[1] Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.
[2] Ecosystem Dynamics Group, Research School of Biological Sciences, Institute of Advanced Studies, Australian National University, Canberra, ACT 0020, Australia.

DUNE SLACK VEGETATION IN SOUTHERN NEW ZEALAND

Summary: A range of slack vegetation in southern New Zealand was described by detailed sampling of four dune slacks, contrasting in topographic situation and in vegetation. Comparison is made with a slack previously sampled on Stewart Island. The five slacks differed markedly in the plant communities present. One slack, where there was considerable peat accumulation, was dominated by the megaherb *Phormium tenax* and the restiad *Leptocarpus similis*. In another, the peat was deep and had apparently accumulated over a long period; the vegetation contained the trunked sedge *Carex secta* and was similar in species composition to carr vegetation described from the region. These two slacks were predominantly native in species composition, though the European *Erica lusitanica* was a component at the second. The other two slack sites were on substrate largely comprising sand; the vegetation was shorter, and included a mixture of native and exotic species. Many of the exotic species found in these sites have been recorded in European slacks.

Communities were defined by Cluster analysis. With rare exceptions, each plant community was specific to one or another of the five sites. Even the few community/site overlaps were in the vegetation of the surrounding dune areas, not of the slack itself. The communities within a site generally formed discrete zones, related to small differences in elevation.

The environment was characterised in terms of elevation, water table level, and soil salinity (chloridity), organic content, pH, physical texture and fertility (assessed by bioassay). There were varying amounts of organic matter accumulation, but the mineral part of the substrate was almost pure sand throughout, except that at one site a stream had brought in silt. In three of the sites, the mineral base was below high tide level. The water table fluctuated through the year, with the same pattern as described for Northern Hemisphere slacks. Chloridity was low, but varied through the year. Some features of the yearly variation could be related to weather events.

It is concluded that slacks in the area show considerable variation in vegetation, much of which can be correlated with peat accumulation.

Key words: Chloridity; fen; New Zealand; salinity; sand dune; slack; water table.

Introduction

Slacks are damp or wet depressions between coastal dunes, where the ground water is often close to the sand surface, and is above it for part of the year (Tansley, 1939; Gitay and Agnew, 1989). They form where sand loss has been limited at some time by the level of the water table. The environment contrasts with that on the adjacent dunes, and fluctuates through the year, with standing water in winter, but possible drought stress in summer. In contrast to salt marshes, sea-water influence is low.

The vegetation and environment of slacks have been of interest to ecologists throughout the world, e.g., in Europe (van der Maarel and Westhoff, 1964), Britain (Crawford and Wishart, 1966), South Africa (McLachlan, Ascaray and du Toit, 1987) and North America (Tyndall and Levy, 1978). Slack vegetation in New Zealand is not well known (Ranwell, 1972). New Zealand slacks were briefly described by Cockayne (1928) and Esler (1969, 1970, 1974, 1978). The first description, based on sampling, of New Zealand slack vegetation was by Sykes and Wilson (1987) for a slack at Mason Bay, Stewart Island (known locally as Mutton Flat). However, the amount of variation in slack vegetation within New Zealand remains unknown. Many such sites have been destroyed by ‘development’, and conservation of the remaining sites requires a knowledge of the types of community found. We therefore sampled the vegetation of four slacks in southern New Zealand. The sites were selected as being less disturbed than other slacks in the area, and also covering a range of geomorphological situations. Records were made of several environmental factors: elevation, water table, and several soil characteristics.

Sites

Aramoana

The dune/slack/saltmarsh area at Aramoana, Otago harbour (170° 42.5' E, 45° 47' S) lies behind an estuary bar (Partridge and Wilson, 1975). There is a series of parallel, low fossil sand dunes, of Holocene age, probably < 6000 years B.P. (C.A. Landis and P.D. McIntosh, *pers. comm.*). The slack surveyed lies between two such sand ridges, and is closed to seawater ingress at both ends. Depressions beyond the two ridges are open to the estuary, and contain salt marsh. The vegetation of the slack is dominated by the tall liliaceous (*s.l.*) herb *Phormium tenax*[1]. The slack is mentioned by Johnson (1992).

Measley Beach

The slack, 60 km southwest of Dunedin (170° 00' E, 46° 15' S) occurs in a long depression between the fixed rear dune and the hillside, the latter apparently a very old dune, confirming the depression as a slack, be it an ancient one. The vegetation is *c*. 2 m tall, with the trunked sedge *Carex secta* visually predominating. Species composition is predominantly native, except for the presence of *Erica lusitanica*, an exotic from Southwest Europe.

Toko Mouth

The small slack examined, 55 km southwest of Dunedin (170° 03' E, 46° 14' S), is entirely surrounded by high dunes. The dunes are dominated by the exotic dune builder *Ammophila arenaria*, but in a few places the native dune builder *Desmoschoenus spiralis* is still present. The vegetation of the slack comprises a low turf, with a close mixture of native and exotic species, between scattered clumps of *Juncus gregiflorus, Carex virgata* and *Isolepis nodosa* (= *Scirpoides nodosa*). There is evidence of rabbit browsing.

Westwood

The slack, 12 km southwest of Dunedin city centre (170° 22' E, 45° 56.5' S) is a small and shallow depression towards the rear of a sand plain behind the main dune ridge. The dune vegetation is largely exotic, but natives are significant in the slack itself. Rabbit browsing is again in evidence.

Mason Bay, Stewart Island

Described by Sykes and Wilson (1987), this site was included in the vegetation analyses to make the communities produced as general as possible from the available data.

Methods

Vegetation sampling

In each site a sample area was delimited, to cover the range of variation in the slack (or the complete slack when small), and to follow what we name the *Sykes Principle*: 'Always sample into the next community'.

The vegetation physiognomy, and the scale of the community pattern, were quite different at the five sites. In order to perform effective sampling, it was necessary to use quadrat sizes appropriate to the vegetation. Therefore, a 0.2 x 0.2 m quadrat was used at Toko Mouth and Westwood (80 quadrats at each), and a circular quadrat of up to 1 m radius, sampling the closest seven species, at Aramoana and Measley Beach (60 quadrats at each). A 0.5 x 0.5 m quadrat had been used at Mason Bay. At each site, the quadrats were placed by restricted randomisation. Shoot presence of all macroscopic plant species was recorded.

In order to compare communities between sites, we analysed together all quadrats from all five sites sampled. This gave 428 quadrats in total. Cluster analysis was performed with the Jaccard measure of dissimilarity, and flexible sorting strategy (beta = -0.25) (Clifford and Stephenson, 1975).

