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Soil-vegetation relationships on a sequence of sand dunes, Tautuku Beach, South-east Otago, New Zealand

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Soil-vegetation relationships on a sequence of sand dunes, Tautuku Beach, South-east Otago, New Zealand.

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Soil development and plant communities are described on three sand dunes estimated to be 130, 440 and 1,000 years old, respectively, at Tautuku Bay, South-east Otago. A comparison of chemical and morphological properties of soils beneath a plant sequence from *Ammophila arenaria* through low forest of *Metrosideros umbellata* and other broadleaved tree species to tall forest of *Weinmannia racemosa* and *M. umbellata* with occasional podocarps, shows an increase in organic matter from less than one to greater than 40%C, and a decline in pH from 8.0 to 4.3.

Keywords: Soil development, sand dunes, vegetation sequence, Ammophila arenaria, Metrosideros umbellata, Weinmannia racemosa, *soil chemistry, organic content, leaching, plant succession.*

INTRODUCTION

The development of soils on sand dunes in New Zealand has not been studied in the South Island other than in an investigation by Wright and Miller (1952), which described podzol formation on dunes in Fiordland. In the North Island, Pullar and Cowie (1967) described the morphology of dune soils at Mt Maunganui; and the pedology of a chronosequence of coastal dune soils in the Manawatu District has been described in detail by Cowie (1963, 1968). Other workers have examined phosphorus transformations (Syers and Walker, 1969a, 1969b; Shah *et al.*, 1968) and the accumulation of organic matter (Syers *et al.*, 1970) in the same sequence.

Published descriptions of indigenous vegetation on sand dunes are also few. Cockayne (1911) gave an account of the botany of New Zealand dunes with respect to control of sand movement and conversion to productive use. Manawatu dune and sand plain vegetation was described by Esler (1969, 1970); Carnahan (1957), Williamson (1953) and Esler (1974, 1975) recorded the vegetation of modified dunes on north Auckland beaches; and Wardle (1979) briefly described dune vegetation in Westland, all in areas considerably disturbed by human activity. More comprehensive studies were carried out by Mark *et al.*, (1962) on two intact dune systems on the Catlins coast of south-east Otago. These described a primary succession in a dune-impounded small lake, and dune forest patterns associated with distance from the coast.

This paper presents the results of a study of the relationships between soil development and relatively unmodified vegetation on three distinct dunes and associated hollows, at Tautuku Bay, south-east Otago.

Location and Physiography

The study area lies approximately 4 km south of MacLennan (Fig. 1), between the Tahakopa and Tautuku Rivers.

Three long transverse dunes (Bloom, 1978) run parellel to the coast, occasionally reducing to two where the landward pair of ridges coalesce for short distances. Dune crests occur at 40, 67, and 97 m respectively inland from, and 8, 13.5 and 11.5 m above, mean high water level (Fig. 2).

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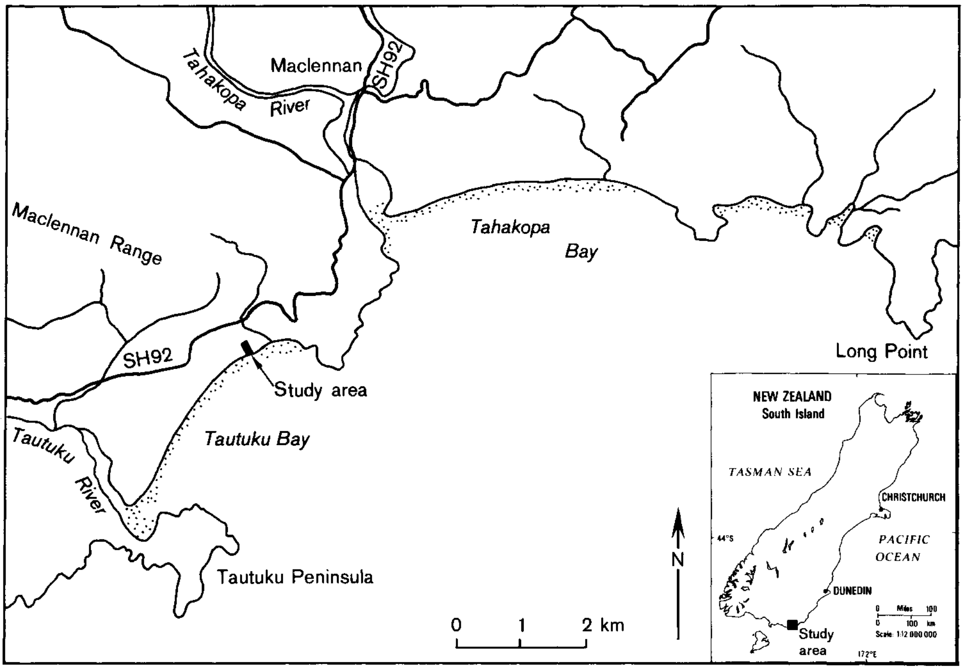

Fig. 1—Locality map.

Climate

Prevailing moisture-laden westerly to south-westerly winds and the coastal location give a continually cloudy, cool, damp climate.

Cold, wet weather commonly occurs from April to September, but frosts are infrequent and seldom severe, and snowfalls are rare. The remainder of the year is generally cool. Daily mean air temperatures at Tautuku for 1980 (N.Z. Meteorological Service, 1980) varied from a high of 14.1°C in February to a low of 6.0°C in July, with a daily mean range varying from 6.2°C (July) to 9.8°C (October).

Mean annual rainfall (1972-1980) at Papatowai, on the coast 3 km north-east of Tautuku, is 1,237 mm, spread almost evenly throughout the year (N.Z. Meteorological Service, 1980). Rain occurs usually as a steady light fall, with few heavy downpours.

Sunshine hours are usually fewer than 1,750 per annum (Hamel, 1977). Presumably evapotranspiration rates are correspondingly low.

Soil Parent Materials

Soil parent material is largely wind-blown sand from the beach containing predominantly quartz (50%) and feldspar (41%) with minor amounts of mica (2%), chlorite (2%) and hornblende (5%) (Bardsley, 1977). The beach sediments are moving north-eastwards along the coast under the influence of ocean currents and southerly swell, causing sand to be concentrated in a narrow offshore zone closely following the coastline (Bardsley, 1977).

Size and sorting of the sand is determined by the local depositional environment with exposure to wind playing a dominant role. The sand has most grains between 0.2 mm and 0.02 mm in diameter, and negligible amounts of silt and clay.

Soil Classification

The soils discussed in this paper are included in the Riverton set of hygrous yellow-brown sands (N.Z. Soil Bureau, 1968). More detailed classifications according to Taylor and Pohlen (1979) and Soil Survey Staff (1975) are given in Table 3.

