

Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.

¹ Present address: Abteilung Oecologie, Universität Bielefeld, Universitätsstrasse 25, 33615, Bielefeld, Germany.

² Author for correspondence.

THE SAND DUNE VEGETATION OF CHRYSTALLS BEACH, SOUTHERN NEW ZEALAND, WITH PARTICULAR REFERENCE TO THE CUSHION COMMUNITY

Summary: The sand dune system at Chrystalls Beach, New Zealand comprises front dune, dune hollow and rear dune areas. On the front dunes are two communities: one on the seaward face of the dunes, and another on the landward face. Most of the dune hollow is occupied by a series of grassland communities, but there are areas of a distinctive cushion community, still largely native in its species composition. It is suggested that the cushion community is maintained against invasion by a switch, possibly involving sand grain size, soil organic content, water supply, wind and magnesium:calcium ratio. The coarse sandy/pebbly substrate, with its low organic content, causes water stress. The water stress permits only low vegetation, which exacerbates the low soil organic content. The low vegetation results in high wind, again favouring cushion species. The water regime has also allowed a buildup of Mg:Ca ratio, especially in the lower layers of the soil.

Keywords: Cushion community; dry slacks; magnesium; sand dune; switch; wind.

Introduction

Sand dune vegetation is common throughout New Zealand (Partridge, 1992a; Johnson, 1992), but few dune systems have been sampled and described in detail (e.g., Brown, 1978; Sykes and Wilson, 1991). The dunes at Chrystalls Beach, Otago (Patrick, 1992), are of particular interest because they retain a larger native component than other dune systems in the region (Johnson, 1992), and also because the dune hollow bears a largely-native cushion community, of a type not previously described from a New Zealand dune system (Fig. 1).

We sampled to describe an area of the dune system that included the cushion community, and made environmental measurements to provide some explanation of the factors controlling community distributions.

Study site

Chrystalls Beach is situated c. 60 km south of Dunedin, in southern South Island of New Zealand (46°12' S, 170°05' E). The substrate is quartz sand. A 24 m high basalt plug, named Cooks Head, occurs in



Figure 1: *The cushionfield, with Cooks Head in the background.*

the middle of the beach (Fig. 1). Mean annual rainfall is 725 mm, spread rather evenly through the year. Temperatures at Taieri Mouth, 18 km further up the coast, shew a mean daily range in July from 1.8 to 9.9 °C, and in February from 9.3 to 18.4 °C.

Methods

The sampling area (Fig. 2) extended from the edge of Cooks Head for 560 m southwest, and from maximum high tide level to the inland edge of the dunes (separated by a fence from agricultural pasture).

One hundred quadrats, each 1 m x 1 m, were placed over this area by restricted randomisation. In each quadrat, the shoot presence of all bryophyte and vascular plant species was recorded, and a soil sample taken (to 10 cm depth). Vegetation data were analysed by Cluster analysis using Flexible sorting strategy ($\beta = -0.25$), and with dissimilarity measured by the complement of Jaccard's coefficient (Clifford and Stephenson, 1975). The soil was analysed for pH, water content by loss-on-drying at 80 °C, organic matter by loss-on-ignition at 500 °C, and conductivity by electrical measurement on a water extract.

For additional environmental measurements, two transects were placed (Fig. 2), one perpendicular to the shore from the high tide mark to the rear dunes (the 'Sea-to-rear' transect) and one parallel to the shore in the dune hollow (the 'Dune-hollow' transect).

Wind speed was measured every 5 m along the Sea-to-rear transect and every 20 m along the Dune-

hollow transect, with a non-directional anemometer. At each point, measurements were made at 10 cm and at 1 m above the ground. To allow for wind variation as the points were measured, whenever wind was measured at any point a simultaneous measurement was taken at a reference position. Values at the reference position were used to remove the effect of variation through the sampling period from the simultaneous point readings. The whole sampling procedure was performed on three separate days.

Additional soil samples (again 0-10 cm depth) were taken every 5 m along the Sea-to-rear transect and every 10 m along the Dune-hollow transect. In each sample, 'available' Mg, Ca, Na and K were determined by atomic absorption spectrophotometry on a 1 M ammonium acetate extract. Particle-size fractions in the sand were determined by dry sieving. In the cushionfield, further soil samples were taken at eight random points, at each point at three depths: 0-5 cm, 5-10 cm and 10-15 cm.