Soil and topography

After vegetation classification, the distribution of the communities was mapped onto each site. Four soil samples were then taken at random from each of the communities. (No samples were taken from the few communities not shewing a clear topographic pattern, or limited in extent.)

Soil characteristics determined were pH, organic matter (by loss on ignition at 500°C) and sand, clay and silt fractions in the inorganic fraction (by hydrometer). Soil fertility was determined by bioassay, mixing a soil sample with an equal volume of washed sand, placing in 9 cm x 9 cm x 7 cm deep pots, and sowing 0.8 g of *Lolium perenne* seed per pot. The pots were sown on January 22 and shoot dry weight per pot determined by harvest on March 13, after growing in an unheated greenhouse. John Innes Potting

[1] Nomenclature follows, in order of priority, Stace (1991), Webb, Sykes and Garnock-Jones (1988), Connor and Edgar (1987) and references therein for higher plants, Sainsbury (1955) for mosses and Hamlin (1972) for liverworts.

Compost No. 1 was included, and biomass results are expressed relative to this.

Elevation relative to the apparent high tide mark was measured at each quadrat. (This was intended to give some meaning to between-site comparisons, not as accurate calibration to tidal levels.) More detailed topography was measured along a transect through the sampled area to the sea. Within the slack, depth was recorded to the water table at vegetation-sampling time (within a few days for the four sites). The chloridity of the ground water was determined by silver chloride titration. Where there was peat, its depth was measured with a sampling probe.

Variation in water table and chloridity

At Aramoana and Westwood a series of perforated tubes was sunk into the substrate at intervals along a transect through the centre of the sampled area. The elevation of the water table was measured monthly from January 1991 to January/February 1992, and a water sample taken for chloridity determination as above.

Results

Vegetation classification: general

The vegetation grouping closely parallelled the sites sampled, all groups comprising predominantly quadrats from one site. At our basic (arbitrary) level of six groups per site, the vegetation groups characteristic of Aramoana contained one quadrat from Toko Mouth and one from Westwood; the Measley Beach groups contained no quadrats from any other site; the Toko Mouth groups contained three Measley Beach quadrats and one Mason Bay (Stewart Island) quadrat; the Westwood groups included two Aramoana quadrats; the Mason Bay groups contained one Westwood quadrat. This represents only nine out of the 428 quadrats bearing vegetation similar to that at another site.

At a more general level of classification, that of eight groups, quadrats from different sites were again distinct, with:

- one Aramoana group,
- one mixed Aramoana and Measley Beach group,
- one Measley Beach group,
- one Toko Mouth group,
- two Westwood groups,
- two Mason Bay (Stewart Island) groups.

Aramoana

Topography

The slack sampled at Aramoana is surrounded by sand ridges. Levelling demonstrated these to be 0.25 - 0.5 m above the base of the slack, thus preventing the ingress of sea water and explaining its difference in vegetation from that in the neighbouring intra-ridge depressions, which are open to the sea and contain salt marsh. The topography within the slack is quite flat, though uneven on a small scale because of the growth form of the *Leptocarpus similis* (Fig. 1).

Water table

The water table at the time of vegetation sampling was almost horizontal, with some undulations that can be attributed to the slowness of lateral drainage through the peat, and slight indication of a lower table at the edges of the slack, under the two dune ridges (Fig. 1). Its depth varied through time (Fig. 2; in analysis of variance: $F = 51.4$, $P < 0.0001$) and between positions A-E (Figs. 1, 2; $F = 149.0$, $P < 0.0001$), but changes at different positions across the slack paralleled each other closely (Fig. 2). Water table depth was quite constant from January through to October, but then dropped. The decrease in November can be correlated with low rainfall in October and November that year (a total of 86.2 mm in Dunedin, 20 km away, compared with the long-term monthly norms of 131 mm). By the next January-February, water table depth had not recovered to its position at the same time a year earlier. The yearly-mean elevation of the water table relative to high-tide mark decreased from +5 cm above high tide level at Position D to high-tide level at Position E and -3 cm at Positions C, B and A. This confirms that drainage is away from the slack under the two ridges. At position A, the water table elevation was less variable than all other positions, probably reflecting the tidal influence there.

Chloridity

Overall, chloridity at Aramoana was somewhat higher than at other sites, an average of 164 mg l^{-1} through the main part of the slack at the time of vegetation sampling. Over the year, Position A, on the edge of the salt marsh, was clearly more saline than the others ($F = 29.2$, $P < 0.000001$), having a mean chloride value of 3 569 mg l^{-1}, but with considerable variation, reflecting tidal influence; the highest chloridity recorded at Position A was 7948 mg l^{-1}, about half sea water. Even removing