METHODS

Soils and vegetation were examined along a 2 m wide transect selected to represent as undisturbed a vegetation sequence as possible running inland from the high water mark. Soil profiles were described in pits for five out of six soil sampling sites, and samples collected for analyses. The site in the third dune hollow was described and sampled using a Dutch clay auger because the water table there was very high.

Soil descriptions follow the Soil Survey Method of Taylor and Pohlen (1979), except that horizon designation follows FAO (FAO, 1974) for mineral horizons and the System of Soil Classification for Canada (Canada Department of Agriculture, 1970) for organic horizons. Profile descriptions are given in Appendix 2.

Soils were analysed for pH by the method of Mountier *et al.* (1966); for phosphate-extractable sulphur by the method of Sinclair and Enright (1982); for available phosphate by the method of Olsen *et al.* (1954), with volumetric modification and half hour shake (Grigg, 1977); and for total nitrogen by the method of Bassan (1976) and Gehrke *et al.* (1972). The remainder of the analyses were made using methods described by Blakemore *et al.* (1981).

Species and position (metres from high water mark) were recorded for all plants found within the transect. Plant canopy height, canopy diameter, and, for trees, stem diameter at 1.2 m above ground level, were also recorded.

At the highest point of each dune, single increment cores were taken from *Metrosideros umbellata, Weinmannia racemosa* and podocarp stems where these were available within a few metres of the transect. Cores were mounted transverse face uppermost on strips of wood, then shaved with a sharp scalpel blade. Ring counts and width measurements were carried out at low magnification using a micrometer eyepiece in a binocular dissecting miscroscope. Growth rings were assumed to be annual (Wardle, 1966, 1971; Franklin, 1968).

RESULTS AND DISCUSSION

Vegetation

A representative vegetation sequence is shown in Fig. 2, which illustrates a transect 2 m wide and 120 m long from high water mark to hollow 3 (behind dune 3). Trends in species distribution across the dune sequence are shown in Appendix 1.

Dune 1

Bare sand forms a moderately steep beach to about 5 m inland from the high tide line. A more gentle slope to the foot of the dune then carries scattered small tufts of *Ammophila arenaria* with a ground cover of about 40%. Patches or individual plants of herbs such as *Lagenifera pumila, Trifolium repens, Hydrocotyle novae-zealandiae* var. *montana*, and *Hypochoeris radicata*, with occasional plants of the prostrate shrub *Coprosma acerosa*, grow amongst the *Ammophila*.

Seaward faces of the dune carry *Ammophila* 0.8 m tall, growing densely except where blowouts have caused areas of bare sand. Other species are found only at low densities.

Stabilised sand on the dune beyond 25 m has an estimated 70% cover of herbs and prostrate shrubs, dominated by *Coprosma acerosa*. There are also small tufts of *Phormium tenax*, clumps of the sedge *Scirpus nodosus*, and rare *Desmoschoenus spiralis*, a sand-binding sedge.

Flax density increases at 35-40 metres from the high tide mark, and young plants of the adjacent forest begin to appear amongst those found closer to the sea. On the summit and rear slope of the dune, *Metrosideros umbellata* is establishing in association with scattered shrubs and small trees such as *Griselinia littoralis, Pseudopanax colensoi, Myrsine australis* and *Coprosma propinqua*. However, much of the ground surface is bare sand, with only scattered herbs including *Lagenifera pumila, Corybas macranthus* and *Mycelis muralis*.

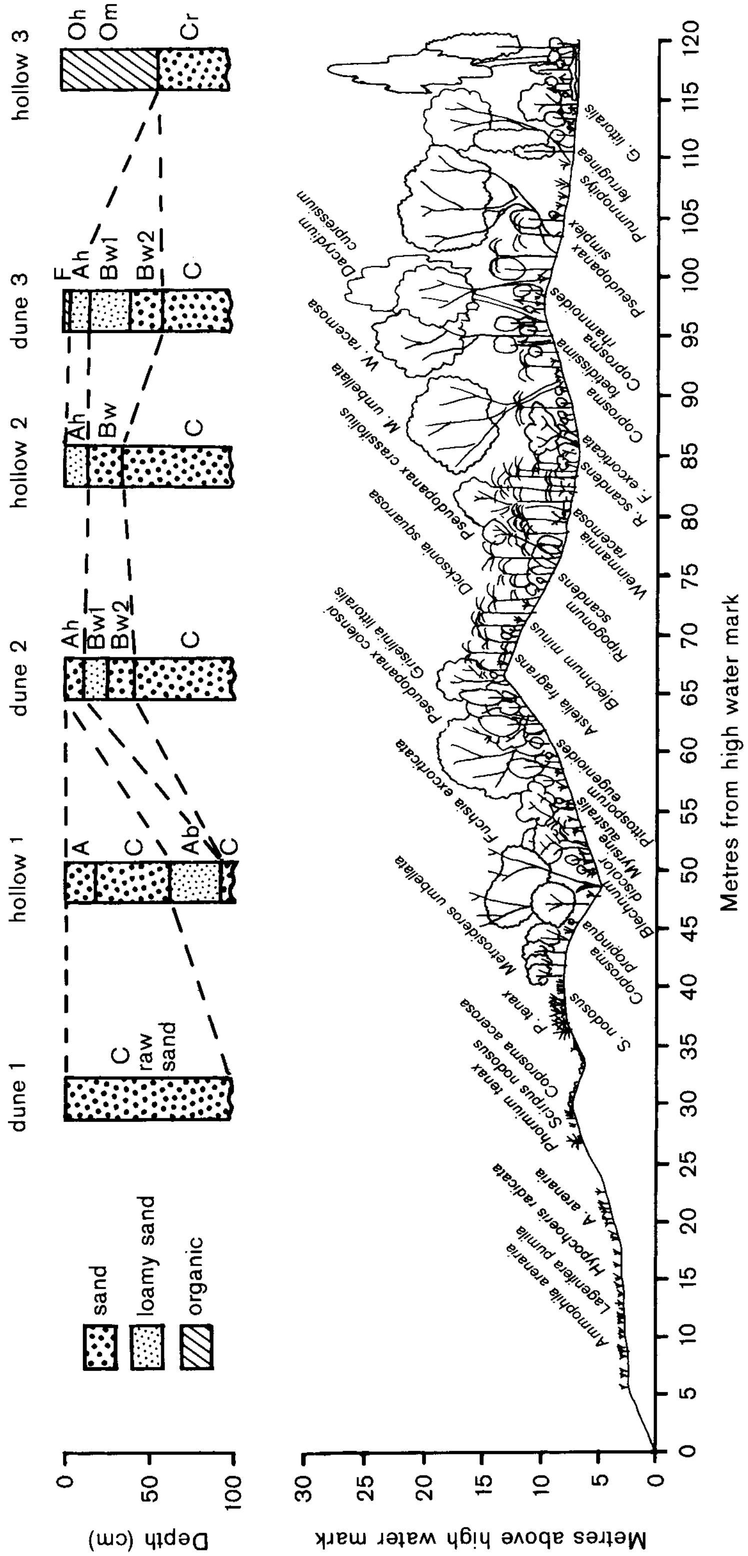

Fig. 2 – Soil and vegetation profile, dune sequence, Tautuku Bay.