Six sand traps were placed in November along the Sea-to-rear transect, and eight further ones in a line parallel to the shore and 5 m from high tide, i.e., along the crest of the front dune ridge. Each trap comprised a closed cylinder half-buried in the sand, with an opening 20 mm high x 70 mm wide facing the sea, the bottom of the opening being 20 mm above the sand surface. The sand traps were left to accumulate sand for 25 days, and then for a further 18 days. At the end of each period the sand trapped was dry weighted.

Elevation was measured with a surveyor's level along five transects perpendicular to the shore, and in addition along the Sea-to-rear and Dune-hollow transects.

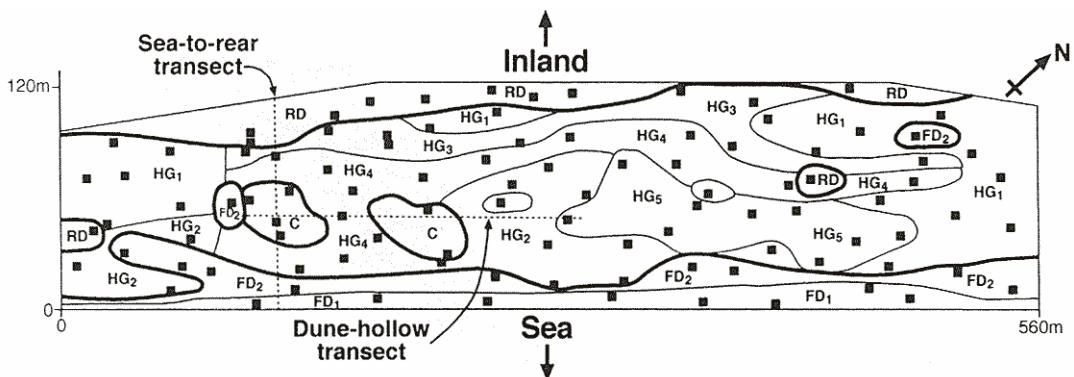


Figure 2: Map of the four community-types and the nine communities. Single occurrences of a community amid the same community-type are not labelled. Some quadrats with only one species, or none, and therefore not included in the vegetation analyses, are included within the area of Community FD_1 .

Nomenclature follows Connor and Edgar (1987) and references therein for native vascular plants, Webb, Sykes and Garnock-Jones (1988) for exotic species, except when superseded by Stace (1991), and Beever, Allison and Child (1992) for mosses (several of the mosses were present only as small, non-reproductive specimens, which it was possible to identify only to genus).

Results

Communities

The Cluster analysis is interpreted at the arbitrary general level of four Community types (**FD**, **RD**, **HG** and **C**, explained below), and also at the finer level of nine Communities. (The terms ‘Community’ and ‘Community-type’ are used for convenience; they are not intended to imply any particular degree of community organisation, cf. Wilson, 1994.)

Front dune community-type **FD** occurs along the front dune ridge (Figs. 2, 3). The sampled soil water content and organic content were both low (Table 1). The vegetation is open, dominated by *Ammophila arenaria*, with *Sonchus oleraceus* in 50% of the quadrats, though both species occur frequently in other community-types. Species richness is low (Table 1). Community-type **FD** is here subdivided into two communities:

Community **FD₁** occurs on the seaward slope of the front dune ridge (Figs. 1, 2). *Ammophila arenaria* occurs more sparsely than in community **FD₂**, but still achieves 100% frequency (Table 2). *Lupinus arboreus* is quite frequent, *Sonchus oleraceus* is constant¹, and *Senecio elegans* reaches its peak frequency. **FD₁** is the only community with no *Holcus lanatus*. Species richness is lower than anywhere else in the dune system (Table 1).

On the landward slope of the front dunes, community **FD₂** occurs. *Acaena novae-zelandiae* reaches its peak frequency here, and *Cirsium vulgare* is frequent. *Calystegia soldanella*, a typical sand dune pioneer (Sykes and Wilson, 1991), occurs occasionally, though it is more frequent inland. The latter two species are both absent from community **FD₁**. Communities **FD₁** and **FD₂** are distinguishable on the soil factors measured only by **FD₁** having even lower organic content (Table 1).

