

Plant succession and dune dynamics on actively prograding dunes, Whatipu Beach, northern New Zealand

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Abstract Whatipu Beach, north Manukau Harbour, Auckland, has prograded episodically over 1.5 centuries. Sand dune vegetation is quantitatively described, and related to successional stage, local environment, and progradation dynamics. Foredunes, with fine, mobile, infertile sand, occupy the most recently prograded areas and are partially vegetated by native species. Instead of a dune slack, a stream which changed course to flow between dune ridges has created wet “sand river” vegetation. Relict foredunes and a dune slack persist inland of the sand river, disrupting a lineal spatial sequence, as do rear dune wetlands. Less-mobile grass and shrub communities, derived from *Ammophila arenaria* dunes, occupy surfaces >50 years old. No climax communities are present. In contrast to spatial analogues, the Whatipu dunes demonstrate how rapidly succession proceeds in response to the formation of new habitat, while freshwater movements generate non-seral sand-river communities. Succession is modified by invading exotics and by the absence of many disturbance-intolerant native shrub species. Coastal progradation rates at Whatipu indicate that shrubland develops within 50 years, suggesting that spatial analogues of dune succession can misrepresent the longevity of early seral stages. These unusual successional patterns on dateable surfaces, and

the presence of rare flora and fauna, make Whatipu Beach important for conservation.

Keywords dune-slack; dynamic; sandplain; nutrient; rare; foredune; linear succession; primary succession; secondary succession; succession

INTRODUCTION

Sand dune habitats are still relatively common in New Zealand, though most have been extensively modified. Vegetation of only a few of the remaining natural dune systems has been quantitatively sampled and described in detail (Esler 1969, 1970; Sykes & Wilson 1987, 1991; Roxburgh et al. 1994; Drobner et al. 1995). The dunes of Whatipu Beach, north Manukau Heads, Auckland, are of particular interest because they have detailed recorded histories (Esler 1974; Cameron 1989), extensive natural areas, and are of recent origin. Active coastal progradation or accretion is occurring, which has been periodically recorded since c. 1853 (Fig. 1), allowing a dated study of dune succession.

Dynamic, mobile coastal dune systems have a characteristic ecology and vegetation (Cockayne 1928). Specialised dune species occur near the sea, capable of withstanding mobile sand, burial, drought, high temperatures, salt winds, and low substrate nutrient levels (Pegg 1913; Sykes & Wilson 1989, 1990; Roxburgh et al. 1994; Wilson & Sykes 1999; Hesp 2000). Dune slack specialists are expected in damp hollows with variable water tables (Esler 1969; Roxburgh et al. 1994; Singers 1997). Mid-seral shrub species occupy older surfaces due to greater substrate stability, accumulation of organic matter and nutrients, and decreased sand movement and salt spray levels (Sykes & Wilson 1991; Hesp 2000). Coastal forest develops next, dominated by podocarps in wetter areas (Logan & Holloway 1934; Robertson et al. 1991; Sykes & Wilson 1991), *Metrosideros umbellata* in southern areas (Smith et al. 1985), and *Metrosideros excelsa* in northern areas (Wardle 1991).

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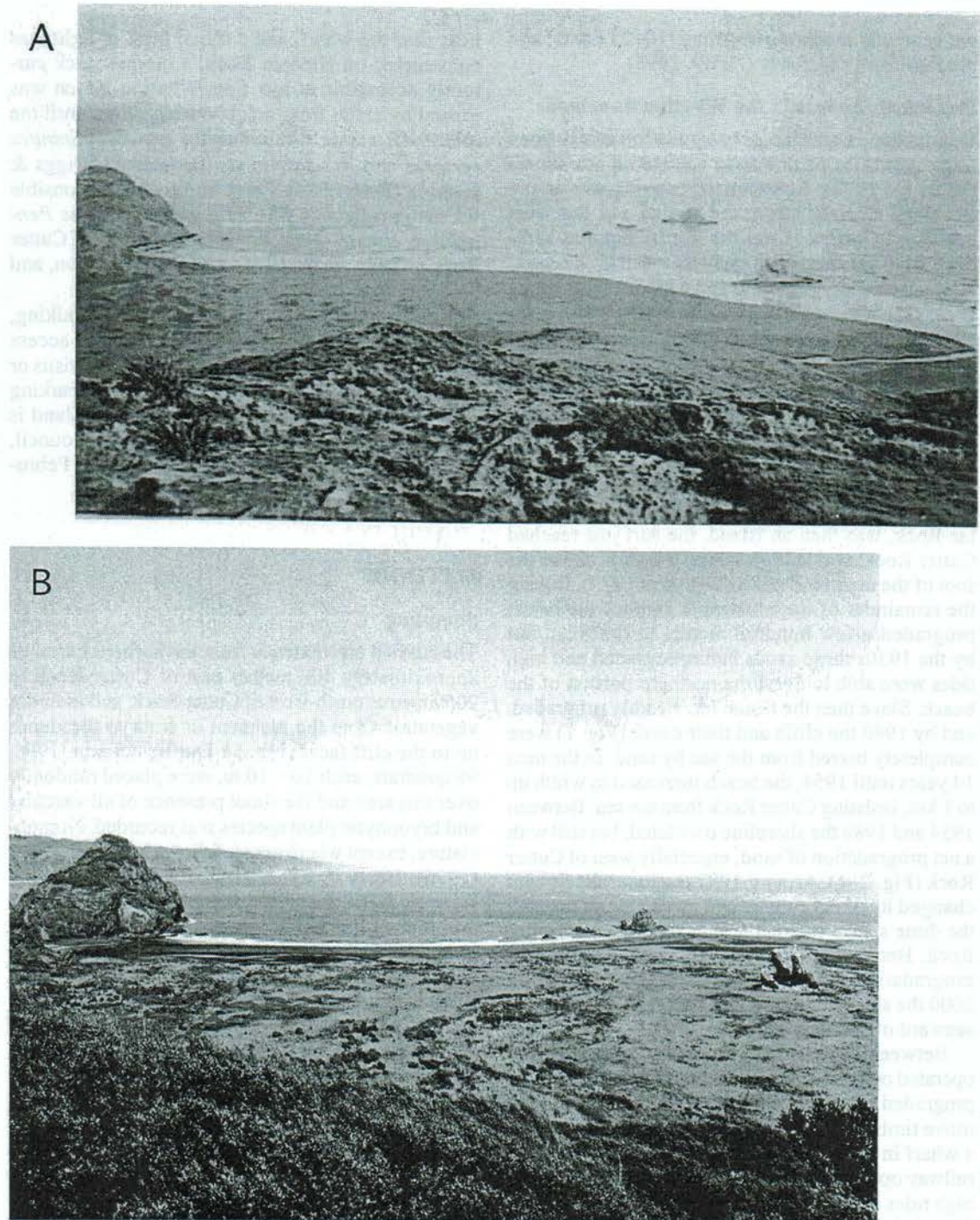