Hollow 1

Metrosideros umbellata dominates the first dune hollow, 45 to 50 metres inland, and plant species of open dunes are virtually absent. Under, or sometimes reaching, the 10 m high *Metrosideros* canopy are *Griselinia littoralis, Fuchsia excorticata, Pittosporum eugenioides, Myrsine australis, Pseudopanax colensoi, Schefflera digitata, Coprosma propinqua* and *C. lucida*. Ferns such as *Blechnum discolor, Blechnum capense, B. lanceolatum* and *Aspelium obtusatum* provide nearly continuous ground cover, and bare sand areas are rare. Epiphytes on larger *Metrosideros* branches include the ferns *Ctenopteris heterophylla, Asplenium flaccidum, Hymenophyllum sanguinolentum* and *Phymatosorus diversifolius.*

Dune 2

Under an open canopy (up to 50% cover) of *Pseudopanax colensoi, Griselinia littoralis, Fuchsia, Myrsine australis, Pittosporum eugenioides* and occasional *Metrosideros umbellata,* the seaward slope of the second dune carries dense ground vegetation dominated by *Blechnum discolor* 1.2 m tall, with occasional taller *Dicksonia squarrosa*. Leaf litter covers the ground surface between plants.

Where the canopy is denser, *B. discolor* is partially replaced by other species such as *Asplenium bulbiferum, Astelia fragrans*, shrubs of *Coprosma* species, and small plants of canopy tree species.

Much of the seaward slope and summit of the second dune carries a dense cover of the fern *Histiopteris incisa* under dead or moribund canopies of *Metrosideros umbellata,* other small trees and tree ferns.

Areas of the landward slope of dune 2 are dominated by dense *Dicksonia squarrosa* up to 6 m tall. Only occasional trees, mainly *M. umbellata*, occur within the *Dicksonia* stands, where the sparse understorey and ground vegetation are provided by *Blechnum discolor, Astelia fragrans* and a few shrubs. Ground cover is almost entirely litter.

Entanglements of the liane *Ripogonum scandens* are common on the lower slope, with *Weinmannia racemosa* appearing as a canopy tree. *Dicksonia* remains dominant at most levels of vegetation, and ground cover is still provided mainly by litter.

Hollow 2

The floor of the second hollow is periodically waterlogged, with bare, peaty soil and occasional patches of surface water. Vegetation is sparse: *Ripogonum* predominates, with occasional small *Dicksonia* and a few small trees, mainly *Fuchsia* and *Coprosma* species. Fallen logs provide habitats for epiphytes such as *Metrosideros diffusa, Phymatosorus diversifolius* and *Hymenophyllum* species, and support seedlings and saplings of a range of shrub and tree species.

Dune 3

Weinmannia is dominant on the third dune, with trees 20-50 cm diameter at breast height (dbh). Occasional large *Metrosideros umbellata* up to 200 cm dbh contribute to the 15 m high canopy, and a few *Dacrydium cupressinum* emerge above it. The heterogeneous understorey includes shrubs and small trees of *Pseudopanax crassifolius, Griselinia, Coprosma foetidissima, Coprosma rhamnoides* and *Pseudopanax simplex*, up to 6 m tall. *Dicksonia squarrosa* is moderately common. *Blechnum discolor* covers 40% of the ground, *Phymatosorus* 40%, and a variety of other ferns, small shrubs of *Coprosma* species, and small plants of *Weinmannia* and understorey tree species contribute the balance. Occasional seedlings and small saplings of *Prumnopitys ferruginea* occur, with fewer of *Dacrydium cupressinum* and *Podocarpus hallii*. Frequent fallen logs, mostly *Metrosideros* and *Weinmannia*, support cushions of bryophytes and *Hymenophyllum* species, with dense regeneration of most species of woody plants. Litter is continuous.

Hollow 3

Beyond dune 3, the ground is flat or slightly undulating, with considerable areas of surface water present throughout the year. *Weinmannia* forms a canopy up to 14 m high from which emerge frequent tall (20-25 m) *Dacrydium* and fewer smaller-statured *Prumnopitys*. The moderately dense understorey includes *Coprosma feotidissima, Pseudopanax crassifolius, P. colensoi, Dicksonia, Griselinia, Coprosma rhamnoides* and *C. colensoi*, up to 4 m tall. Fallen logs cover much of the ground, supporting virtually continuous cushions of bryophytes and ferns, and prolific regeneration of shrub and tree species. *Blechnum discolor* provides about 10% ground cover, bryophytes 40%, and litter 30%. Lesser contributions come from species such as the sedge *Uncinia angustifolia* and the ferns *Rumohra adiantiformis, Blechnum minus, Phymatosorus* and *Hymenophyllum dilatatum.*

Age Determinations

Results of age determinations on vegetation are given in Table 1, which also shows the range of diameters exhibited by plants occupying the dune summits within a few metres of the transect.

Growth rates (annual ring width) of all *Dacrydium* sampled on dune 3 showed a sharp decline at about 380 years B.P. and remained low until the present. Age estimates for *Dacrydium* were weighted to take this into account. Variability in growth rate of other species showed no consistent pattern, and age estimates were derived from an overall mean for each increment core.

Soil Morphology

Soil morphology and degree of development of soil horizons in the six soil profiles are shown in Figure 2. Soil on dune 1 shows no horizon differentiation and the sand is very pale brown in colour and unaggregated with very fine shell fragments throughout. The profile in the first dune hollow has a buried soil at 65 cm with loamy texture. The soil

Table 1—Diameter and estimated age of trees on dune summits

SPECIES	DUNE 1		DUNE 2		DUNE 3	
	Diameter cm	Age Years	Diameter cm	Age Years	Diameter cm	Age Years
Metrosideros umbellata	8	52	34	221	59	383
	9	58	40.5	304*	91	591
	9.5	62	43	279	94	610
	12	67*	59	383	110	752*
	14	91	70.5	458	165	1084*
	16	127*	82	436		
	21	136	100	649		
	22	143				
	32	202				
Weinmannia racemosa			31	145*	40	364*
			32.5	233	64	694*
			36	367*	74	530
			48	260*		
			56	401		
Dacrydium cupressinum					71	795*
					79	632*
					87	844*
Prumnopitys ferruginea					54	577*

