gleichenia dicarpa* (tangle fern). Three graminoids are also present, with *Lepidosperma australe* and *Baumea tenax* more common than *Leptocarpus similis*.

**Type D: *Baumea* - *Leptocarpus* marsh**

**Community D<sub>1</sub>: *Baumea* marsh**

Increasingly extensive areas of almost pure *Baumea tenax* occur towards the southern end of the lagoon.

**Community D<sub>2</sub>: *Baumea* - *Leptocarpus* marsh**

This community is generally similar to community D<sub>1</sub> but with the addition of *Leptocarpus similis*. The small graminoid cushion *Centrolepis ciliata* is frequently present. This community occurs in isolated patches among the *Baumea* marsh community and seems to be associated with slightly shallower water.

**Type (Community) E: *Eleocharis* - *Potamogeton* lagoon**

This community was found towards the northern end of the lagoon and consists of *Eleocharis sphacelata*, frequent plants of *Potamogeton cheesemani*, and an unidentified aquatic macrophyte.

**Type (Community) F: pure *Eleocharis* lagoon**

Occasional sites throughout the lagoon contain pure stands of *E. sphacelata*.

**Type (Community) G: *Eleocharis* - *Myriophyllum* lagoon**

In the central parts of the lagoon, in deep water, *E. sphacelata* and *Myriophyllum* spp. are accompanied by occasional plants of *Potamogeton cheesemani*.

**Type (Community) H: *Eleocharis* - *Baumea* lagoon**

In water more shallow than that associated with the *Eleocharis* - *Potamogeton* community, mostly at the southern end of the lagoon, *E. sphacelata* and *B. tenax* co-dominant. *Myriophyllum robustum* is less frequent, occurring in about half the quadrats.

**Zonation**

Results of three of the transects are summarised as profile diagrams (Fig. 6) which also show the distribution of the 14 communities.

In the ordination (Fig. 5), Axis 1 accounts for most of the variation in species composition and

reveals a gradient of increasing wetness with increasing ordination score. Axis 2 is less obviously related to the communities.

**Correlations with environmental parameters**

Mean values for four environmental variables among the plant communities previously described are shown in Table 2, together with results of Duncan's New Multiple Range Tests.

**Elevation**

Both analysis of variance and Duncan's test (Table 2) indicate that elevation is a significant factor in differentiating many of the 14 communities recognised. Moreover, a regression of mean elevation of a quadrat against its ordination scores showed a strong relationship with Axis 1 scores for quadrats less than 2 m above the lagoon surface (negative;  $R^2 = 0.75$ ;  $n = 281$ ;  $P < 0.001$ ). The importance of water (depth or drainage) is again implied in determining the vegetation pattern, though other effects of elevation, e.g., on salt spray, may also be important.

There was no significant relation between elevation of quadrats more than 2 m above the lagoon and ordination values on either axis. A weaker relation occurred between quadrat elevation and Axis 2 (positive;  $R^2 = 0.13$ ;  $n = 281$ ;  $P < 0.001$ ), again excluding those quadrats more than 2 m above the lagoon.

**Soil organic content**

There were significant differences in the organic content (% of dry weight) of soil associated with the five forest types that occur above the water level (Table 2).

The lower values in the three B-type communities are related to their location on sandier and steeper sites than the more or less permanently waterlogged sites that characterise A-type forest. Significant regressions were found between soil organic content and ordination scores on both Axis 1 (positive;  $R^2 = 0.28$ ;  $n = 141$ ;  $P < 0.001$ ) and Axis 2 (negative;  $R^2 = 0.25$ ;  $n = 141$ ;  $P < 0.001$ ).

**Soil acidity**

Soil pH varied significantly with vegetation, the A-type forest associations being more acidic than the B-type (Table 2). Only Axis 2 of the ordination, however, relates to pH (positive;  $R^2 = 0.28$ ;  $n = 141$ ;  $P < 0.001$ ).

**Soil colour**

$\chi^2$  tests showed significant differences in soil colour between communities (Table 2), confirmed for both axes of the ordination with ANOVA.

**Water analysis**

There was no indication of a difference between water samples taken from the two different parts of the lagoon. Overall means are therefore presented (Table 3).