Fig. 2 The mobile sands of Whatipu Beach from the same location by the cliffs about 70 years apart. **A**, in the 1930s; Wentworth private collection, **B**, Harvey pers. comm.; **B**, in 2001. Note in **A** the presence of Cutter Rock at the edge of the waves, and Ninepin Rock surrounded by water. In **B**, Cutter Rock is surrounded by vegetation of the Rush, Old Fore Dune, and *Ammophila* Dune communities.

A



B



Fig. 3 The mobile sands of Whatipu Beach from the same location 28 years apart, showing the view towards Cutter Rock with *Paratutae* in the background. **A**, in 1973; A. E. Esler private collection; **B**, in 2001. The abundant vegetation of 2001 is of the *Ammophila* Dune Community.

seed on each mixed sand sample, grown in pots behind glass in direct sunlight, and watered on demand. Weeds present in the sand were removed as necessary. After 3 months the browntop shoots were excised, and the roots washed; tissues were dried separately at 98°C for 72 h and weighed.

Two transects were placed across the sampling area at right angles to recorded zones of sand progradation (Fig. 1, 5; Esler 1974). The Cutter Rock transect ran 900 m at 27° true north, from high tide to 50 m north of Cutter Rock (Fig. 5), where it terminated in an extensive patch of the exotic grass *Pennisetum clandestinum*. The Large Cave transect (1350 m long) was placed at 91° true north, across the longest sequence of prograded beach surfaces, toward a large cave (Fig. 5). Elevation was measured every 10 m along each transect with a surveyor's level, and presence and depth of surface water noted. Sand samples, 10 cm deep, were taken using a 7.5 cm diam. corer every 50 m along both transects, and stored in sealed bags at 4°C until determination of percentage organic matter (in dry sand samples by loss on ignition at 550°C for 5 h).

Sand traps were used to monitor sand movement. Each consisted of an empty 1.5 litre soft-drink bottle with an opening cut in the side 70 mm wide and 20 mm high. The trap was buried cap-down in the sand, facing the sea, with the bottom of the opening c. 40 mm above the sand surface (following Drobner et al. 1995). Seven sand traps were placed for 14 days (28 Apr to 12 May 1996) on the seaward faces of the foredunes at the Large Cave Transect, and five further sand traps were placed along this transect on the rear-dune faces, and in the old fixed dunes beyond the dune slack towards the cliffs. The trapped sand was collected, dried at 80°C, and weighed. From 25 May to 29 Jun 1996 a second trial, of 7 sand traps placed on the dune tops and 2 on the rear dune faces in the middle of the sampling area, ran for 36 days.

Analysis

Aerial photographs from 1940–2000 (New Zealand Aerial Mapping (NZAM); Air Logistics (AL)) were used to draw shorelines on the locality map (Fig. 1) to supplement earlier coastal boundaries as outlined in Esler (1974) and Williams (1977). Beach progradation rates were calculated from Fig. 1, assuming each front was laid down at the end of the named year and there was no beach opposite the sea caves in the 1930s.

The presence/absence vegetation data were analysed for community patterns by cluster analysis, using Jaccard's dissimilarity coefficient (for binary

data), and average linkage (Systat 1996). Fourteen quadrats lacking vegetation were excluded from the vegetation analysis, although nine containing only bare sand contribute to the Beach Front zone, and the other five were assigned to the Sand River habitat, based on their locations (see below). Thirty species, each present in only one quadrat, were excluded from the cluster analysis. Analysis of the remaining 75 plant species produced a dendrogram which was truncated at a dissimilarity of 0.75, yielding 12 vegetation types, designated "communities". Mean % occurrence of species in each community was calculated. Communities were mapped and boundaries interpolated from field observations and the aerial photograph closest in date to the study period (AL 1993, Serial No. 235729/235731, run 21/22; Fig. 5). The quadrat environmental data were used in descriptions of the communities. Environmental data, including those for the Beach Front, were analysed by Analysis of Variance, or by Pearson's correlation.