Note: Ages marked * are derived from individual increment core ring counts, extrapolated to the length of the stem radius where cores did not reach the centre of trees, others from mean growth rates for each species as estimated from these ring counts: 1.54 mm diam./ann. (*M. umbellata*), 1.40 mm diam./ann. (*W. racemosa*).

overlying it appears to be considerably younger as its topsoil is paler, coarser textured, and unstructured. Very fine shell fragments are also visible in the C horizon of the upper soil, a feature not evident in the buried C horizon. The soil on dune 2 shows a thin humified A horizon and the development of a B horizon distinguished by colour and weakly developed nut structure. Hollow 2 has a much darker A horizon and the B horizon is shallower than in the preceeding soil. Dune 3 soil has a significant litter layer at the surface, and a moderately thick B horizon with weakly developed nut structure. The lower B and C horizon contain many very thin (1-2 mm) lamellae, probably composed of clay-organic complexes. Hollow 3 is very poorly drained and the water table is at or near the surface for a large part of the year. Peat has developed to a depth of approximately 50 cm and overlies sand stained with organic matter.

Soil Chemistry

Results of analysis of soil profiles are shown in Table 2.

The amount of organic matter (%C and %N) in the surface horizons of both dune and hollow soils increases from very low levels in dune 1 to a maximum in hollow 3. C/N ratios are much higher in soils occurring in hollows, suggesting slower breakdown and greater accumulation of organic matter in these wetter sites compared with similar age dune soils. The high C/N ratios in dune 1 may be an analytical artifact caused by the very low values for %C and %N.

No calcium carbonate was detected in samples taken inland of hollow 1. The seaward dune has a surface pH of 7.8. As the calcium carbonate disappears the pH falls and the surface pH on dune 2 is 5.4. The reaction of the lower layers of the soil is similar to that of the surface. Beyond dune 2, pH values generally decrease to a minimum of 4.3 in hollow 3.

The two most seaward profiles have very low total exchangeable bases related to their very low cation exchange capacities (CEC), which are dominated by calcium from shell fragments (Table 2). The older, more landward soils have much higher levels of exchangeable bases but exhibit more leaching (lower %BS). This is because the older soils have higher cation exchange capacities which are related to higher amounts of organic matter.

Acid oxalate extractable Al and Fe levels are low to very low but increase with increasing soil age. No appreciable amounts of secondary iron and aluminium compounds occur in dune 1 or hollow 1, although in the latter, oxalate extractable iron and aluminium levels are higher in the buried soil than in horizons above. The remaining soils all show the accumulation of some secondary iron and aluminium compounds. Oxalate-extractable silicon is negligible.

Available P (Olsen) remains relatively constant in topsoils. In soils of dunes 2 and 3 and hollow 3, Olsen P values are higher in subsoils than in topsoils. P retention values are generally low, with highest values occurring in the soil of hollow 3 which also has highest oxalate extractable Al and Fe. This is consistent with the accumulation of secondary iron and aluminium compounds.

Chemical analyses support the classification (Table 3) of the two youngest soils as recent soils rejuvenating by air-borne accumulation, rather than yellow-brown sands. The distinct buried soil in hollow 1 indicates the site has been stable for considerable periods without receiving significant deposists of sand and is therefore classified as a recent soil—yellow-brown sand. There is also a distinct break in the leaching regime of the sequence, with the two youngest soils having base saturation levels of 100%, and the remaining soils an average of between 30% and 50%. Calcium carbonate is still present in dune 1 and hollow 1. Older soils in the sequence have no free calcium carbonate and have correspondingly lower pH values (<6). These chemical parameters in association with the morphological criteria may provide a useful separation between recent soils and yellow-brown sands.

According to Soil Taxonomy (Soil Survey Staff, 1975) the soils are Udipsamments except for the peaty soil in hollow 3 which is a Medihemist.

Table 2 — Soil Chemical Analyses

	Depth (cm)	pH	CaCO3 %	C %	N %	C/N	CEC me.%	Σ bases me.%	BS %	Exchangeable Ca me.%	Exchangeable Mg me.%	Exchangeable K me.%	Exchangeable Na me.%	Ex-change acidity me.%	P retn %	Olsen P ppm	PO_4 extract-able SO_4 ppm S	Pyro-phosphate extractable Fe %	Pyro-phosphate extractable Al %	Acid oxalate extractable Fe %	Acid oxalate extractable Al %	Acid oxalate extractable Si %	Dithionite-citrate extractable Fe %	Dithionite-citrate extractable Al %	ODOE*
1st Dune Crest																									
T347a	0- 50	7.8	1.0	0.2	0.01	20	0.3	Free	lime	—	0.42	0.03	0.25	0.0	5	4	1	0.00	0.00	0.01	0.01	0.00	0.16	0.04	0.00
b	50-100	8.0	0.7	0.9	0.03	30	0.3	Free	lime	—	0.43	0.01	0.25	0.0	4	2	1	0.00	0.00	0.02	0.01	0.00	0.14	0.02	0.00
1st Dune Hollow																									
T348a	0- 17	7.3	0.1	3.8	0.13	29	14.3	Free	lime	—	2.37	0.05	0.28	3.0	4	2	3	0.00	0.00	0.02	0.01	0.01	0.17	0.02	0.07
b	17- 65	8.0	2.0	0.3	0.02	15	0.9	Free	lime	—	0.49	0.02	0.38	0.0	3	2	1	0.00	0.00	0.02	0.01	0.01	0.18	0.03	0.02
c	65- 92	7.6	0.1	1.2	0.07	17	6.9	10.0	(100)	8.4	1.31	0.03	0.22	1.5	6	2	1	0.06	0.01	0.07	0.03	0.00	0.28	0.05	0.20
d	92-100	7.5	0.1	0.6	0.04	15	3.6	3.8	(100)	2.7	0.93	0.04	0.15	1.8	6	3	1	0.08	0.02	0.08	0.04	0.00	0.32	0.06	0.16
2nd Dune Crest																									
T349a	0- 10	5.4		4.7	0.35	13	12.5	8.8	70	4.7	3.34	0.19	0.52	11.7	6	5	10	0.08	0.03	0.07	0.05	0.01	0.24	0.05	0.31
b	10- 24	5.1		3.0	0.23	13	10.0	3.6	36	1.8	1.33	0.09	0.37	15.2	12	8	5	0.12	0.07	0.10	0.08	0.01	0.33	0.11	0.56
c	24- 43	5.6		0.5	0.04	13	3.4	1.1	32	0.5	0.40	0.04	0.11	6.0	7	14	4	0.07	0.04	0.07	0.06	0.01	0.26	0.06	0.31
d	43-100	6.0		0.3	0.03	10	1.9	0.6	32	0.3	0.18	0.04	0.08	4.0	4	16	3	0.05	0.03	0.04	0.06	0.02	0.27	0.08	0.16
2nd Dune Hollow																									
T350a	0- 13	4.5		19.0	1.1	17	50.7	19.6	39	11.3	6.93	0.34	1.02	51.6	6	5	5	0.08	0.04	0.07	0.06	0.00	0.24	0.09	0.10
b	13- 34	4.8		3.6	0.18	20	8.9	2.2	25	1.0	0.92	0.06	0.22	12.4	10	4	1	0.08	0.04	0.05	0.05	0.00	0.31	0.07	0.31
c	34- 80	5.7		0.6	0.05	12	5.8	2.1	36	1.0	0.91	0.02	0.16	10.2	15	4	1	0.24	0.09	0.21	0.11	0.01	0.46	0.14	0.47
3rd Dune Crest																									
T351a	3- 15	5.2		5.5	0.36	15	15.8	8.6	54	4.7	3.11	0.09	0.67	18.8	16	4	4	0.13	0.05	0.10	0.06	0.01	0.35	0.09	0.38
b	15- 40	5.3		2.5	0.16	16	10.2	4.7	46	2.4	1.58	0.08	0.60	14.8	17	3	2	0.15	0.08	0.13	0.09	0.01	0.41	0.13	0.68
c	40- 59	5.7		0.5	0.04	13	5.1	1.2	24	0.4	0.61	0.01	0.20	10.0	15	107	2	0.13	0.08	0.11	0.10	0.01	0.38	0.13	0.44
d	59-100	5.9		0.5	0.02	25	3.3	0.7	21	0.2	0.35	0.01	0.14	7.0	13	130	2	0.09	0.07	0.07	0.09	0.02	0.31	0.12	0.27
3rd Dune Hollow																									
T352a	0- 10	4.3		44.0	1.4	31	105.8	38.6	36	18.8	13.0	1.66	5.12	134.5	12	9	39	0.19	0.15	0.11	0.16	0.01	0.31	0.20	0.16
b	10- 60	4.3		48.0	1.4	34	99.1	26.7	27	10.1	10.3	0.97	5.28	143.2	35	8	31	0.38	0.29	0.42	0.16	0.02	0.49	0.32	0.65
c	60-100	5.4		4.0	0.16	25	7.8	3.9	50	1.8	1.49	0.09	0.50	11.1	14	18	11	0.05	0.06	0.03	0.26	0.01	0.08	0.08	0.13