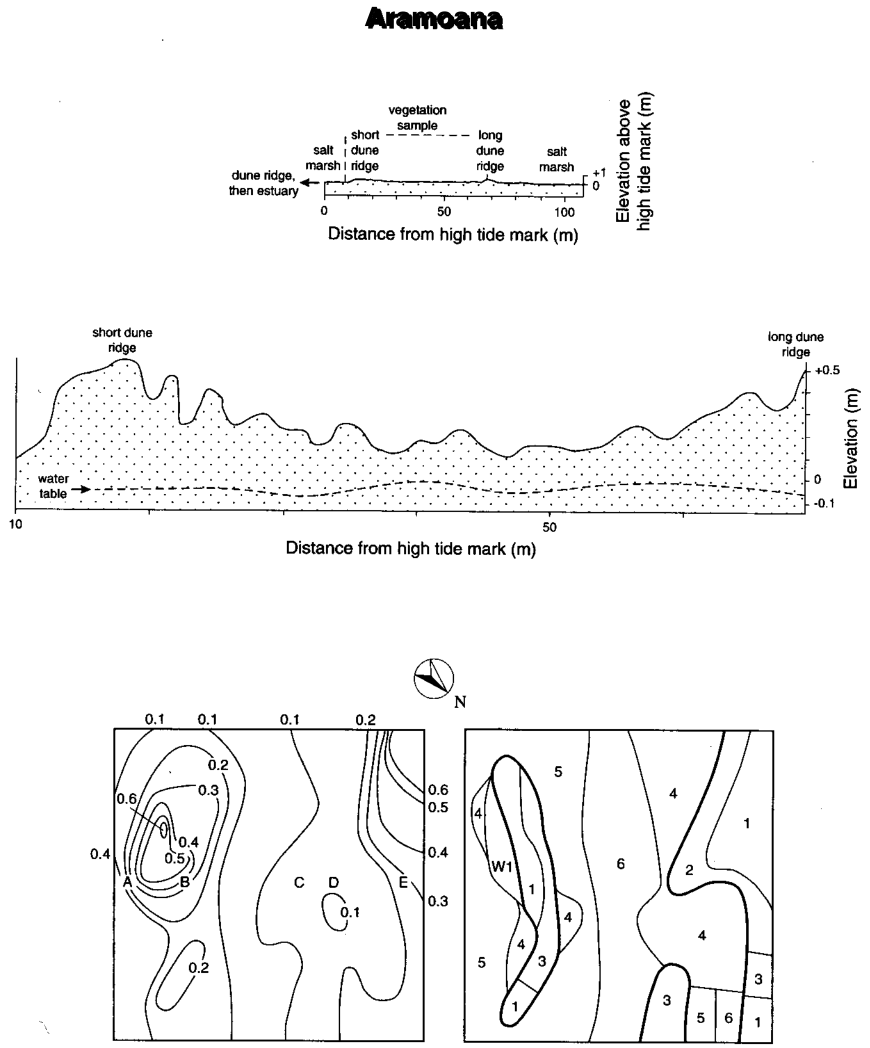

Figure 1: *The Aramoana slack: Profile of the site (top), profile of the area sampled for vegetation (middle), contour map (bottom left) and vegetation map (bottom right). Bold lines separate major groups of communities. 1 to 6 = Aramoana communities, W1 = Westwood community 1. The water table on the enlarged profile is at the time of vegetation sampling. A to E on the contour map are the positions of tubes for monthly water table sampling. Contours in metres.*

Table 1 (opposite): *Species composition of communities in the four southern New Zealand slacks, Aramoana (A), Measley Beach (M), Toko Mouth (T) and Westwood (W). C = constant (i.e. frequency 100%), 9 = frequency 90-99%, 8 = frequency 80-89%, etc., + = frequency 0.1-0.9%, space = species absent. Bold figures indicate occurrences mentioned in the text. Horizontal lines separate groups of species that differ in the sites at which they are most frequent.*

	Aramoana						Measley Beach						Toko Mouth						Westwood						
	A 1	A 2	A 3	A 4	A 5	A 6	M 1	M 2	M 3	M 4	M 5	M 6	T 1	T 2	T 3	T 4	T 5	T 6	W 1	W 2	W 3	W 4	W 5	W 6a	W 6b
Blechnum penna-marina	1				**3**																				
Chiloscypus normalis	2		8	3	**1**	**C**																			
Gonocarpus aggregatus	1				4																				
Leptocarpus similis	+			**9**	**8**	**C**																			
Lophlocloea sp.	2	4		**5**	3	4																			
Peltigera sp.	+				1	2								+			+								
Racopilum sp.					+	**3**																			
Blechnum minus	1			3	2	4	6	5	**7**	**C**	**C**	**C**													
Coprosma propinqua	+	2	**C**	9	1	4	6		2	+		4							+						
Lepidosperma australe	3	4	**C**	+	2				2		**8**	**8**													
Ranunculus glabrifolius		4	4	2		+			2																
* *Anthoxanthum odoratum*	**C**	2		3	+	+							5	1		1	2				+				
* *Cerastium fontanum*		2			+								3	2	4	2					1				
Hydrocotyle novae-zeelandiae	+		4	+	+	2							7	6	2	1	**7**	2							
* *Hypochaeris radicata*	3	2	4	+																	4	+	**6**	3	
* *Lupinus arboreus*	+	2																	**3**						
* *Ranunculus repens*		2																			7			1	**C**
* *Agrostis capillaris*	2	2	2		+		3		5				**+**	**8**	8		**6**	2							1
Plagiochila sp.	+				**3**	3	3						8	8		6	9	1							
Phormium tenax	3	4	**C**	**C**	**9**	**C**		2	**7**	9	**8**	2							+	**6**					
* *Trifolium repens*	+	**8**											6	8	6	5	6	3			3	+	3	**7**	1
* *Poa pratensis*		**C**		1		2							2	+							**8**	+	2	6	5
* *Juncus articulatus*		**4**									+		+	+			2	**6**			2	+	+	**C**	**C**
Hypnum sp.		2													2	1							+	**5**	
Isolepis nodosa	1	6	4	**8**	4	**+**							+			1								+	2
Carex virgata			2	+	+	+							2	+		1	4	1							4
Thuidium sp.	1		2		2								9	9	**C**	1	C	C			+				2
* *Holcus lanatus*	**8**	**8**	**6**	+	1		3		**7**		+		9	9	**C**	7	3		**9**	**C**	**7**	**C**	**C**	2	1
Astelia fragrans							3	**4**																	
Carex coriacea	+						6			+	2						1								
Carex secta							3		**5**	**7**	**6**	**C**													
Coprosma lucida								**4**																	
Coriaria arborea										**2**															
Eleocharis acuta						1			**5**		**7**														
* *Erica lusitanica*										+	**5**	**C**													
Fuchsia excorticata								**1**																	
Hebe salicifolia							**C**	**7**		+															
Myrsine australis								**1**																	
Olearia avicenniifolia							3	1	2	3	+	8													
Pittosporum tenuifolium								**5**		+		2													
Pseudopanax colensoi								**7**																	
Pteridium esculentum							**6**	**7**		1		4													
Weinmannia racemosa								1				**8**													
Juncus gregiflorus							3						**5**	1		1	+	**6**					+		
Marchantia berteroana									2				**5**	2		1		**3**							
* *Cirsium vulgare*									5												1	**2**		+	
Aneura sp.													2	4		1	+								
Collema sp.													1				1	1							
Epilobium brunnescens													**3**	1		2									
* *Festuca rubra*													3	1		3	+				+				
Fossombronia sp.													6	9		1									
Gnaphalium audax													2	+											
Hydrocotyle heteromeria													1	+	**6**	1									
Isolepis aucklandica													1	1		3	**9**	6							
Isolepis cernuua														+		2	1	4							
* *Juncus bufonius*													2	**6**		1	4								
Nertera setulosa	+												3	3		**6**	2	2							
Ranunculus acaulis													+	+		1	1								
Ranunculus cheesemanii														**5**	2	1	+								
Riccardia sp.													3	3		2	5	1							
* *Sagina procumbens*													5	7		1	+								
Tortula sp.													7	5	6	5	C	2							
Trichocolea rigida								1						1		2	2	1							
* *Rumex acetosella*															4						**C**	**C**		3	2
Acaena novae-zelandiae																			+		4	2	**7**	1	
* *Agrostis stolonifera*					1															8	8	4	7	**C**	**8**
* *Carduus* sp.																			**5**			+	2		
* *Dactylis glomerata*	+																		1			1	+		
* *Galium aparine*																			**5**			+	1		
Muehlenbeckia australis																			+	C					
Potentilla anserinoides																					+			**7**	**8**
* *Rumex crispus*																			+		2	1	**4**	1	