Along each transect, topography and the organic content of sand samples were plotted, and the plant communities from the vegetation survey superimposed.

Mean sand movement for the two periods was calculated as $g \text{ day}^{-1}$.

To investigate species' relationships to the environment, a Canonical Correspondence Analysis (using Canoco 4.5; ter Braak & Smilauer (2002); selecting direct gradient analysis, and interpreting relationships among species) was considered appropriate as it constrained the ordination axes of the vegetation data to be linear combinations of the environmental data. Aspects (in radians) were expressed as northings and eastings using cosine and sine transformations. Flat sites were given an arbitrary true north aspect for analytical purposes. Additional variates, to represent beach progradation rates, and opportunities for vegetation succession, were calculated. Distance to the coast (To Coast) was derived for each quadrat from Fig. 5. Minimum age (Min.Age) of each quadrat, the most recent time that location was "dry land", was taken as the age of the front closest to and seaward of it (Fig. 1). Time since disturbance (TSD) by sand movement was calculated as:

$$\text{Min. Age} - 8 - \frac{\text{distance of quadrat inland from the Min.Age front}}{\text{rate of accretion between that front and the next earliest}}$$

assuming linear progradation between known fronts, and where 8 is the number of years for vegetation

to occupy a new foredune (determined from aerial photos). Quadrats at the back of the beach, where waves cut in during the 1930s, were given an earliest front age of 61 (1996–1935), while quadrats on the 1853 surface, unaffected by the high tides of the 1930s, were given an earliest front age of 85, to reflect the time of cessation of operation of the railway (1996–1911). Quadrats affected by the Pararaha Stream diversion were given a TSD of 9 years (being the time interval between the estimated diversion and sampling, i.e., 1987–1996). Canoco variates which were mathematical combinations of others were excluded, as was one member of each highly correlated pair (Pearson $r > 0.65$). Assuming both multivariate methods were responding to the same patterns in the data, the community labels from the classification were assigned to quadrats on the CCA plot, to aid interpretation.

RESULTS

Beach dynamics

It is unclear how many changes of beach front there were between the 1850s and 1930s, but from then the beach prograded at an average rate of $0.10 \text{ km}^2 \text{ yr}^{-1}$ (Table 1). The beach prograded steadily from the 1930s until 1954 ($0.38 \text{ km}^2 \text{ yr}^{-1}$), to be followed by a period of erosion over the 1955–1960 period. The beach was more stable over the next two decades, to retrograde over 1987–1993 (average: $-0.59 \text{ km}^2 \text{ yr}^{-1}$). Since then sand has moved northwards along the beach, with no net addition of dry land but considerable erosion of foredunes (Table 1).

Floristics

The flora of Whatipu comprises 110 species, of which 105 were encountered in sampling, the others being rare. Exotic species are 47% of the 105 species sampled, increasing to 51% in the analysed species due to a high number of infrequent native species. Native and exotic shrub species are few (9 and 3 species analysed, respectively), but frequent (in 38% and 33% of quadrats).

Categorisation of vegetation

The dendrogram of quadrats separated the mobile foredune community, two types of herb meadow, four extremely wet communities, relict foredune and sand river communities, and a pair of mixed, more developed communities (Fig. 5; Table 2). The CCA of sites (Fig. 6) reflected this division, although

the wet communities were seen as more disparate from the sandy communities, while the old and new foredunes were closely allied, and adjacent to the diffusely positioned sand river sites.

Foredune community

The New Fore Dune (NFD) community is closest to the sea (Fig. 5), and consists of relatively steeply sloping sand dunes with open vegetation (6% cover), high shell cover, and little litter (Table 3). Substrate moisture and fertility by bioassay are as low as for the unvegetated Beach Front (BF, bare sand; Table 3). Only two native sand dune binders occur. *Desmoschoenus spiralis* tends to form small, low and scattered dunes of fine sand, usually facing seaward, while *Spinifex sericeus* dunes are taller, extend further along the shore, and appear less prone to wind and water erosion. These foredunes exist in the same location as incipient seaward unvegetated dunes in 1954, according to aerial photographs (NZAM 1954, serial no. 192, run 271, frames 1–7), but have grown considerably since the early 1980s.

Spinifex
taller
dunes.

Herb-meadow communities

Two small species-poor Herb-meadow communities, with few exotics (Table 2; Fig. 5), occur behind the foredune community, on flat, wet sites, and with areas of high water-borne sand movement.

Three small *Schoenoplectus* Herb-meadow H(S) patches, on the inland side of the NFD community (Fig. 5, 7), in shallow (10–15 cm deep), slow-moving water, all contain *Schoenoplectus pungens*, sometimes with *Carex pumila*, and tall, submerged *Triglochin striata*.

The *Nostoc-Triglochin* Herb-meadow H(NT) community comprises two small areas with 50% water cover amongst the Sand River community (see below), with abundant *Triglochin striata* and *Nostoc* spp., and some *Lilaeopsis novae-zelandiae* and *Isolepis cernua* var. *cernua*.