* Optical density of the oxalate extract.

Table 3—Classification of Soils

SOIL	Taylor and Pohlen (1979) (At Category VI)	Soil Survey Staff (1975) (to family level)
Dune crest 1	Very weakly leached, hygrous recent soil from quartzo-feldspathic sand	Typic Udipsamment, sandy, mixed, mesic
Dune hollow 1	Very weakly leached, scrub melanised hygrous intergrade between recent soils and yellow-brown sands from quartzo-feldspathic sand	Typic Udipsamment, sandy, mixed, mesic
Dune crest 2	Moderately leached, forest melanised hygrous yellow-brown sand from quartzo-feldspathic sand	Typic Udipsamment, sandy, mixed mesic
Dune hollow 2	Moderately leached, forest melanised hygrous yellow-brown sand from quartzo-feldspathic sand	Typic Udipsamment, sandy, mixed, mesic
Dune crest 3	Moderately leached, forest melanised hygrous yellow-brown sand from quartzo-feldspathic sand	Typic Udipsamment, sandy, mixed, mesic
Dune hollow 3	Organic soil	Terric Medihemist, sandy, mixed, dysic, mesic

None of the soils have a horizon meeting the chemical criteria for spodic horizon (Soil Survey Staff, 1975) because of low values for pyrophosphate extractable Al and Fe, although there are small maxima of these values in B horizons of dune crest soils. A method of separating podzols or Spodosols from other soils based on measurement of the optical density of acid oxalate extracts (ODOE) for soils (Daly, 1982) was applied to the sequence. The ODOE values are proposed as a measure of the amount of the soluble organic matter component (fulvic acid) which is formed and translocated under podzolising conditions. Daly proposed a B horizon/A horizon ODOE ratio of 1.0 or more as the criterion for separating podzolised soils and podzols from other New Zealand soils.

The ODOE values do show evidence of fulvic acid formation and translocation in the four most inland soils; fulvic acid formation was most pronounced on dune 3. Here the fulvic acid has also been translocated to a greater depth. (The small maxima in the third horizon of hollow 1 corresponds with a buried topsoil). The reason for the lack of agreement between spodic horizon criteria and the ODOE as to whether the soils are Spodosols is related to the sensitivity of the methods. Soil processes in these sandy soils take place in thin amorphous mineral-organic layers surrounding largely inert sand grains. Therefore, expressed as a percentage of the whole soil, pyrophosphate extractable Al and Fe are low, but because most of the soil is relatively inert these small amounts have a pronounced effect on soil processes. There is some morphological evidence of podzol formation in the oldest dune crest soil. Here B horizons are dark brown to strong brown in colour merging to dark yellowish brown with depth. The presence of several thin lamellae in B and C horizons also indicates the presence of translocated materials.

Dune Ages

Species and diameter distribution of plants across the dune system clearly indicate the sequence of dune formation (Table 1). *Metrosideros umbellata* stems are progressively larger inland, and *Weinmannia* and podocarps were recorded establishing only on the second and third dunes, respectively. The apparent overlap of diameter ranges in *M. umbellata* between dunes may be due to burial of some tree bases by sand (P. Wardle, *pers. comm.* 1984). Measurement of the younger, exposed stem of such plants would result in under-representation of their true diameter 1.2 m above original ground level.

Wardle (1971) stated that in forest, *M. umbellata* "seedlings occur on stumps, logs, rocks, and on the ground in well lit sites such as beneath canopy gaps, on the crests of spurs and ridges, and on the edges of terraces". He also contended that beneath dense canopies *M. umbellata* seedlings were probably rarely successful except as high epiphytes. No *M. umbellata* seedlings were recorded within forest on dunes 2 and 3 at Tautuku, and given the conditions necessary for *M. umbellata* establishment it is reasonable to assume that the very large tree recorded on dune 3 established there when it was exposed to the coast as a seaward dune. *M. umbellata* recorded on dune 2 of the sequence are smaller and younger than those on dune 3, evidence for the later establishment of this dune seaward of the former. The presence of relatively young *M. umbellata* on the existing seaward dune (Dune 1) attests to its more recent origin.

Conversely, the establishment of *Weinmannia racemosa* (Wardle, 1966) and *Dacrydium cupressinum* (Franklin, 1968) requires conditions which are not available on the present seaward dune. Neither species would have appeared on the dune that it occupies at present until sufficient distance from the coast and the presence of other vegetation provided a suitable environment. Formation of dunes seaward of that now occupied by *W. racemosa* or *D. cupressinum* fulfilled these requirements.