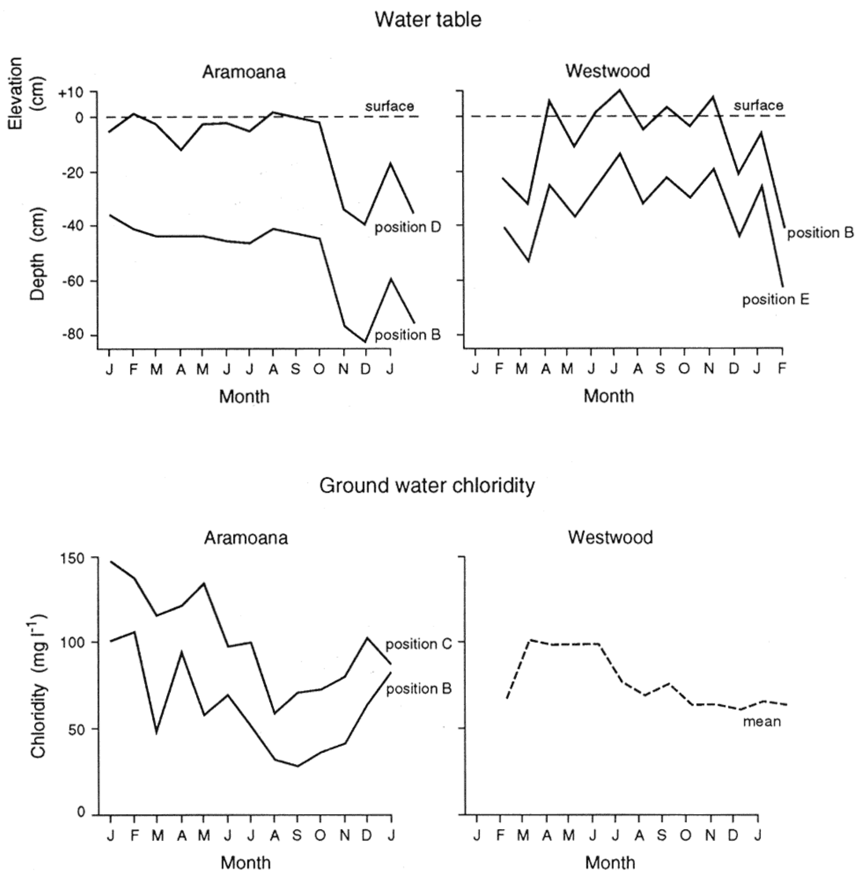

Figure 2: *Water table and ground water chloridity for 13-14 months in the Westwood and Aramoana slacks.*

Position A from analyses, there were still significant difference between Positions B-E ($F = 19.1$, $P < 0.000001$), and variation between months ($F = 9.7$, $P < 0.000001$). Chloridity decreased until August-September and then rose until midsummer (Fig. 2). The low chloridity in winter would be expected from lower evaporation during winter, with input by seepage and salt spray occurring all year. There was no clear relation between water table height and chloridity.

Vegetation

Communities A1-A3 (Table 1), indicated among the Aramoana communities by the presence of *Holcus lanatus*, represent the sand ridge vegetation, occurring on the landward long dune ridge and also on the short dune ridge towards the estuary.

The higher parts of both ridges bear community A1, with *Anthoxanthum odoratum* constant (Table 1, Fig. 1). The substrate is quite pure sand, with a much lower organic content than in any other community in the Aramoana sampled area (Table 2). Bordering the slack on the long ridge is Community A2, with constant *Poa pratensis* and frequent *Trifolium repens* and *Juncus articulatus*. The latter species indicates wetter conditions. Fertility, as estimated by bioassay, is low in Community A2. At the NE edge of the long dune ridge, and at the NW edge of the short ridge, is

Community A3, with the cyperad *Lepidosperma australe*, shrub *Coprosma propinqua* and megaherb *Phormium tenax* always present. The latter two species are typical of fens (Sykes *et al.*, 1991), and indicate transition to the wetter communities. Indeed, both *Holcus lanatus* from the drier communities and *Phormium tenax* from the wetter ones are present.

Communities A4-A6 are in the slack proper. *Leptocarpus similis* and *Phormium tenax* are almost constant. Vegetation height is *c.* 2 m. Community A4 occurs adjacent to both dune ridges. The soil has a high organic content. The community is species-poor, the best indicators being the liverwort *Lophlocloea* sp. and the cyperad *Isolepis nodosa*. Around the short ridge and adjacent to the salt marsh, Community A5 occurs. It is rather heterogeneous, with the fern *Blechnum penna-marina* common in one sub-community (i.e., below the level of classification shewn in Table 1) and *Plagiochila* sp. common in another. *Gonocarpus aggregatus* is more common here than anywhere else among the sampled slacks. Soil fertility is the highest found. Community A6 occurs in some of the lowest parts of the slack. *Phormium tenax* and *Leptocarpus similis* are constant, and beneath the dense stand of *L. similis* little else can grow, especially after lodging (i.e., flattening). The best indicator species for Community A6 are bryophytes *Chiloscypus normalis* and *Racopilum* sp., almost