The Hollow-grassland community-type (**HG**) occurs through most of the shallow dune hollow between the front and rear dunes (Figs. 1, 2), save where the Cushion community-type (**C**) is present. Soil conductivity is high (Table 1). The community is dominated by tall grasses, with occasional shrubs, and shorter species, including a few cushion species, between. There is high constancy of exotic species, including the grass *Holcus lanatus*, herbs such as *Cerastium fontanum* and *Hypochoeris radicata*, and the shrub *Lupinus arboreus*. Exotic herbs *Crepis capillaris*, *Solanum dulcamara* and *Stellaria media* are faithful¹, as are several mosses: a *Bryum* species, a *Thuidium* and *Ceratodon purpureus*. *Sonchus oleraceus* is frequent, a similarity with community-type **FD**. Scattered native species occur, the most noticeable being *Poa cita* and *Phormium tenax*. Organic matter is relatively high, and pH relatively low. Community-type **HG** is subdivided into five communities:

¹ Following normal usage, ‘faithful’ indicates that the species occurs in no other community or community-type in the study area; ‘constant’ indicates that the species occurs in all samples from that community or community-type.

Table 1. Soil environmental factor means, and mean species richness, of the nine communities. Values within a column not sharing a letter are significantly different by Duncan’s Multiple Range Test (at P = 0.05).

Community	Conductivity (µmhos)	Water content (% dry weight)	Organic matter (% dry weight)	pH	Species richness
FD1	37 abc	3.5 ab	0.3 a	6.2 bc	3.6
FD2	56 bcd	5.2 abc	1.3 b	6.1 bc	5.6
HG1	98 e	12.7 d	4.1 d	5.8 ab	8.1
HG2	61 cde	7.3 bcd	1.6 bc	6.1 bc	8.8
HG3	59 cd	5.8 abc	3.0 cd	6.0 ab	9.3
HG4	35 ab	3.3 a	1.3 b	5.9 ab	10.6
HG5	107 e	10.6 cd	3.7 d	5.7 a	10.6
C	21 a	3.5 ab	0.9 b	6.4 c	16.5
RD	84 de	11.9 d	4.0 d	5.8 ab	4.4

Table 2. Frequency of species in the nine communities, and the number of quadrats of each community. * = species exotic to New Zealand.