Using the age estimates derived from increment core ring counts, only very approximate minimum ages can be attributed to the dunes. Assuming that the oldest tree recorded on the summit of each dune established there soon after dune stabilisation, minimum ages of 127, 436 and 1084 years are obtained, all from *M. umbellata* stems, for dunes 1, 2 and 3 respectively.

Wardle (1971) bases a life span estimate of 400-500 years for *M. umbellata* in Westland on correlation with glacial chronology, casting some doubt on the reliability of *M. umbellata* age estimates on the third dune at Tautuku. However, the conservative age estimates for *D. cupressinum* on that dune confirm that the age of the dune is at least 844 years, and suggest that on the Catlins coast, *M. umbellata* is able to achieve considerably greater longevity than the Westland estimates imply.

Darcrydium cupressinum growth rates fall within the range suggested by Franklin (1968) for suppressed poles, semi-mature trees, or over-mature stems. They are considerably slower than those of unsuppressed trees on favourable North Island sites, as should be expected on the low-fertility, cool climate, southern latitude dunes at Tautuku.

The chronology of soil development largely supports dune ages derived from tree ages. For instance, there is considerable uniformity in the figures obtained by various workers for the time taken to remove calcium carbonate by leaching. At Woy Woy, New South Wales, Burgess and Drover (1953) estimated that a period of about 200 years was required to remove all the calcium carbonate from surface horizons. Salisbury (1925) found that in the Blakeney Point dunes, in England, where the initial calcium carbonate content was 0.42%, between 200 and 300 years were necessary for its complete removal from surface horizons; this is approximately the same as the figure for the Southport dunes, which contained 6.9% of calcium carbonate. From the low calcium carbonate figures in the first dune hollow (Table 2) it is assumed that the buried soil is approximately 200 years old and the soil on dune 2 at least 200 to 300 years old.

Plant Succession and Soil Development

Abrasion, salt spray, substrate instability and desiccation allow few plant species to establish on the open beach (Esler, 1978). *Cakile edulenta* is a succulent herb which is able to tolerate these harsh conditions, and is thus found in a zone above high tide mark at Tautuku. *Desmoschoenus spiralis* would have occupied and stabilised mobile sand at the top of the beach, initiating dune formation. However, it has been largely displaced from this role by the more aggressive introduced grass *Ammophila arenaria*, and is now restricted to a few small remnant clumps on the foredune. *Ammophila* is the major coloniser of mobile sand, stabilising the substrate and facilitating the establishment of a few species of prostrate herbs, such as *Hypochoeris radicata* and *Lagenifera pumila*.

With no further addition of large quantities of fresh sand on a stabilised site, *Ammophila* dies out (Cockayne, 1911) and is replaced by a mosaic of vegetation. Within these patches of herbs, grasses, sedges, prostrate shrubs and *Phormium tenax*, woody species such as *Coprosma propinqua and Metrosideros umbellata* establish.

M. umbellata establishment is confined to the exposed seaward dune because the harsh conditions there preclude establishment of other tree species with which *M. umbellata* is unable to compete on more favourable sites further inland, a pattern observed in *M. umbellata* regeneration elsewhere (Wardle, 1971). Under a low *M. umbellata* canopy, light levels are insufficient to support *Phormium tenax*, sedges and most other species of the open dune.

Because of the relatively sparse cover, low biomass and short period of establishment of plants on this dune, very little litter has accumulated. Hence the soil organic carbon content is very low (0.2-0.9%) and the pH moderately alkaline (7.8-8.0%). The presence of free lime throughout the profile indicates that the soil is relatively young and weakly leached.

Levels of some exchangeable bases are very low mainly because of the very low CEC levels resulting from the paucity of soil organic matter. Exchangeable potassium is derived from the parent material, but not in an easily soluble form (as for calcium), nor is it constantly added from the environment in salt spray (as for magnesium and sodium).

Episodes of fresh sand deposition have occurred on and immediately behind the first dune at the transect site, as is demonstrated by the buried soil in the first dune hollow. Elsewhere on the dune system, burial has extended to the seaward face and summit of dune 2, killing well-established low forest dominated by *Metrosideros umbellata*. In these areas *Histiopteris incisa* has formed a dense cover up to 2 m tall between the dead or moribund stems of trees and tree ferns.

The *M. umbellata* canopy and hollow 1 provide shelter from salt spray and wind damage, which can cause dieback of the outer foliage of *M. umbellata* branches. Humidity and soil moisture increase, and light intensity decreases. These factors favour establishment of ferns and broadleaved small tree and shrub species, interspersed with groves of *Dicksonia squarrosa* tree ferns which probably originate from rhizomatous growth in response to localised damage or death of the tree canopy caused by wind or salt spray. This pattern prevails over most of dune 2.

Associated with the increased biomass and the corresponding increase in litter deposition is the marked increase in organic carbon content of both the surface and buried soil examined in hollow 1. Surface pH drops slightly to 7.3 as a result, although free lime is still present throughout the profile, with lower levels in the buried soil reflecting its greater age.

Towards the rear of the second dune, the availability of suitable establishment sites for *Weinmannia racemosa*, notably *Dicksonia* trunks (Wardle, 1966), leads to *W. racemosa* sharing canopy dominance with the remaining large *Metrosideros umbellata*. Light-demanding broadleaved tree species common on the seaward face of the dune become sparser, and are joined as an understorey by more shade-tolerant species such as *Pseudopanax simplex*.

The further increase in litter deposition under this taller canopy leads to the higher organic carbon level of 4.7% in the soil surface layers (Table 2). The consequent decrease in surface pH to 5.4 results from significant leaching and removal of all free lime. Leaching also considerably lowers base saturation levels.

Secondary compounds of iron and aluminium increase in importance, and higher levels of exchangeable bases in this and older soils in the sequence (Table 2) result from higher CEC levels due to the increase in soil organic matter.

In the loose consistency of the sand substrate, deep-growing tree roots abstract nutrients which are returned to the soil surface via litter, promoting a deep organic cycle. Exchangeable potassium and organic matter levels are linked, with potassium released by weathering from the parent material being incorporated into the organic cycle.

Permanent waterlogging of the soil in hollow 2 prevents establishment of most species. Vegetation is restricted to plants such as *Ripogonum scandens* which are rooted on adjacent better-drained sites and spread into the hollow, or to those which grow as epiphytes on branches, logs, or other raised surfaces.