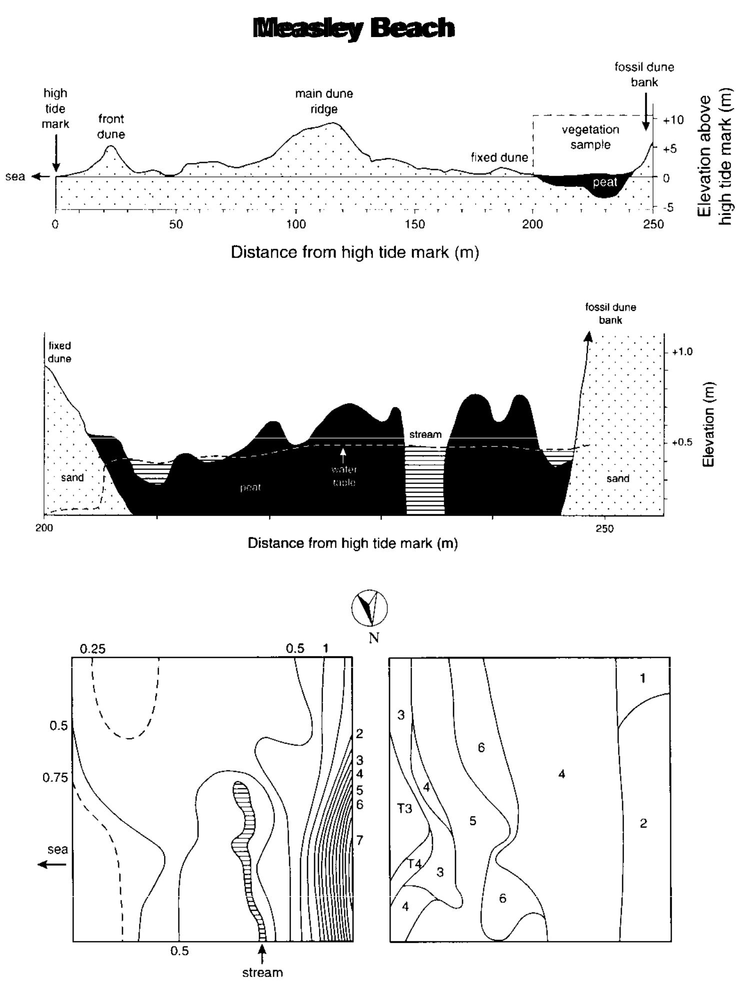

Figure 3: *The Measley Beach slack, arrangement as in Fig. 1. 1 to 6 = Measley Beach communities, T3 and T4 = Toko Mouth communities 3 and 4.*

Table 2: *Soil characteristics of plant communities in four slacks in southern New Zealand. - = organic content too high for texture analysis to be performed. The bioassay index is based on J.I.P. compost No. 1 = 100.*

Community	pH	Inorganic Sand (%)	Clay (%)	Silt (%)	Organic (%)	Bioassay index
Aramoana						
A1	4.3	91.9	4.1	4.0	8.9	93
A2	4.2	91.4	5.5	3.1	41.5	83
A3		*no samples*				
A4	4.3	-	-	-	53.2	94
A5	4.1	90.2	4.8	5.0	13.7	107
A6	5.2	-	-	-	63.7	82
Measley Beach						
T3+T4	4.4	64.5	11.1	24.4	12.6	78
M1	5.1	77.4	2.7	19.9	6.4	90
M2		*no samples*				
M3	4.5	38.0	21.4	40.6	6.5	83
M4	5.9	0.0	24.3	75.7	40.7	79
M6	5.9	0.0	35.6	64.4	39.6	82
M5	5.6	0.0	26.3	73.7	45.8	75
Toko Mouth						
T1	5.2	89.3	4.5	6.2	7.3	80
T2	5.4	90.3	3.0	6.7	6.2	95
T5	4.9	89.1	3.5	7.4	7.6	91
T6	4.7	89.9	3.7	6.4	7.4	100
T3		*no samples*				
T4	5.0	88.2	4.6	7.2	7.7	100
Westwood						
W1	5.3	93.7	3.7	2.6	4.2	84
W2		*no samples*				
W5	5.9	92.2	3.9	3.9	5.1	106
W3	5.7	93.1	3.7	3.2	3.2	91
W4	6.7	93.5	3.7	2.8	2.6	106
W6a	6.6	91.6	5.0	3.4	4.2	100
W6b	5.9	93.0	4.0	3.0	2.9	87

always as epiphytes on the base of *Phormium tenax* leaves. The soil has higher pH, and the highest organic content. A notable difference from Communities A4 and A5 is the rarity of *Isolepis nodosa*, common in the latter two.

Community W1, found otherwise on the dune slopes at Westwood, occurs on the estuary edge of the short dune ridge at Aramoana, with species such as *Holcus lanatus* and *Galium aparine*.

Measley Beach

Environment

The slack vegetation at Measley Beach occurs on a substrate of deep peat, down to 3.5 m depth (Fig. 3). The peat is very liquid, solid material being only 3% by weight. The peat surface is at about high tide level but the sand surface on which peat started to form is now well below this.

A stream, with water *c*. 3 m deep, enters the area, but it is very slow-flowing, with no surface outlet, outflow being by seepage through the sand.

Levelling shews the steep bank on the landward edge (Fig. 3), which comprises the slope of a fossil (i.e., non-active) dune, and the shallower slope on the seaward edge where the slack ends in a fixed dune. The water table was very close to the surface across most of the slack, with standing water present at some points. It dropped slightly towards the fixed dune and markedly within it, indicating the direction of drainage below the dunes towards the sea. Mean chloridity at time of vegetation sampling was 35 mg l^{-1}.

Vegetation

Communities M1-M2 at Measley Beach are the communities of the inland fossil dune bank. Community M1 has constantly the shrub *Hebe salicifolia* and frequently the bracken *Pteridium esculentum.* It represents an early seral stage in succession to native forest, after disturbance. In M2, some parts are open scrub, related to M1, with *Hebe salicifolia, Pteridium esculentum* and the small tree *Pseudopanax colensoi*. Other patches comprise low forest of the small trees *Coprosma lucida*, *Fuchsia excorticata*, *Myrsine australis* and *Pittosporum tenuifolium*, with the megaherb *Astelia fragrans* below. The whole community is typical of secondary native forest.

Communities M1 and M2 are both seral to the climax native forest of the area. They might represent a salt-spray subclimax, but they probably reflect also some disturbance associated with the building of a road nearby.

The fixed dune bears two communities found more extensively at Toko Mouth. T3 occurs on the dunes at both Measley Beach and Toko Mouth (Figs. 3, 4); it is characterised best by the near-faithful *Hydrocotyle heteromeria*, but the more widespread *Thuidium* sp. and *Holcus lanatus* are constant. T4 is characteristic of the outer slack at Toko Mouth and the slack edge at Measley Beach (Table 2), adjacent to the dunes; *Nertera setulosa* is the most notable species. The soil on which these communities occur at Measley beach is somewhat higher in organic content and lower in sand content than where T4 occurs at Toko Mouth (Table 2).

Just below T3 and T4, on the seaward edge of the slack is an ecotonal community, M3. It contains species typical of the fixed dune, such as *Holcus lanatus*, but also slack species typical of M4-M6, such as *Blechnum minus, Carex secta* and *Phormium tenax*.