Former foredune communities

Two speciose (23–35 species) communities occurring in conspicuous bands immediately behind the foredunes are in the place of former foredunes and a beach front (Fig. 5). Their grouping with the more localised *Ammophila* Dune (AD) community in the dendrogram is due to a shared flora of wetland and dune species (Table 2).

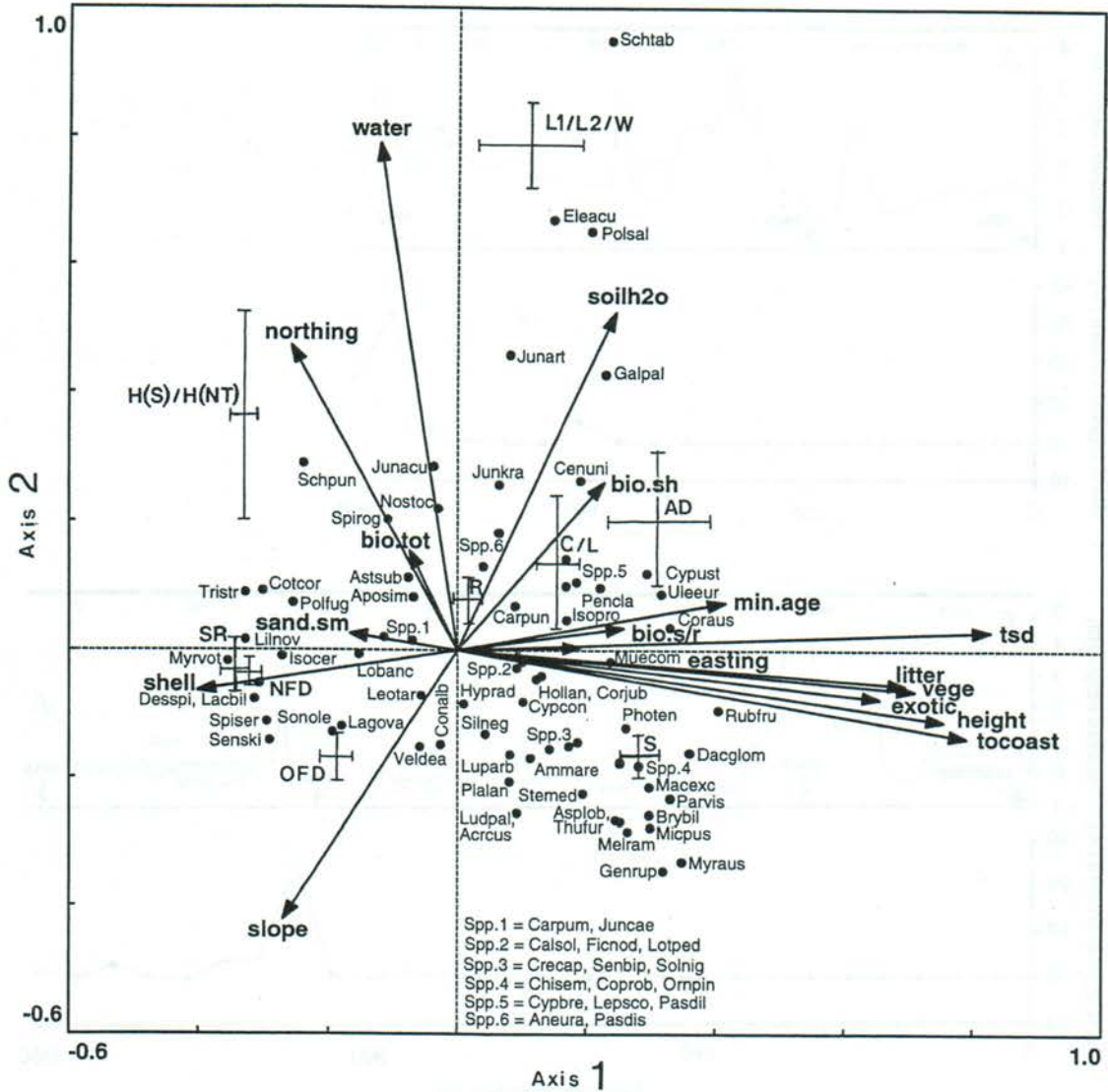
The large Sand River (SR) community occurs very close to sea level with shallow, flowing, fresh water at 32% cover on a sand substrate. Five quadrats under water and containing no vegetation are

Table 2 (Continued)

Community	NFD	H(S)	H(NT)	SR	OFD	AD	C/L	S	R	W	L ₁	L ₂
<i>Phormium tenax</i>	-	-	-	-	-	-	-	33	15	-	-	-
<i>Polygonum salicifolium</i>	-	-	-	-	-	-	22	-	-	50	-	100
* <i>Polypogon fugax</i>	-	-	50	12	-	-	-	-	8	-	-	-
<i>Schoenoplectus pungens</i>	-	100	-	6	-	-	11	-	15	-	-	-
<i>S. tabernaemontani</i>	-	-	-	-	-	-	-	-	-	-	50	100
* <i>Senecio skirrhodon</i>	-	-	-	47	71	-	-	8	8	-	-	-
* <i>Silene gallica</i>	-	-	-	12	14	-	-	25	0	-	-	-
* <i>Sonchus oleraceus</i>	-	-	-	29	43	-	-	-	8	-	-	-
<i>Spinifex sericeus</i>	42	-	-	59	100	-	-	8	8	-	-	-
<i>Triglochin striatum</i>	-	67	100	82	14	-	-	-	23	-	-	-
* <i>Ulex europaeus</i>	-	-	-	-	-	25	33	25	8	-	-	-
No. of other species	0	1	0	4	3	4	15	23	16	1	1	1