Podocarps first become prominent on dune 3. The marked increase in *Prumnopitys ferruginea* frequency is a result of establishment on fallen logs: virtually all the stems recorded of this species were seedlings or saplings on this substrate. *Dacrydium cupressinum* appears as scattered, mainly mature, trees, suggesting opportunist origin. It shows no particular habitat preference beyond a tendency to establish on the dune crest, perhaps reflecting its preference for only partial shade (Franklin, 1968).

The abundance and variety of fern species established on the second dune continues to the third, with changes in relative frequency and species composition again reflecting changes in light intensity, humidity and soil moisture. A wider range of establishment sites becomes available as older trees collapse. Understorey plants typical of tall forest become prominent, with *Coprosma* species, *Pseudopanax* species and *Hymenophyllum* ferns particularly evident. These frequently grow on rotting logs, a substrate which may have higher nutrient status than the soil A horizon (June and Ogden, 1975).

Soils on dune 3 are generally less fertile than those on the second dune (Table 2), because illuviation is more pronounced, and a greater proportion of plant nutrients is contained in the standing biomass of the forest. Organic carbon levels have increased slightly (5.5%) and pH shows a corresponding decline (5.2). Associated with these factors is a further reduction in base saturation and a significant increase in the levels of secondary iron and aluminium compounds (Table 2).

The dense podocarp forest occurring beyond the dune sequence is unrelated in origin to that on the dunes. It occupies a site which has developed as a result of gradual infilling by vegetation of a wetland impounded by the beach, a process evident behind most Catlins beaches (Mark *et al.*, 1962).

It is evident that as the plant succession proceeds, the leaching of soil nutrients becomes accelerated by the solution and mobilisation of elements, and by biological activity. The increase in soil organic matter with time has the most pronounced effect on these processes. Exchangeable fractions of all major nutrients increase in topsoils because there are only very small amounts of clay in all the soils (Table 2). The increase in organic carbon is also reflected in a corresponding increase in acidity. Decreasing pH is also a result of increased leaching with time: free lime is removed early in the sequence, and there is a reduction in base saturation with increased soil age, a pattern demonstrated in other dune studies (Cowie, 1968; Burgess and Drover, 1953).

CONCLUSIONS

The variation in vegetation structure and species composition, and in the morphological and chemical properties of soils, on each of the three dunes at Tautuku, demonstrates that there is a successional sequence from bare, unconsolidated sand, to a heavily-forested podzolised soil.

With increasing distance from the coast, vegetation stature and complexity increase, as does the age of the largest trees. Similarly, soil profiles show an increasing number of horizons, accumulation of organic matter at the surface and in mineral horizons, changes towards redder hues in B and C horizons, and textures becoming increasingly loamy.

It is apparent that increasing plant biomass with time has led to organic matter accumulation and establishment of a deep organic cycle which, with leaching, have been the major soil-forming processes operating in the development of the soil sequence.

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APPENDIX 1.

Distribution of plant species on seaward (S) and landward (L) sides of three dunes (Seaward—Landward, 1—3) at Tautuku Bay.*

	1		2		3	
SPECIES	S	L	S	L	S	L
Trees, Shrubs and Lianes:						
Aristotelia serrata			+	+	+	+
Carpodetus serratus					+	+
Coprosma acerosa	+					
C. colensoi					+	+
C. foetidissima			+	+	+	+
C. lucida			+	+	+	+
C. propinqua	+	+	+			
C. rhamnoides					+	+
Dacrydium cupressinum						+
Fuchsia excorticata		+	+	+	+	+
Griselinia littoralis		+	+	+	+	+
+ *Lupinus arboreus*	+	+				
Metrosideros diffusa			+	+	+	+
M. umbellata		+	+	+	+	+
Muehlenbeckia australis			+	+		
Myrsine australis		+	+	+	+	+
M. divaricata		+			+	+
Pimelea lyallii	+	+				
Pittosporum colensoi			+			
P. eugenioides		+	+	+	+	+
P. tenuifolium	+		+			
Podocarpus hallii					+	+
Prumnopitys ferruginea (D.Don) de Laubenfels				+	+	+
Pseudopanax colensoi		+	+	+	+	+
P. crassifolius				+	+	+
P. simplex					+	+
Rubus cissoides			+			
Schefflera digitata			+	+	+	+
Weinmannia racemosa				+	+	+
Dicot herbs:						
Australina pusilla		+				
+ *Cakile edulenta* (Bigel.) Hook.	+					
+ *Cerastium glomeratum*	+					
Colobanthus muelleri		+				
+ *Fumaria muralis*	+	+				
Gentiana saxosa	+					
Geranium microphyllum	+					
Hydrocotyle novae-zelandiae var. *montana*	+	+				
+ *Hypochoeris radicata*	+	+				
Lagenifera pumila (Forst.f.) Cheesem.	+	+				
+ *Mycelis muralis*		+	+			
Nertera dichondraefolia				+	+	+
+ *Plantago lanceolata*	+					
+ *Prunella vulgaris*	+					
Seneco biserratus Belcher	+					
+ *S. jacobaea*	+					
S. minimus	+					
+ *Sonchus oleraceus*		+				
+ *Trifolium repens*	+					
Monocots:						
+ *Ammophila arenaria*	+					
+ *Anthoxanthum odoratum*	+					
Astelia fragrans			+	+	+	+
Carex flagellifera	+					
Corybas macranthus		+	+			
C. trilobus			+	+	+	+
+ *Dactylis glomerata*	+					
Desmoschoenus spiralis	+					
Dichelachne crinita Hook. f.	+					

APPENDIX 1 —*continued*

SPECIES	1 S	1 L	2 S	2 L	3 S	3 L
Earina autumnalis			+			
+ *Festuca arundinacea*	+	+				
Gastrodia cunninghamii			+	+	+	+
+ *Holcus lanatus*	+					
Lachnagrostis sp. Trin.	+					
Libertia peregrinans		+				
Phormium tenax	+	+				
Poe laevis R. Br.	+					
Pterostylis graminea			+	+	+	+
Ripogonum scandens				+	+	+
Scirpus nodosus	+	+				
Uncinia angustifolia						+
U. uncinata						+
Ferns:						
Alsophila smithii (Hook.f.) R. Tryon						+
Asplenium bulbiferum			+	+	+	+
A. obtusatum			+			
A. flaccidum			+	+	+	+
A. terrestre Brownsey			+	+	+	+
Blechnum discolor			+	+	+	+
B. lanceolatum			+			
B. minus			+	+	+	+
Ctenitis heterophylla (Labill.) Tind.		+	+			
Dicksonia squarrosa			+	+	+	+
Grammitis billardieri			+	+	+	+
Hymenophyllum demissum			+	+	+	+
H. dilatatum			+	+	+	+
H. ferrugineum				+		
H. flabellatum					+	+
H. rarum					+	+
H. revolutum					+	+
H. sanguinolentum				+	+	+
Phymatosorus diversifolius (Willd.) Pic.Ser.		+	+	+	+	+
Polystichum vestitum			+	+		
Pyrrosia serpens			+	+		
Rumohra adiantiformis			+	+	+	+
R. hispida						+
Trichomanes venosum			+	+	+	+

* Nomenclature follows Allan (1961), Moore and Edgar (1970) or Clapham *et al.* (1962) except where otherwise indicated by the addition of authority names.
\+ Indicates adventive species.