	FD ₁	FD ₂	HG ₁	HG ₂	HG ₃	HG ₄	HG ₅	C	RD
<i>Acaena microphylla</i>	-	-	-	-	-	7	-	67	-
<i>Acaena novae-zelandiae</i>	-	45	22	-	-	-	11	-	-
* <i>Agrostis capillaris</i>	-	-	6	-	-	-	-	-	27
* <i>Agrostis stolonifera</i>	-	-	11	-	-	-	-	-	-
* <i>Ammophila arenaria</i>	100	100	11	100	45	53	11	33	27
* <i>Anthoxanthum odoratum</i>	-	9	33	-	64	33	22	-	9
* <i>Bromus diandrus</i>	-	-	-	9	-	-	22	-	-
<i>Bryum</i> sp.	-	-	6	9	9	20	11	-	-
<i>Calystegia soldanella</i>	-	18	-	-	82	13	-	-	9
<i>Campylopus introflexus</i>	-	-	-	-	-	20	-	100	-
<i>Cardamine debilis</i>	-	-	6	-	-	7	-	-	-
* <i>Cerastium fontanum</i>	-	-	22	100	64	80	100	50	-
<i>Ceratodon purpureus</i>	-	-	6	9	9	40	33	-	-
* <i>Cirsium arvense</i>	20	9	11	9	-	7	22	-	-
* <i>Cirsium vulgare</i>	-	55	17	36	9	13	89	-	-
<i>Colobanthus muelleri</i>	-	-	-	-	-	7	-	100	-
* <i>Crepis capillaris</i>	-	-	17	36	18	20	67	-	-
* <i>Dactylis glomerata</i>	-	18	33	9	100	7	-	-	82
<i>Dichelachne crinita</i>	-	-	6	-	18	27	-	-	9
<i>Epilobium komarovianum</i>	-	-	-	-	-	-	-	83	-
<i>Geranium sessiliflorum</i> var. <i>arenarium</i>	-	-	-	-	-	7	-	100	-
* <i>Hieracium pilosella</i>	-	-	-	-	-	-	-	33	-
* <i>Holcus lanatus</i>	-	91	94	100	64	80	100	100	45
<i>Hydrocotyle heteromeria</i>	-	18	-	-	-	13	-	33	-
<i>Hydrocotyle novae-zelandiae</i> var. <i>montana</i>	-	-	6	-	-	7	-	100	-
* <i>Hypochaeris radicata</i>	20	45	89	82	82	100	100	83	9
<i>Isolepis nodosa</i>	-	9	22	-	64	13	33	17	73
* <i>Leontodon taraxacoides</i>	-	6	18	9	33	-	83	-	-
<i>Leucopogon fraseri</i>	-	-	-	-	-	13	-	17	-
<i>Lophocolea semiteres</i>	-	-	6	-	18	7	-	17	-
* <i>Lupinus arboreus</i>	60	36	44	27	100	73	89	17	9
<i>Luzula celata</i>	-	-	-	-	-	-	-	33	-
<i>Microtis unifolia</i>	-	-	-	-	-	13	-	-	-
<i>Muehlenbeckia australis</i>	-	-	28	9	9	7	11	-	18
<i>Muehlenbeckia axillaris</i>	-	-	-	9	-	7	-	-	-
<i>Myosotis pygmaea</i>	-	-	-	-	-	-	-	33	-
<i>Phormium tenax</i>	-	-	6	-	9	-	-	-	-
<i>Poa cita</i>	-	9	6	9	-	27	22	-	18
<i>Poa maniototo</i>	-	-	6	-	-	7	-	33	-
<i>Pseudognaphalium luteoalbum</i>	-	9	-	-	-	7	-	-	-
<i>Pteridium esculentum</i>	-	18	39	-	18	-	-	-	82
<i>Raoulia australis</i>	-	-	-	-	-	-	-	100	-
* <i>Rubus fruticosus</i>	-	-	11	-	-	-	-	-	-
* <i>Rumex acetosella</i>	-	-	11	-	-	40	-	67	-
<i>Scleranthus uniflorus</i>	-	-	-	-	-	7	-	100	-
<i>Senecio biserratus</i>	-	9	-	55	-	7	-	-	-
* <i>Senecio elegans</i>	40	9	-	9	-	7	-	-	-
* <i>Solanum dulcamara</i>	-	-	22	36	36	7	56	-	-
<i>Solanum laciniatum</i>	-	-	-	-	-	13	44	-	-
* <i>Sonchus oleraceus</i>	100	27	22	73	18	13	100	-	-
* <i>Stellaria media</i>	-	-	72	64	55	27	89	-	-
<i>Stokesiella praelongum</i>	-	9	6	-	9	13	-	-	-
<i>Thuidium</i> sp.	-	-	28	9	18	13	11	-	-
<i>Tortula</i> sp.	-	-	-	-	-	-	-	33	-
* <i>Trifolium repens</i>	-	9	11	27	-	73	27	100	9
* <i>Trifolium dubium</i>	-	-	-	9	-	20	-	50	-
* <i>Ulex europaeus</i>	-	-	33	18	-	-	-	-	9
Number of quadrats	5	11	18	11	11	15	9	6	11

HG₁ is a community that occurs at the northern and southern boundary of the study site (Fig. 2), on flat land at a moderate distance from the shore. *Agrostis stolonifera* and *Rubus fruticosus* are faithful, and *Ulex europaeus* reaches its peak frequency. In common with community **HG₅**, soil conductivity is high (Table 1).

Community **HG₂** occurs beside Cushion community-type **C**. *Ammophila arenaria* is more frequent than in other **HG** communities, *Cerastium fontanum* and *Holcus lanatus* are constant, and the community contains the highest frequency of *Senecio biserratus*.

In **HG₃**, adjacent to the rear dunes, *Anthoxanthum odoratum*, *Calystegia soldanella*, *Dactylis glomerata* and *Lupinus arboreus* all reach their peak, *D. glomerata* being constant.

The **HG₄** community occurs towards the rear of the dune hollow, just seaward of community **HG₃**. *Trifolium repens* is frequent, the native grass *Dichelachne crinita* reaches a peak, and the orchid *Microtis unifolia* is faithful. The sand has the lowest conductivity of all the **HG** communities, and the lowest water content at time of sampling (but not significantly different from **HG₃**). Soil organic content is the lowest of the **HG** communities (but similar to **HG₂**).