Table 3 Environmental factor means, species diversity (no. per quadrat), and exotic diversity in communities, and BF (Beach Front, or bare sand between apparent high tide and foredune vegetation). Community codes are explained in the text. Communities are plotted in dendrogram order (see Table 2). Northings and eastings are in radians; flat sites are given an arbitrary aspect of due north. Values in brackets for SR are the means of the 5 quadrats lacking species, and assigned to that vegetation belt, though they were excluded from the vegetation analysis and community means. Mean, mean value of variable for all communities, excluding Beach Front; wt, weight; NS, non-significant by ANOVA for all communities including Beach Front; diversity values were not tested by ANOVA.

Community	BF	NFD	H(S)	H(NT)	SR	OFD	AD	C/L	S	R	W	L ₁	L ₂	Mean
Number of quadrats	9	12	3	2	17 (5)	7	4	9	12	13	2	2	2	
Distance to coast (m)	349	275	440	488	546 (349)	639	979	1007	1269	956	913	980	1086	798
Species diversity	0	2	4	6	35	23	21	45	59	59	12	6	6	19
Exotic diversity (%)	0	0	0	33	52 (0)	67	57	53	49	44	25	40	60	37
Species diversity	0	2.3	3.0	6.8	30.0 (0)	15.8	10.5	24.0	29.3	38.3	11.3	5.3	5.3	14.0
Slope (°)	4.0	6.6	0	1.0	3.4 (0)	7.9	4.5	1.8	2.8	2.3	0	0	0	2.6
Northing	0.94	0.06	1	0.25	0.16 (1)	-0.43	-0.63	0.25	-0.35	-0.08	1	1	1	0.27
Eastings NS	0.26	0.11	0	0.43	-0.10 (0)	0.35	0.23	0.30	0.04	0.01	0	0	0	0.11
Min. front age (years)	45	43	44	45	46 (45)	46	100	72	71	50	52	56	56	56.5
Time since last disturbance (years)	39	38	9	9	9 (9)	42	63	55	55	46	30	51	51	38
Max. vegetation height (m)	0	0.92	0.33	0.22	0.90 (0)	0.98	1.99	2.06	2.56	1.61	1.50	1.00	1.95	1.3
Vegetation cover (%)	0	6	12	55	37 (0)	36	98	88	94	81	37	43	33	52
Exotics cover (%)	0	0	0	1	1 (0)	16	97	43	60	10	3	5	60	25
Sand cover (%)	100	94	0	45	40 (97)	64	1	1	6	19	0	0	0	19
Litter cover (%)	1	1	1	1	1 (0)	2	37	18	51	7.4	1	100	90	25
Shell cover (%)	0.4	0.2	0	0	0.2 (0.1)	0	0	0	0	0.1	0	0	0	0.04
Water cover (%)	0	0	100	50	32 (100)	0	13	32	1	43	100	100	100	48
Substrate moisture (% wet wt)	3.3	4.0	17.6	12.3	13.1 (13.4)	3.3	22.3	17.8	11.2	17.6	21.9	16.7	16.7	14.5
Substrates (% dry wt)														
Coarse NS	0	0	0	0	0 (0)	0	0.2	0.5	0.1	0	0.2	0	0	0.0
Medium	0.4	0.9	1.2	0.6	1.0 (0.8)	0.8	2.9	1.7	1.1	0.8	0.4	0.5	0.7	1.1
Fine	99.6	99.1	98.8	99.4	99.0 (99.3)	99.2	96.9	97.8	98.8	99.2	99.4	99.5	99.3	98.9
Bioassay total dry wt (g)	0.44	0.51	0.85	0.57	0.75 (0.69)	0.79	1.12	0.76	0.64	0.64	0.78	0.75	0.75	0.74
Bioassay shoot dry wt (g)	0.09	0.12	0.24	0.21	0.20 (0.18)	0.14	0.34	0.21	0.19	0.17	0.17	0.24	0.24	0.21
Bioassay shoot/root ratio NS	0.40	0.39	0.41	0.57	0.42 (0.37)	0.28	0.56	0.49	0.46	0.44	0.28	0.48	0.48	0.44