**Species richness**

Defined as the number of species per quadrat, this is a simple but meaningful measure of species diversity.

It showed overall a significant decrease (negative;  $R^2 = 0.77$ ;  $n = 322$ ;  $P < 0.001$ ) towards the positive (dry) end of ordination Axis 1.

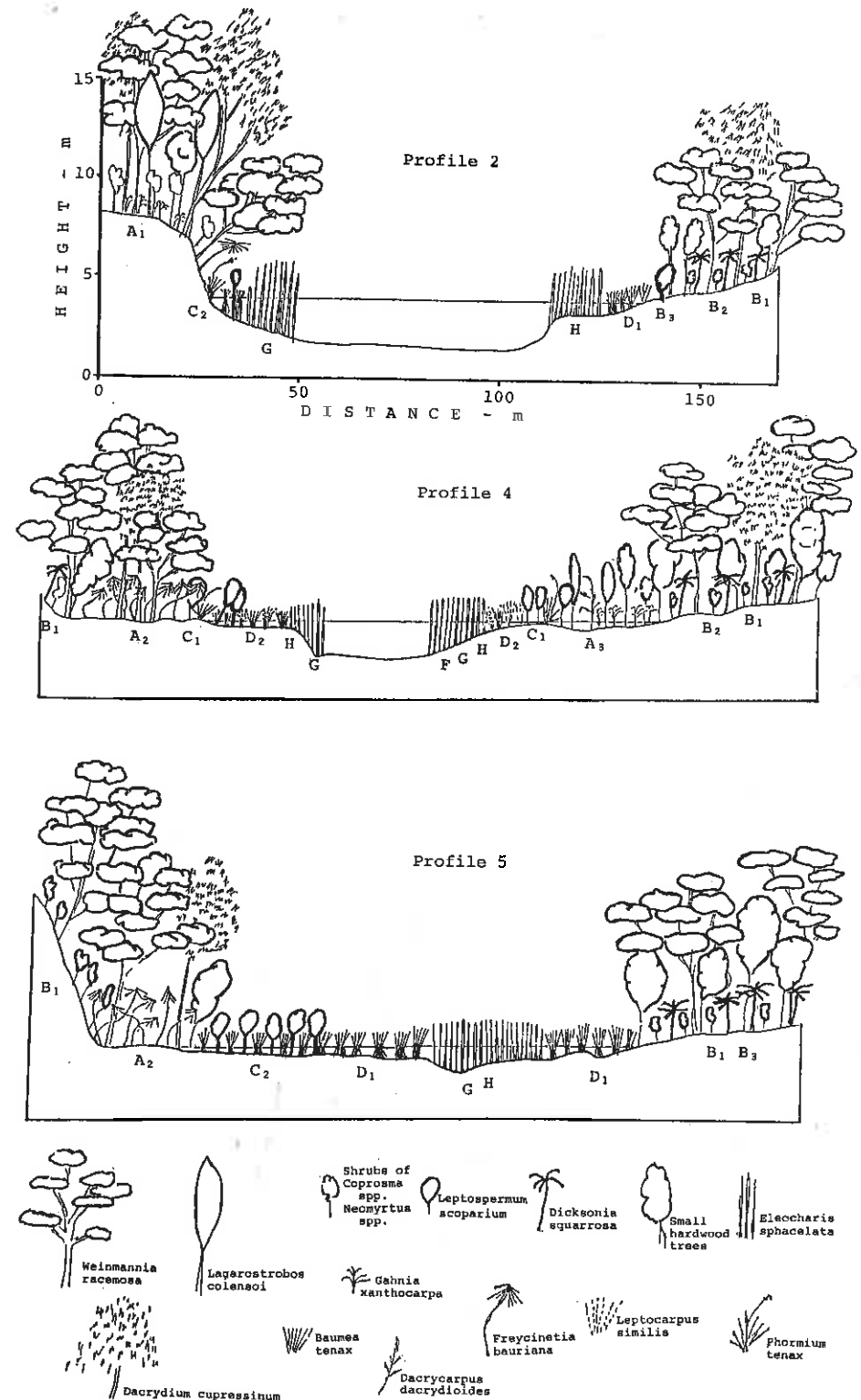
**CONCLUSIONS**

Ordination Axis 1 has been shown to represent the pattern of the dune-hollow sequence which is

**Table 2** Mean values for four environmental parameters associated with the 14 plant associations recognised. Elevation is shown in relation to the lagoon surface. Letters shared within each factor indicate no significant difference with Duncan's New Multiple Range Tests at  $P < 0.05$ . For soil colour, "brownish-black" was the most frequent in all communities and the "characteristic soil colour" indicates the next most frequent.