Community **HG₅** occurs at the same distance from the sea as the Cushion community, but further northeast. *Cerastium fontanum* and *Sonchus oleraceus* are constant, *Cirsium vulgare*, *Bromus diandrus* and *Solanum laciniatum* reach their peaks, and *Holcus lanatus* is constant. Conductivity is high (comparable with **HG₁**).

Cushion community-type **C** occurs in one particular part of the dune hollow. This area had low conductivity and water content at the time of sampling. Soil organic content is nearly as low as in the **FD** community-type, and pH the highest. About 50% of the surface is covered by plants of low stature (c. 5 cm). Some form cushions (e.g., *Raoulia australis*), others are present as isolated rosettes (e.g., *Geranium sessiliflorum*). The area between these low plants is mostly covered by mosses and/or a layer of quartz pebbles. Occasional taller plants occur, especially towards the periphery of the cushion area (e.g., *Isolepis nodosa*). Several species are faithful, or almost so, to Cushion community **C**: mosses *Tortula* sp. and *Campylopus introflexus*, and native herbs *Acaena microphylla*, *Colobanthus muelleri*, *Epilobium komarovianum*, *Geranium sessiliflorum*, *Hydrocotyle novae-zeelandiae*, *Luzula celata*, *Myosotis pygmaea* var. *pygmaea*, *Raoulia australis* and *Scleranthus uniflorus*. The tiny native grass *Poa maniototo*, and exotic herbs *Leontodon taraxacoides*, *Rumex acetosella* and *Trifolium repens* all reach their

peak in the Cushion community-type. Other native species present in the Cushion community-type, which our quadrats did not include, are *Neopaxia australasica*, *Pernettya macrostigma*, *Pimelea prostrata* and *Selliera radicans* (*pers. obs.*; Patrick, 1992). Species richness at the 1 x 1 m scale is the highest in the dune system (Table 1).

Rear dune community-type (**RD**) occurs as a band at the rear of the dunes (the term 'rear dune' follows Wardle, 1991). The soils here had high conductivity and water content at the time of sampling, high organic content and low pH. The native cyperad *Isolepis nodosa* and *Dactylis glomerata* occur frequently, and tend to be physiognomic dominants. *Pteridium esculentum* and *Agrostis capillaris* reach their peaks. The tussock grass *Poa cita* occurs mainly here and in community-type **HG**, though occasionally elsewhere.

Elevation

All six levelled lines from high tide to the rear dunes shewed a similar profile: the front dune ridge, dune hollow sloping backwards, and rear dunes (one is illustrated: Fig. 3). The cushion area (Community-type **C**) occurred at a slightly higher elevation than the Hollow-grassland (**HG**) community type beside it (Fig. 4).

Physical substrate

The substrate of the whole area is quartz sand (SiO₂), the colour (Oyama and Takehara, 1970) varying from greyish-yellow on the front dune to dark greyish-yellow on the rear dune, where more organic matter has accumulated. The shape of the sand grains is equant, and angular to subangular (Tucker, 1991).

The proportions of sand grains in the larger sizes were higher in the dune hollow, and very low in the front dunes (Fig. 3). Along the Dune-hollow transect (Fig. 4), the tendency was for the sand to be coarser in the cushionfield than in the hollow-grassland alongside, but the difference was not significant. In the cushionfield, the sand was coarser below the surface (Fig. 5). There was a smaller proportion of fine (< 1mm) particles at 5-10 cm and 10-15 cm than at the surface, and a correspondingly larger proportion of 1-2 mm particles. ($P = 0.00097$ for difference between depths for the < 1 mm fraction, and $P = 0.022$ for the 1-2 mm fraction, by analysis of variance after arcsine transformation).

Soil nutrients

Soil sodium levels were generally higher in the front dunes and the rear dunes (Fig. 3), but they were (by analysis of variance) not significantly different in the