Communities M4-M6 represent the slack proper, quite uniform in species composition, with high frequency of *Blechnum minus* and the trunked sedge *Carex secta*, and mean vegetation height *c*. 1.7 m.

Community M4 occurs on the deep peat adjacent to the bank. The stream is situated within this area. *Coriaria arborea* is common in one sub-community. M4 also occurs as a narrow band at the edge of the fixed dune at the seaward side of the slack. In both M5 and M6 the exotic shrub *Erica lusitanica* is common, and also the native cyperad *Lepidosperma australe*. Community M5 occurs on the seaward side of M6, intermediate between it and M3; *Phormium tenax* and *Eleocharis acuta* are frequent, but in general the community is species-poor. Community M6 occurs in the middle of the slack. Shrubs of the normally arborescent species *Weinmannia racemosa* are common in this community. The community is again species-poor. None of the substrate factors measured (Table 2) distinguish between Communities M4-M6, but the geomorphology does, in that M4 occurs most consistently on the deepest peat, M5 occurs on shallower peat towards the dunes, and M6 between them.

The substrate of communities M4-M6 is peat, with a high water content. Cut off from the substrate, there is no sand content, but there is an appreciable content of silt and to a lesser extent clay (Table 2), presumably brought down from the hills in the stream.

Toko Mouth

Environment

This site is the nearest of the four to open sea (Fig. 4), with only one high dune ridge between it and the ocean. It is the closest to a typical slack in geomorphological position, with high dunes almost all round it. The main slack plain is slightly below high tide level.

The water table was almost level, but at greater depth than at other sites. Mean chloridity at vegetation sampling time was 78 mg l^{-1}. Organic content was quite low in all communities, certainly lower than in most communities at Aramoana or Measley Beach. The mineral component was almost pure sand, with negligible silt and clay fractions.

Vegetation

Communities T1, T2 and T3 occur on the dunes surrounding the slack (Fig. 4). T1 occurs mainly to the south and east. In the areas of T1 to the south, *Epilobium brunnescens* is quite frequent, and *Marchantia berteroana* and *Juncus gregiflorus* very common. *Agrostis capillaris* is notably infrequent. Fertility is lower than in other Toko Mouth communities (Table 2). Community T2 occurs on the steep NW slope, and again on the shallower SE slopes. It contains frequent *Agrostis capillaris*, *Juncus bufonius* and *Ranunculus cheesemanii*. On these lower slopes, organic content is even lower than in the other Toko Mouth communities, and pH the highest. Community T3 occurs as two quadrats on the inland dune slope; *Hydrocotyle heteromeria* is frequent. The composition and position of the community may relate to human use, since there is a vague track here.

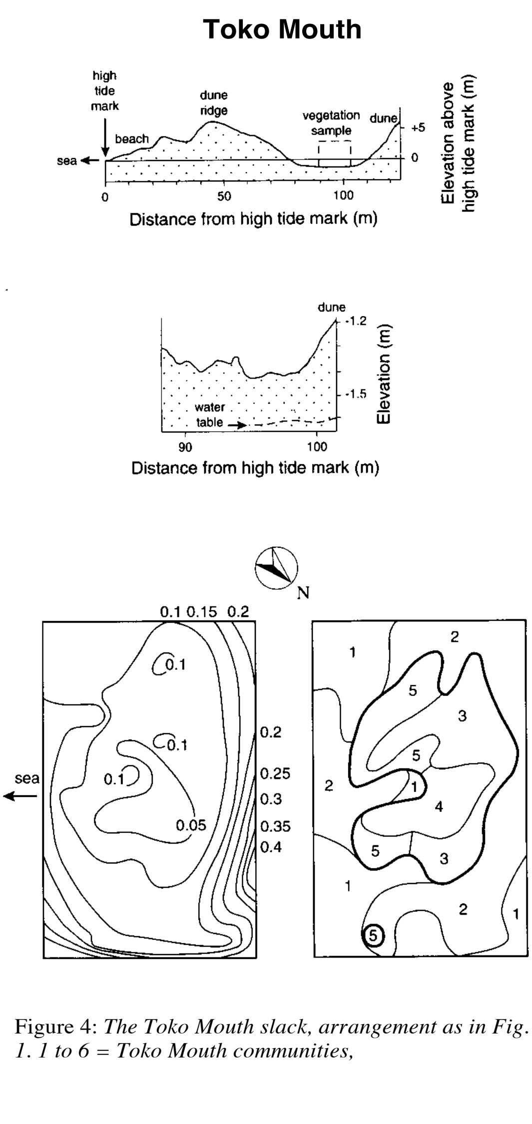

Figure 4: *The Toko Mouth slack, arrangement as in Fig. 1. 1 to 6 = Toko Mouth communities,*

Communities T4-T6 represent the slack proper. T4, with frequent *Nertera setulosa*, occurs around T6 on the SE side. Community T5 occurs around T6 on slightly higher ground to the NW; *Agrostis capillaris* and *Hydrocotyle novae-zelandiae* are very common, in contrast to T4 and T6; *Isolepis aucklandica* is an indicator species. Community T6 occupies the lowest part of the slack. It comprises two phases, with *Marchantia berteroana* and *Juncus gregiflorus* frequent in some patches, *Juncus articulatus* constant in others. T4 and T6 are on the most fertile soils.

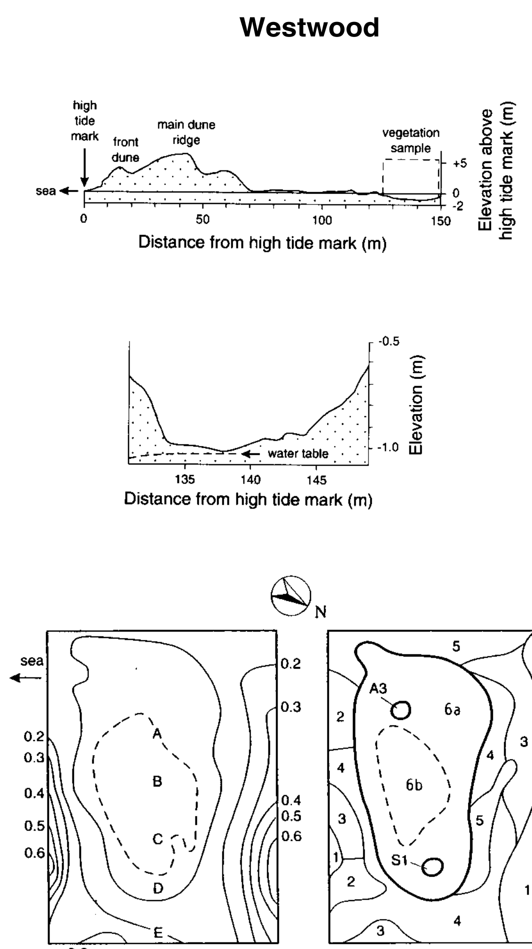

Figure 5: *The Westwood slack, arrangement as in Fig. 1. 1 to 6b = Westwood communities, A3 = Aramoana community 3, S1 = Mason bay (Stewart Island) community 1. A to E on the contour map are the positions of tubes for monthly water table sampling.*

Westwood

Topography

The slack itself is below high tide level (Fig. 5), 125-150 m inland. The Kaikorai estuary/lagoon is to the east, too far to exert any influence.