APPENDIX 2.

Profile descriptions

Dune 1

Location: NZMS 1 S184 282842
Topography: Crest of undulating sand dune—slightly convex
Slope: 1—2 degrees   Aspect: East
Parent Material: Wind blown sand derived from quartzo-feldspathic rocks
Drainage: Excessively drained
Site Vegetation: *Coprosma*, herbs
Moisture Conditions: Slightly moist
Profile:

Horizon	cm	
D	0-100 (100)	very pale brown (10YR 7/3) sand; loose; single grain; some faint laminations of grey (10YR 6/1) sand; few fine roots throughout.

Hollow 1

Location: NZMS 1 S184 282842

Topography: Depression between two dunes—concave

Slope: 0 degrees Aspect: —

Parent Material: Wind blown sand derived from quartzo-feldspathic rocks

Drainage: Somewhat excessively drained

Site Vegetation: *Metrosideros, Coprosma, Blechnum*

Moisture Conditions: Moist

Profile:

Horizon	cm	
Au	0-17 (17)	dark greyish brown (10YR 4/2) sand; loose; single grain; non-sticky and non-plastic; many fine and medium roots; distinct smooth boundary,
C	17-65 (48)	very pale brown (10YR 7/4) sand; loose; single grain; non-sticky and non-plastic; common fine and medium roots; distinct irregular boundary,
Ab	65-92 (27)	dark brown (10YR 3/3) loamy sand; very friable; single grain plus weakly developed medium nut structure; non-sticky and non-plastic; common fine and medium roots; distinct smooth boundary,
Cb	92-100+ (8+)	brown to dark brown (10YR 4/3) sand; loose; single grain; non-sticky and non-plastic; few fine and medium roots.

Dune 2

Location: NZMS 1 S184 282842

Topography: Crest of undulating sand dune—convex

Slope: 3 degrees Aspect: North-east

Parent Material: Wind blown sand derived from quartzo-feldspathic rocks

Drainage: Somewhat excessively drained

Site Vegetation: *Griselinia, Pseudopanax colensoi, Blechnum*

Moisture Conditions: Moist

Profile:

Horizon	cm	
Ah	0-10 (10)	very dark brown (10YR 2/2) sand; loose to very friable; single grain plus weakly developed very fine nut structure; non-sticky and non-plastic; abundant fine and medium roots; indistinct smooth boundary,
Bw1	10-24 (14)	dark brown (7.5YR 3/2) loamy sand; very friable; weakly developed medium nut structure plus single grain; non-sticky and non-plastic; many fine and medium roots; distinct smooth boundary,
Bw2	24-43 (19)	brown to strong brown (7.5YR 4/5) sand; loose; weakly developed nut and single grain structure; non-sticky and non-plastic; few fine roots; distinct smooth boundary,
C	43-100 (57)	yellowish brown (10YR 5/4) sand; loose; single grain; non-sticky and non-plastic; no roots.

Hollow 2

Location: NZMS 1 S184 281843

Topography: Depression between two sand dunes—slightly concave

Slope: 1—2 degrees Aspect: East

Parent Material: Wind blown sand derived from quartzo-feldspathic rocks

Drainage: Moderately well drained

Site vegetation: *Ripogonum, Coprosma, Fuschia*

Moisture Conditions: Very moist

Profile:

Horizon	cm	
Ah	0-13 (13)	black (5YR 2.5/1) loamy sand; very friable; single grain plus weakly developed very fine nut structure; non-sticky and non-plastic; abundant fine roots; indistinct smooth boundary,

Bw	13-34 (21)	dark brown (7.5YR 3/2) sand; very friable; weakly developed medium nut structure plus single grain; non-sticky and non-plastic; many fine and common medium roots; distinct wavy boundary,
C	34-100 (66)	dark yellowish brown (10YR 4/4) sand; loose; single grain; non-sticky and non-plastic; no roots.

Dune 3

Location: NZMS 1 S184 281843

Topography: Crest of undulating dune—flat

Slope: 0 degrees Aspect: —

Parent Material: Wind blown sand derived from quartzo-feldspathic rocks

Drainage: Somewhat excessively drained

Site Vegetation: *Weinmannia, Metrosideros umbellata, Pseudopanax crassifolius, Coprosma*

Moisture Conditions: Moist

Profile:

Horizon	cm	
F	0-3 (3)	dark brown (7.5YR 3/4) moderately decomposed leaf litter; loose; abundant very fine roots; distinct smooth boundary,
Ah	3-15 (12)	very dark grey (10YR 3/1) loamy sand; loose; single grain plus weakly developed fine nut structure; non-sticky and non-plastic; many fine roots; indistinct smooth boundary,
Bw1	15-40 (25)	dark brown (7.5YR 3/2) loamy sand; friable; weakly developed medium nut structure; non-sticky and non-plastic; common fine roots; indistinct smooth boundary,
Bw2	40-59 (19)	brown to strong brown (7.5YR 4/5) sand; loose; very weakly developed medium nut and single grain structure; non-sticky and non-plastic; few fine (3-4 mm) distinct very dark greyish brown (10YR 3/2) clay-humus lamellae throughout horizon; few fine roots; diffuse boundary,
C	59-100 (41)	dark yellowish brown (10YR 4/4) sand; loose; single grain; non-sticky and non-plastic; few fine (3-4 mm) distinct very dark greyish brown (10YR 3/2) clay-humus lamellae throughout horizon; few fine roots.

Hollow 3

Location: NZMS 1 S184 281843

Topography: Gently undulating depression behind dune

Slope: 0 degrees Aspect: —

Parent Material: Wind blown sand derived from quartzo-feldspathic rocks and weakly to moderately decomposed peat

Drainage: Very poorly drained

Site Vegetation: *Weinmannia, Dacrydium, Griselinia*

Moisture Conditions: Wet

Profile:

Horizon	cm	
Oh	0-10 (10)	very dark grey (7.5YR 3/0) peat; structureless; weakly to moderately decomposed; sharp smooth boundary,
Om	10-60 (50)	dark reddish brown (5YR 3/4) peat; structureless; saturated; moderately to strongly decomposed; sharp boundary,
Cr	60+	strong brown (7.5YR 4/6) sand; loose; single grain; non-sticky and non-plastic; saturated; sand becomes light brownish grey (10YR 6/2) with increasing depth.