Community	No. of quadrats	Elevation (cm)	Soil organic content (%)	Soil pH	Characteristic soil colour
A <sub>1</sub> <i>Dacrydium</i> - <i>Lagarostrobos</i> - <i>Weinmannia</i> forest	28	+473 a	30.2 b	4.09 a	olive-black
A <sub>2</sub> <i>Dacrydium</i> - <i>Lagarostrobos</i> - <i>Weinmannia</i> / <i>Freyinetia</i> forest	35	+106 b	56.0 a	4.30 b	black
A <sub>3</sub> <i>Lagarostrobos</i> - <i>Dacrycarpus</i> forest margin	15	+11 cde	-	-	-
B <sub>1</sub> <i>Weinmannia</i> - mixed broadleaved tall forest	43	+129 b	23.8 b	4.47 bc	black/dark brown
B <sub>2</sub> <i>Podocarp</i> - broadleaved / <i>Dicksonia</i> forest	27	+42 cd	9.7 c	4.86 d	olive-black
B <sub>3</sub> Windshorn broadleaved / <i>Dicksonia</i> forest	25	+41 c	12.1 c	4.67 cd	dark olive brown
C <sub>1</sub> <i>Leptospermum</i> - <i>Phormium</i> shrubland	20	-26	def	-	-
C <sub>2</sub> <i>Gleichenia</i> - <i>Leptospermum</i> shrubland	14	-16	cdef	-	-
D <sub>1</sub> <i>Baumea</i> marsh	28	-40 ef	-	-	-
D <sub>2</sub> <i>Baumea</i> - <i>Leptocarpus</i> marsh	14	-29 def	-	-	-
E <i>Eleocharis</i> - <i>Potamogeton</i> lagoon	7	-68 efg	-	-	-
F pure <i>Eleocharis</i> lagoon	11	-148 g	-	-	-
G <i>Eleocharis</i> - <i>Myriophyllum</i> lagoon	21	-143 g	-	-	-
H <i>Eleocharis</i> - <i>Baumea</i> lagoon	34	-78 fg	-	-	-

**Fig. 6** Profile diagrams for three of the belt transects sampled across the lagoon. Vegetation types (notation as in Fig. 4) and important species (dominant or frequent) are shown. All profiles are drawn with the inland side to the left.



correlated with site elevation, water depth and soil organic content. For purely terrestrial sites, this will represent soil water availability; for aquatic sites it will represent depth of water, possibly acting via light limitation on the bed; for intermediate sites it represents the frequency and duration of waterlogging. Sites at higher elevation will also be more subject to salt spray.

The zonation we recorded suggests that succession within the lagoon starts with establishment of a bed of tall emergent *Eleocharis sphacelata*. This contributes organic matter while probably trapping wind-blown sand and other material. The substrate is gradually built up, we suggest, until at a water depth of c. 1 m (Table 2) the site comes within the tolerance range of *Baumea tenax*. Later, with continued accumulation of substrate, *Leptocarpus similis* and *Lepidosperma australe* invade, then, in approximate order, *Leptospermum scoparium*, *Gleichenia dicarpa*, *Phormium tenax*, and *Blechnum procerum*. Pedestals of turf build up around the bases of *L. scoparium* and *P. tenax* plants and provide sites for seedling establishment of forest tree species such as *Lagarostrobos colensoi*, *Dacrydium dacrydioides* and *Phyllocladus alpinus*. These species also dominate the first forest stand on the dunes.