Soil organic content is consistently low. The mineral soil component is overwhelmingly sand, most of the apparent silt and clay probably being the unavoidable analysis artefacts of organic matter.

Water table

The water table at vegetation-sampling time shewed a very slight fall in elevation away from the centre of the slack (Fig. 5). Its depth varied with time ($F = 324.7$, $P < 0.000001$) and position ($F = 367.0$, $P < 0.000001$). Standing water was present to a depth of 10 cm in the centre of the slack (Position B) intermittently during the winter (Fig. 2), but the water table, even in the bottom of the slack, retreated to *c.* 40 cm depth in summer. Depths of the water table at different positions followed each other closely (Fig. 2). The rise in water table from February to March can be related to the rainfall in February, 178 mm compared to the monthly norm of 61 mm. Similarly, the lower water table in November can be correlated with low rainfall the previous month (see above), though there was an unexplained increase in December. In absolute elevation (i.e., after compensating for differences in the elevation of the soil surface) water table at Position E was on average 4 cm above that at B.

Chloridity

Chloridity varied with time ($F = 4.9$, $P = 0.00005$), but was low overall (mean 77 mg l^{-1}). The chloridity was not significantly different between positions ($F = 0.57$, ns), reflecting the distance from tidal influence. Chloridity rose in February, reflecting a storm on 1992 February 18-19, and resulting salt spray; it subsequently decreased.

Vegetation

Communities W1-W5 represent the surrounding sand dune and transitional communities. *Holcus lanatus* is almost constant through these communities. Community W1 occurs on the raised ground to either side of the slack, inland and seaward. *Carduus* sp. and *Galium aparine* are frequent, especially in the patch of the community at the inland side. This is the only Westwood community where *Lupinus arboreus* occurred. *Agrostis stolonifera* is absent, in contrast to all other Westwood communities. Soil fertility is the lowest of the Westwood communities. Community W2 occurs also around the edge of the sampled area, but on slightly lower ground than W1. The megaherb *Phormium tenax* is characteristic of W2. Organic content is slightly higher than in the other Westwood communities, but still lower than in any community in any of the other sites. In W3, *Rumex acetosella* is constant. *Poa pratensis* is most common here among the Westwood communities. The community is intermediate in position between Communities W1 and W4. In W4, *Rumex acetosella* is common too, but the community is species-poor, with *Cirsium vulgare* the nearest to an indicator species. The community occurs around, and adjacent to, Community W6, the slack proper. Also adjacent to W6 is W5, with *Rumex acetosella* absent, but *Hypochaeris radicata*, *Acaena novae-zelandiae* and *Rumex crispus* more common than elsewhere.

Community W6 is the slack proper. *Holcus lanatus* is rare, in contrast to communities W1-W5. *Juncus articulatus* is constant, *Agrostis stolonifera* and *Potentilla anserinoides* frequent. Although the community is quite uniform, because of its considerable extent it can usefully be divided in two: W6a and W6b. Subcommunity W6a surrounds W6b, with *Trifolium repens* frequent. W6b is in the lowest part of the slack; *Ranunculus repens* is constant, and *Hypnum cupressiform* common.

Discussion

Slack geomorphology

The sites differ in their geomorphology. Toko Mouth and Westwood are very close to the classical slack landform, of a depression bounded by sand ridges. At Aramoana, the site is indeed bounded on all sides by sand ridges, but they are low and sand deposition is not active; moreover, there is saltmarsh nearby. Drainage out of the area is downwards through the sand, conforming to the slack concept. The Measley Beach slack is between sand ridges, but the one inland of the sampled slack is apparently thousands of years old. A stream enters the area but does not leave, water percolating through the sand, again confirming the site as a slack rather than streambank.

All four sites are quite clearly, from their orientation and from the dunes around them, primary slacks, i.e., depressions between successively-formed sand ridges (Willis *et al*., 1959), in contrast to the apparently secondary slack at Mason Bay (Stewart Island), formed in a blow-out (Sykes and Wilson, 1987).

The substrate is similar in all four slacks, a moderately-fine siliceous sand. However, there are varying degrees of peat accumulation. The Mason Bay slack has low-organic soil, up to 5% (Sykes and Wilson, 1987). The composition of the mineral soil component in these slacks is probably even more predominantly sand than the analyses indicate, since it is technically difficult to exclude remnant organic matter from the fine fractions. A sand base is typical of slacks, expected from their origin (e.g., Tyndall and Levy, 1978).

The Measley Beach slack has considerable formation of peat, but this also is known in slacks elsewhere, e.g., 0.38 m depth in a slack described by Sims, Wickware and Cowell (1987). However, this does emphasise its status as an intermediate on a slack to fen gradient.

Water regime

Water table elevations are related to weather patterns, but not simply nor in the same way in all slacks. The notably high rainfall in 1991 February (close to the highest ever recorded for that month) is reflected clearly in the elevation of the water table at Westwood, but not at Aramoana. This can be attributed to surface outflow from the Aramoana site when standing water reaches *c*. 20 cm depth, because of the low dune sills.

Species of slacks are often tolerant of waterlogging (Schat, 1984; Seliskar, 1988), suggesting this may be a limiting factor in the slack environment. The strong relation between community zonation and elevation that we found supports this (cf. Studer-Ehrensberger, Studer and Crawford, 1993; Noest, 1994). Our 13-month sampling (Fig. 2) demonstrated that intermittent winter waterlogging is a feature of the slacks of southern New Zealand, with water table fluctuations similar to those recorded in slacks in Europe (e.g., van der Laan, 1979; Gitay and Agnew, 1989).