australis; Corjub, *Cortaderia jubata*; Cotcor, *Cotula coronopifolia*; Crecep, *Crepis capillaris*; Cypbre, *Cyperus brevifolius*; Cypcon, *Cyperus congestus*; Cypust, *Cyperus ustulatus*; Dacglom, *Dactylis glomerata*; Desspi, *Desmoschoenus spiralis*; Eleacu, *Eleocharis acuta*; Ficnod, *Ficinia nodosa*; Galpal, *Galium palustre*; Genrup, *Geniostoma rupestre*; Hollan, *Holcus lanatus*; Hyprad, *Hypochaeris radicata*; Isocer, *Isolepis cernua* var. *cernua*; Isopro, *Isolepis prolifer*; Junacu, *Juncus acutus*; Juncae, *Juncus* aff. *caespiticius*; Junart, *Juncus articulatus*; Junkra, *Juncus kraussii* var. *australiensis*; Lacbil, *Lachnagrostis billardierei*; Lagova, *Lagarus ovatus*; Leotar, *Leontodon taraxacoides*; Lepsco, *Leptospermum scoparium*; Lilnov, *Lilaeopsis novae-zelandiae*; Lobanc, *Lobelia anceps*; Lotped, *Lotus pedunculatus*; Ludpal, *Ludwigia palustris*; Luparb, *Lupinus arboreus*; Macexc, *Macropiper excelsum* var. *excelsum*; Melram, *Melicytus ramiflorus*; Micpus, *Microsorium pustulatum*; Muecom, *Muehlenbeckia complexa*; Myrvot, *Myriophyllum votschii*; Myraus, *Myrsine australis*; Nostoc, *Nostoc* sp.; Ormpin, *Ornithopus pinnatus*; Parvis, *Parentucellia viscosa*; Pasdil, *Paspalum dilatatum*; Pasdis, *Paspalum distichum*; Pencla, *Pennisetum clandestinum*; Photen, *Phormium tenax*; Plalan, *Plantago lanceolata*; Polsal, *Polygonum salicifolium*; Polfug, *Polyogon fugax*; Rubfru, *Rubus fruticosus* agg.; Schpun, *Schoenoplectus pungens*; Schtab, *Schoenoplectus tabernaemontani*; Senbip, *Senecio bipinnatisectus*; Senski, *Senecio skirrhodon*; Silgal, *Silene gallica*; Solnig, *Solanum nigrum*; Sonole, *Sonchus oleraceus*; Spiser, *Spinifex sericeus*; Spirog, *Spirogyra* sp.; Stemed, *Stellaria media*; Thufur, *Thuidium furfuriosum* (moss); Tristr, *Triglochin striata*; Uleeur, *Ulex europaeus*; Veldea, *Vellerophyton dealbatum*.

have more than 97% of fine sand (< 0.5 mm diam.; Table 3), community AD (*Ammophila* Dune) has more medium-sized substrate grains (0.5–0.15 mm diam.). The organic content of sand was low overall, but slightly higher in the sand river and herb meadow communities, and much higher in the rear communities on both transects (Fig. 7). Sand movement on the rear dunes is an order of magnitude less (0 and 53 g day⁻¹ trap⁻¹, respectively for Large Cave Transect and mid study site trap complexes) than on the foredunes at both sites investigated (135 and 443 g day⁻¹ trap⁻¹). Fore-dune sand movement was very high under the predominantly westerly wind flows of the second time period, when winds were moderate to strong (10–25 knots) with gales on some days.

Mean exotic plant cover and exotic richness (as a percentage of total species richness) are positively correlated with increasing average distance of a community from the sea (Cover: $r = 0.653$; Diversity: $r = 0.603$; Fig. 8). Communities NFD and H(S) near the shore have no exotic plants. Communities H(NT), SR, OFD, R, L₁, and W have a wide range in richness of exotic plants (25–67%; Table 3), but these exotic plants have little cover (0.3–16%). However, communities C/L, S, L₂, and AD, closer to the cliffs, have high richness (49–60%) and high exotic plant cover (43–97%).

These species-environment gradients are summarised by the transect profiles (Fig. 7), which show bare sand on the Beach Front where scattered *Desmoschoenus spiralis* seedlings form incipient fore-dunes. The strand-line portion of the beach slopes down towards the recent mobile foredunes (NFD), which are up to 4 m tall and have been prograding since 1949. Behind these a wet (7–10 cm deep) sand river zone is broken by successive sand ridges, which were formed in 1940–1949 during rapid coastal accretion. This zone is below the apparent high spring-tide level on the Large Cave Transect, as is the mid Beach Front on the Cutter Rock transect. Landward are less mobile, older sand dune communities (OFD and R; prograded since the 1930s), then communities with increased exotic invasion (C/L and S). On the Large Cave Transect, low-lying wetland areas occur coastwards of the loose unvegetated sand against the cliffs (see Fig. 5). Underlying the whole area, the freshwater water table drops closer to the sea (Fig. 7).

The first axis of the CCA explained 24.8% of the variation of the species' data (Fig. 6). The presence of shrub and weed species typical of later seral stages (such as *Cordyline australis*, *Phormium tenax*, *Ulex europaeus*, *Dactylis glomerata*, and *Rubus*

fruticosus agg.) was positively associated with cover and height of vegetation, distance to coast, time since last disturbance by sand movement, and higher covers of exotics and litter (Fig. 6). Communities S, AD, and C/L are located in this area of ordination space. The pioneering sand-binders *Desmoschoenus spiralis* and *Spinifex sericeus* and some sandplain species were strongly negatively associated with these vectors, and instead were positively associated with higher shell cover and finer sand. Here the young sandy communities NFD and SR are tightly positioned, close to the older OFD community. Species commonly associated with the rear of fore-dunes (in communities R and AD) occur in the middle of the trend, along with *Ficinia nodosa*, the restiad *Apodasmia similis*, and *Carex pumila*, often a sand-binder but also tolerant of damp sites. Thus, the first axis of the CCA corresponds closely to a successional sequence of species from left (young surfaces) to right (older surfaces; Fig. 6).