Examination of species richness indicates that the deepest water is colonised by a few dominant species. These are replaced by an increasing number of species with narrower alpha niches as water depth decreases. As species diversity increases so also does plant stature and presumably also biomass.

The suggested developmental sequence is expressed as concentric zones around the lagoon. Development appears to have occurred fastest at the southern end of the lagoon, where water enters. Here *Leptospermum* shrubland (Type C) and *Baumea-Leptocarpus* marsh (D) are well established, while small clumps of trees, particularly of *Lagarostrobos colensoi* and *Dacrydium dacrydioides*, up to 2–3 m tall are common. The northern end shows the least development with small patches of *Eleocharis sphacelata* only 2–3 m wide bordering large expanses of open water.

Table 3 Analysis of lagoon water.

	mean	s.e. of mean
pH	5.6	0.15
Conductivity (m Sm <sup>-1</sup> )	3.88	0.174
Chlorinity (mg l <sup>-1</sup> Cl)	13.5	0.15

Development of the wetland sequence proceeds through a pakihi-like phase (community types C and D) with occasional small forest trees. ("Pakihi" is a regional name for an oligotrophic mire amid forest: Mew 1983.) The fate of this community is indicated by forest stands, mostly of communities A<sub>2</sub> and A<sub>3</sub>, on the flat areas adjacent to the marsh vegetation. A narrow fringe of *Gahnia xanthocarpa* and *Blechnum procerum*, characteristic of the A<sub>3</sub> community, forms the initial understorey but as the podocarps increase in size *Weinmannia racemosa* and *Dacrydium cupressinum* become established. *Freycinetia baueriana* largely replaces most other subcanopy species and forest community A<sub>2</sub> apparently persists for an extended period, though a broadleaved forest (Community type B) may substitute for the mixed podocarp-*Weinmannia* type (A).

Results of waterlogging experiments (Robertson, unpublished) indicated that most local species are limited less by decreased waterlogging than by decreased light levels under the developing forest canopy. Absence of *Dacrydium dacrydioides* from the sequence possibly is due to low soil fertility (Wardle 1974).

Vegetation sequences similar to those described here have received some attention from Cockayne (1928), and most recently from Wardle (1980) and Norton (1989). Wardle examined a range of primary successions in Westland, including a sequence very similar to that described here. The mire-forest sequence described by Norton from Saltwater Ecological Area, 130 km to the north, bears some resemblance to that on the lagoon margin, but the substrates and the pH differ and the Saltwater sequence is considered to be essentially static (Norton op. cit.).

The dune ridges obviously support a different development sequence. Soils here derive from sand and are well-drained with the crest freely exposed to salt-laden winds. The vegetation on such sites, towards the top end of ordination Axis 2, is a broadleaved forest community, predominantly of *Weinmannia racemosa* and *Hedycarya arborea* with a *Dicksonia squarrosa* understorey. Such dune forest was not present in or near Westland National Park, some 80 km to the north, presumably because of human disturbance (Wardle 1977). Observations indicate that podocarps become more prominent on the older dunes further from the coast, beyond the study area. We suggest this follows podzolisation and associated impeded drainage. Eventually a forest develops, dominated by *Dacrydium cupressinum*. Decreasing scores on Axis 2 are correlated with

decreasing pH and increasing organic content, both trends associated with soil development (Smith & Lee 1984). Soil colour also changes, with olive-brown soils of the early stages darkening to black as development continues. Several generations of morphing forest species presumably would be involved.

There is evidence that the vegetation sequence described represents two separate processes of vegetational development occurring in the vicinity of the lagoon. Establishment of successive dune crests and their associated hollows has initiated forest development on the well-drained crests, and hydrarch succession in the hollows. While the two temporal sequences are somewhat convergent there is no indication that full convergence is ever achieved.