Soil chemistry

The lowest yearly-mean chloridities at Aramoana (Position E: 72 mg l^{-1}; D: 89 mg l^{-1}) were similar to the yearly mean of 77 at Westwood, and the sampling-time mean of 78 mg l^{-1} at Toko Mouth. This is far below the chloridity of sea water: the open-sea norm is 18 000 - 19 000 mg l^{-1}, and we measured 15 230 mg l^{-1} for local shore seawater. To determine whether the chloridities at these slack sites represented some low level of seawater influence, or whether they were was simply the expected non-marine ionic background, we analysed samples from four small unpolluted streams in the area. The values ranged from 7.2 to 11.1, with a mean of 8.8 mg l^{-1}.

This suggests there is still an impact of sea water at the slack sites, a conclusion strengthened by the seasonal variation in chloridity, and in one case the ability to tie this to a storm event. The lower chloridity at Measley Beach (35 mg l^{-1}) can therefore be seen as reflecting its distance from the sea, and perhaps the sheltering effect of the hill behind. Van der Merwe and McLachlan (1991) found an average of 1400 mg l^{-1} in South African slacks.

Chloridity at Aramoana Positions C (201 mg l^{-1}) and B (162 mg l^{-1}) was higher, suggesting seepage from the saltmarsh beyond the low dune ridges.

Dougherty, Mendelssohn and Monteferrante (1990) found increased growth after treatment of a Louisana slack with fertiliser, especially N and perhaps P. In contrast, the bioassay here shewed little nutrient growth limitation in comparison with fertile soil, and the relatively small difference in fertility within the sites.

Species

The majority of exotic species present in the slacks are also found in slacks in Europe: *Agrostis capillaris*, *A. stolonifera*, *Bellis perennis*, *Cerastium fontanum*, *Cirsium vulgare*, *Crepis capillaris*, *Festuca rubra*, *Holcus lanatus*, *Hypochaeris radicata*, *Juncus articulatus*, *J. bufonius*, *Leontodon taraxacoides*, *Poa pratensis*, *Prunella vulgaris*, *Ranunculus repens*, *Rumex crispus*, *Sagina procumbens* and *Trifolium repens* (Crawford and Wishart, 1966; Gitay and Agnew, 1989; van der Laan, 1979; Ranwell, 1960; van der Maarel and Westhoff, 1964; Willis *et al*., 1959). *Hypnum cupressiforme* and possibly *Potentilla anserinoides* are natives conspecific with the common European slack species. Most of these species are generalists, although the combination of them would be more restricted.

Plant community attributes

It was impossible to use the same sampling unit in all sites because of the varying spatial grain of the vegetation. However, the conclusion that different communities are found in different sites cannot be attributed to this, for even between pairs of sites with identical sampling scheme there was very little community overlap. Indeed *all* the cases of community overlap between sites were between sites with different quadrat sizes. We can therefore see the sampling schemes as a result of the vegetational differences, not the reverse.

The two taller-vegetation slacks are predominantly native, except on the higher, drier, sandy areas. The two shorter slacks contain many exotics. This indicates greater invasion resistance of the taller communities, though there may also be fewer exotics in the species pool that are adapted to wetter conditions. It is general in N.Z. and world-wide for dry areas to be those particularly invaded by exotics (Dansereau, 1964; Williams, 1980; Wardle, 1985; Jackson and Roy, 1989).

On many New Zealand dune systems, slacks seem to be absent (Johnson, 1992), e.g., at Cole Creek on the west coast of South Island (Sykes and Wilson, 1991), probably because of the free-draining sand, and the physiognomy of the dunes and beach.

Vegetation relations

The vegetation at Measley Beach is similar to part of the carr described by Sykes *et al*. (1991), especially in the physiognomic dominants such as *Carex secta*, *Phormium tenax* and *Blechnum* species. There is especial similarity between communities M3-M6 at Measley Beach and Communities ‘4’ and ‘5’ in the carr (Sykes *et al*., 1991). Indeed the latter species are prominent in the photograph of carr community ‘5’ in Fig. 4 of Sykes *et al*. (1991). In Aramoana community A3, the shrub *Coprosma propinqua* and megaherb *Phormium tenax* are always present. These species are also found in other damp communities of the region such as carr (Sykes *et al*., 1991). Here, community A3 is transitional between dune and slack. Another species typical of A3 is *Lepidosperma australe*, found in both wet sites and in heathland (Johnson and Brook, 1989). Others have noted the similarity between slack vegetation and that of inland fens (Sims *et al*., 1987).

There is quite remarkable distinction in vegetation between sites. There are only nine cases of quadrats being classified with those of other sites, 2.1%. Partridge and Wilson (1988) observed that even though many species are in common between saltmarshes of southern New Zealand, the species are assembled in different ways on different marshes. King, Wilson and Sykes (1991) similarly observed that in riverbank marshes, although many of the species are in common with marine marshes, they are rarely associated into the same communities. This geographical variation is even more marked for slacks. All the cases of similarity between slack sites were in communities of drier areas, often the dune above the slack proper, emphasising the differentiation of the slack communities themselves. One reason for the variation may be that sites with different environments are included under the term ‘slack’. Yet the water and chloridity regimes at Aramoana and Westwood, sites with very different slack vegetation, were quite similar (Fig. 2). The four slacks are very different in soil organic content, the organic Aramoana and Measley Beach soils contrasting with the mineral substrate at Toko Mouth and Westwood. This may be largely a function of slack age. It results in marked vegetational differences.

The communities of the short slacks described here bear little relation to the list of slack species given by Cockayne (1928), though there are some obvious similarities with the taller-vegetation slacks: e.g., *Leptospermum scoparium*, *Phormium tenax*, *Coprosma propinqua*. Part of this difference may be due to the age of the slack; that at Measley beach is clearly much older, and since the dunes at Aramoana are inactive the slack there is probably quite old too. However, it may be that the balance between slack vegetation types can be tipped by quite small changes in environment (cf. Studer-Ehrensberger *et al.*, 1993). This suggests the operation of a vegetation switch (Wilson and Agnew, 1992), perhaps with a positive-feedback mechanism between specific composition, vegetation height and peat formation.

Many previous slacks have been destroyed by 'development'. In selecting our four sites to sample, we visited many others, and consulted botanists who had visited further sites. This gives us confidence, increased by the site descriptions in Johnson (1992), that our four sites both cover the range of slack vegetation in the south-east of South Island, and include some of the best preserved sites. Plant community descriptions provide a sound basis for assessment of natural values and hence conservation decisions. It is clear that conservation of the Aramoana, Measley Beach and Toko Mouth slacks is a high priority.

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