The second axis (16.8% of variation) of the CCA is more strongly associated with sunny or flat sites, and the presence of water (in soil or on the surface); it is weakly associated with high fertility (via bioassay). At the positive end, aquatic species abound, such as *Eleocharis acuta*, *Nostoc* sp., *Spirogyra* sp., and *Schoenoplectus tabernaemontani*, along with the herb-meadow and lake communities (H(NT), H(S), W, L₁, and L₂). The opposite end of Axis 2, associated with steep slope and southerly aspects, contains many exotic weedy species. Quadrats of the SR community are dispersed along this axis due to their variable water cover and substrate moisture.

DISCUSSION

Whatipu Beach is a particularly interesting dune system because of its recorded history of sand movement and progradation, and its indigenous vegetation (Esler 1974; Cameron 1989). Here, vegetation dynamics and dune dynamics are described, a successional sequence delineated, and its relationship to dated surfaces determined.

Beach dynamics

Whatipu Beach has a history of progradation episodes, like nearby Piha (Esler 1974, 1975). Sand has prograded episodically over the last 1.5 centuries as a consequence of high sand mobility during periods of high sand supply. In the mid nineteenth century and again in the 1930s no beach was present at all. Since the 1930s, the beach has largely been

radicans, *Tetragonia trigyna*, and *Ozothamnus leptophyllus* (Forst.) Brietw. & Ward. Populations of *Limosella lineata* once dominated Whatipu herbmeadows (Cameron 1989; Denyer et al. 1993), but have recently declined, conceivably due to increased sand erosion or to water table oscillations. *Selliera radicans*, a facultative halophyte, is rare at Whatipu, probably because the only suitable habitat, a dune slack, is now a freshwater sand river. The small herb *Ranunculus acaulis* is present at nearby Kaitarakihi Bay, Huia (APMP pers. obs. 2002; herbarium specimen AK 237029) and may yet migrate to Whatipu. Thus, the total number of native slack plants at Whatipu is low compared with Mason Bay, Stewart Island (Sykes & Wilson 1987) and Manawatu dunelands (Esler 1969; Singers 1997), though the small, disturbed slack at Westerwood Beach, south-west of Dunedin, is still less speciose (Roxburgh et al. 1994). An important sandplain species at Whatipu, although not recorded in any quadrat, is the small "declining" cyperad *Eleocharis neozelandica* (de Lange et al. 1999). It was present beside Cutter Rock in the 1970s but is now absent due to water table changes (A. E. Esler pers. comm. 1996) or to competition with larger rushes or sedges (Singers 1997). Since 1974, the more northern patches of *E. neozelandica* have changed location from beside Pararaha Stream, immediately north of the study area, to further south behind the mobile foredunes in the sand river and herb meadow areas (A. E. Esler & E. K. Cameron pers. comm. 1996; APMP pers. obs. 2005). This migration may have paralleled the altered course of the stream and resultant changes in water table, as *E. neozelandica* copes well with temporary submersion, and is dispersed by fresh water (Singers 1997).

Exotic species are very important at Whatipu, making up about half of the flora and with high cover (60–97%) in communities further from the beach. Typically exotic floras are smaller in other less disturbed dune areas (40% at Chrystalls Beach, Drobner et al. 1995; 30% in southern dune slacks, Roxburgh et al. 1994; 27% of reported species at Kaitorete Spit, Widodo 1997; 15% in Mason Bay slacks, Sykes & Wilson 1987; 12% at Cole Creek beach, Sykes & Wilson 1991). Frequent dune weeds are *Holcus lanatus*, *Hypochaeris radicata*, *Trifolium repens*, *Lotus pedunculatus*, *Lupinus arboreus*, and, of course, *Ammophila arenaria*, all present at Whatipu except for *Trifolium repens*. *Ammophila arenaria* dominated most of the beach in the 1970s (Esler 1974), to recently decline. Currently, the exotic species with greatest coverage are the

larger sward or tussock forming grasses, especially *Cortaderia jubata*, *Cynodon dactylon*, *Pennisetum clandestinum*, and *Paspalum dilatatum*. These were introduced by the lessee of the Whatipu valley farm in about 1953 for sand stabilisation purposes (Esler 1974). Their growth is so vigorous that they smother native dune-building or shrub species, and dominate rear dune communities such as Shrub (S), Rush (R), and *Cortaderia/Leptospermum* (C/L), and will probably continue to dominate until slowly-invading forest shrubs overtop them.

Vegetation dynamics and community succession

The "normal" linear dune succession, as outlined by Cockayne (1928), is derived from observations of spatial analogues, and describes a foredune vegetation followed by more or less temporary wet dune hollows which succeed into shrubland and forest on older sand surfaces. At Whatipu Beach, the ability to date sand surfaces extrinsically, using a combination of maps, early records, and aerial photos, allows these to be related more directly to vegetation dynamics. Nine beach front positions are known over the last 170 years, indicating minimum times since disturbance by sand movement. From the 1930s the beach prograded to reach its greatest known extent in the 1980s (Fig. 1). This active area was examined here, and surveying for the profile diagrams took place directly across the lines of emplacement of new beach fronts. However, disturbance events, especially commercial fishing and logging activities of 1850–1911 (which used coastal railway and sea ports), invasion of exotic plants, and stock grazing until the 1970s, have greatly modified the succession.