The ecological, conservation, and scenic values of the lagoon plus its proximity to a main highway all justify the area being given formal protection. The case for preservation is greatly enhanced by the presence of the aquatic herb *Myriophyllum robustum*, listed as vulnerable by Given (1981). Williams & Given (1981) contend that its future survival outside Fiordland seems doubtful, and report that attempts to relocate previously reported wild populations elsewhere have been largely unsuccessful. Orchard (1979) considers that the combination of draining and burning of the species' habitat will result in its extinction unless conservation measures are taken soon. The species is common in this lagoon. Large areas of open water remain available for it to inhabit and it would seem that survival here could be ensured with the site protected. Formal protection is now assured since the area is included in the South-west New Zealand World Heritage area recently approved by the International Union for the Conservation of Nature and Natural Resources (IUCN). The actual designation of the wetland area has not yet been decided.

#### ACKNOWLEDGMENTS

The authors thank Sharon Quinn and Murray Grant for field assistance and the Zoology Department, University of Otago for loaning levelling equipment and a dinghy. D. Kelly and two anonymous referees provided useful comments on an earlier version.

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## Reproductive phenology, pollination biology, and gynoecium development in *Discaria americana* (Rhamnaceae)

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**Keywords** *Discaria*; phenology; pollination biology; flower morphogenesis; protandry; Diptera; Hymenoptera; Coleoptera; Rhamnaceae

### INTRODUCTION

**Abstract** *Discaria americana* individuals bloom in late winter or early spring and display large numbers of small, white, entomophilous flowers for about a month. Individual flowers contribute to colour display for c. 4 weeks, although they are active in pollen transfer only 5–7 days (male phase = days 1–3, female phase = days 2–5). A strong, foetid smell along with nectar and pollen attract over 50 insect species, of which 19 are probable pollinators. These are mainly Diptera, but include as well Hymenoptera-Apoideae and Coleoptera. Incomplete protandry and reverse herkogamy restrict pollen-stigma interference, but self-incompatibility seems operative in avoiding self-fertilisation. Gynoecium development (from carpel inception to fruit dehiscence) lasts c. 18 weeks, starting with a 33-day-long prefloral period during which most gynoecial structures arise. The floral and postfloral phases occupy c. 18 and 73 days, respectively. The times of starting and ending of several growth processes were determined. Minimum growth rate of the ovary coincides with the active period of the flower, after which some, presumably fertilised, flowers resume ovary growth whereas other ones begin to wither. Pedicels of young fruits become erect which could be beneficial both for seed filling and explosive dispersal. Endocarp maturation apparently sets an upper limit on seed expansion and, indirectly, on size increase of the fruit. Early flowering and erect pedicels are apparently derived traits within *Discaria*.

Most Rhamnaceae bear small, hermaphrodite, inconspicuous, often ill-smelling flowers that are apparently cross-pollinated by a variety of nectar and/or pollen-consuming insects (Suessenguth 1953; Brizicky 1964; Herrera 1985 1987 1988). Protandry seems to be the rule, but reports of nondichogamy (Warnstorf 1896) or protogyny (Hallé 1962) also exist. In a few genera, unisexuality leads to polygamy, monoecism, or even dioecism (Suessenguth 1953). This perspective results mainly from limited observations or morphological inferences; only a few taxa have been studied in detail. These include *Ziziphus* (e.g., Ackerman 1961; Galil & Zeroni 1967; Lyrene 1983; Mehrotra & Gupta 1985), *Pomaderris* (Harvey & Braggins 1985) and *Discaria* (Primack 1979 1980; Primack & Lloyd 1980; Webb 1985). Appreciable diversity in the breeding systems was found both within *Ziziphus* and *Pomaderris*. The one species of *Discaria* so far studied (*D. toumatou* of New Zealand) was reported as protandrous and self-incompatible, showing also variation in functional gender. Information on the reproductive biology of additional *Discaria* species is relevant to the question of the origin of the disjunction presently shown by this amphiantarctic genus (Primack 1979), and adds to the knowledge of the breeding systems present within the genus and family.

The tetraploid, South American species, *Discaria americana* Gill. & Hook. comprises subaphyllous, spiny shrubs which range from south-eastern Brazil to the north of Patagonia in Argentina (Tortosa 1983). I reported on gynoecium morphogenesis of this species, identifying a sequence of growth processes acting from carpel inception to fruit dehiscence (Medan 1985). Unable to study living material, I located the start, duration and end point of each process on a relative scale, constructed using

B90006

Received 8 March 1990; accepted 5 November 1990