Today the surfaces most clearly undergoing a normal primary succession are the New Fore Dune and Old Fore Dune communities (NFD and OFD). The new foredunes were laid down in the 1950s, but increased in size only in the 1980s, when the native foredune binder *Spinifex sericeus* (Esler 1970; Singers 1997) spread from isolated patches on older dunes (Esler 1974). *Desmoschoenus spiralis*, the weaker native sand-binder (Esler 1970), has expanded in the last 30 years from a small patch near Cutter Rock (A. E. Esler pers. comm. 1996), and now extends along most of the front of the beach. These species were previously widespread throughout New Zealand foredunes (Cockayne 1928), and one or both still dominate Stewart Island and Northland dunes (GLR pers. obs.) and, amongst studied dunes, parts of the Manawatu dunefields (Singers 1997) and the Cole Creek dunes (Sykes & Wilson 1991). At Whatipu a

of the beach, and nutrient impoverishment from the limited sand supply. Instead *Ammophila arenaria* has been largely superseded by exotic kikuyu grass (*Pennisetum clandestinum*), which is also widespread in other non-shrubby older communities (Fig. 5) and is aggressive at nearby Piha (Esler 1975). This community is typical of many other highly modified and weedy duneland areas in New Zealand, which interrupt or terminate natural dune successions.

Esler (1974) recorded an area of "mobile dunes" amongst *Ammophila arenaria* in 1973, which today appears to coincide with the *Cortaderia/Leptospermum* community (C/L). A rather wet, well-vegetated community, with some exotics, it has a range of native species which tolerate water-logging, such as *Apodasmia similis* and *Leptospermum scoparium* (Cook et al. 1980). It differs from the Shrub community by its more recent colonisation, presumably largely by pioneering exotics. It appears to represent a primary succession, initiated by exotics on stable surfaces.

Rear, short-stature dune communities are usually occupied by sand-collecting species or species which can survive modest amounts of sand burial (Sykes & Wilson 1990), such as *Pimelea arenaria* and its congeners, *Coprosma acerosa*, and *Ozothamnus leptophyllus* (Pegg 1913; Cockayne 1928). These occur as scattered individuals in the rear of the expansive Manawatu foredunes (Carnahan 1957; Singers 1997; Dawson 2003), but are otherwise uncommon on New Zealand beaches except for those of Stewart and Great Barrier Islands (Johnson 1992; Partridge 1992; APMP & GLR pers. obs.). All are known to be susceptible to disturbance (Esler 1975). Although dominant behind the foredunes at nearby beaches (Williamson 1953; Asplin & Fuller 1986), *Ozothamnus leptophyllus* was almost eliminated at Piha by 1974 (Esler 1975). At Whatipu, these species are absent, except for *Ozothamnus leptophyllus* which occurs in one quadrat. Instead the shrub community (S), on surfaces more than 70 years old, is dominated by aggressive exotic species such as the tall (2 m) tussock *Cortaderia jubata* and nitrogen fixers from the genera *Lupinus* and *Lotus*, amongst a range of weedy forbs. A few natives, including several forest understorey species, are able to invade despite the dense cover of exotics, possibly even facilitated by their presence.

Although most New Zealand dune systems with indigenous vegetation now lack the expected hinterland vegetation, due to forest clearance or past fires (e.g., Manawatu region, New Zealand; Esler 1970), coastal podocarp or broadleaf forests do occur in the

rear of some dune systems such as in the southern South Island (Smith et al. 1985; Sykes & Wilson 1991; Johnson 1993). At Whatipu the rear of the study site is instead occupied by communities of shrubs and exotic tussock grass (communities AD, S, and C/L). Esler (1974) recorded these areas as having thin topsoil, and a higher organic content was recorded there in this study (Fig. 7). However, it appears that succession at Whatipu Beach is arrested, i.e., proceeding, if at all, only slowly to forest, due to the density of the exotic grass sward, and, probably, the low native seed input on this isolated beach which has an additional dispersal barrier of tall cliffs.

Testing successional analogues

Whatipu Beach gives an opportunity to date the linear dune succession propounded by Cockayne (1928), and to test the approach of determining the pattern and rate of succession from putative spatial analogues. While communities close to the coast are typical of primary succession (i.e., NFD, OFD, and R), those on older surfaces have anomalous characteristics, through being exposed to exotic invasion and cattle browsing. Despite this, a number of native species do establish in rear dune communities, and perhaps are even facilitated by the relatively stable environment provided by species such as *Ammophila arenaria*. The successional sequence described for Whatipu Beach parallels that postulated by Cockayne as early as 1928, at least for the earlier stages.

Although no dates have been applied to the various seral stages perceived under the linear model, at Whatipu succession proceeds very rapidly, with dunes being colonised by 8 years, a dense cover of sandbinders establishing by 20 years, dune slack communities forming within 30 years, and stabilising communities (including exotic species) within 50 years. Forest development is likely to be long-delayed, though, at Whatipu.

Only on a prograding beach, where dunes are rapidly isolated from the sea, is any real primary succession possible, and there it is extremely rapid. The relatively long duration of a dune succession's spatial corollary must be due to ongoing exposure to wind, salt, and sand, the coastal influence permanently holding dune communities in a "neotenic" state. Thus, the development of soil stages, often regarded as crucial to the progress of a succession, does not appear to be a prerequisite in dunes, but rather a consequence of the succession being delayed due to environmental or topographical

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