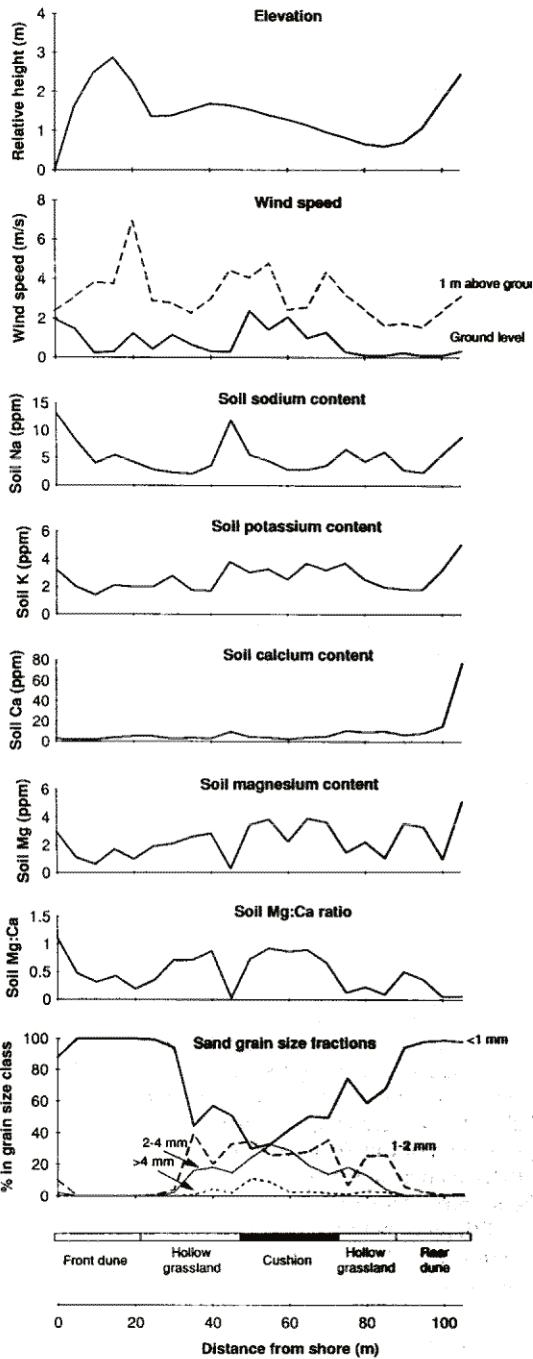


Figure 3: The environment along the Sea-to-rear transect.

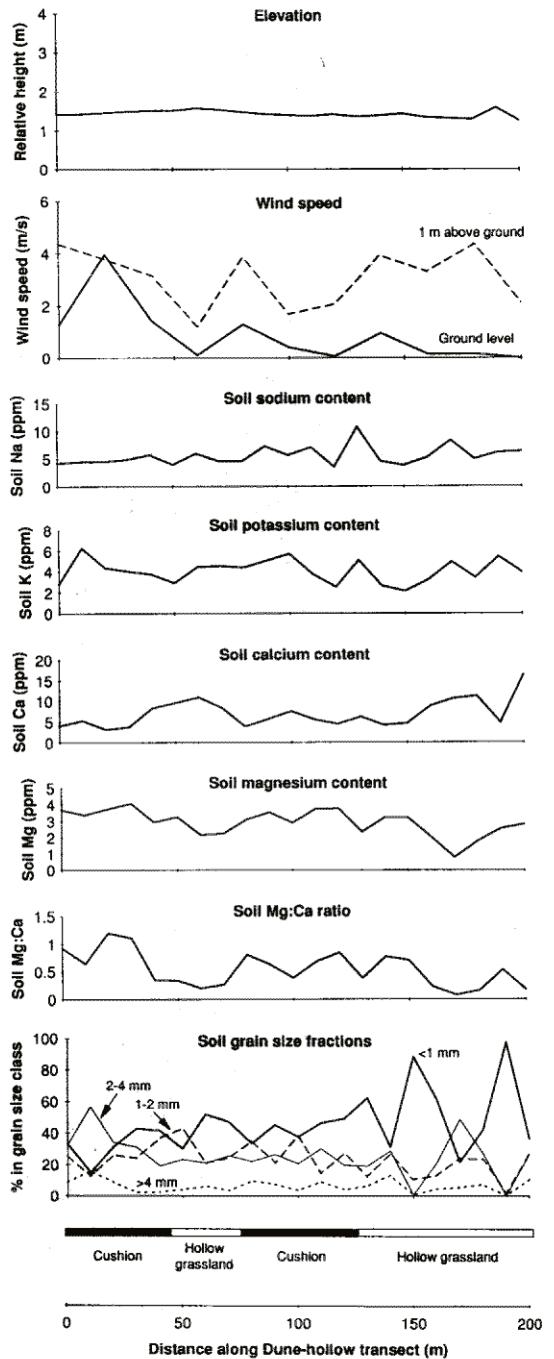


Figure 4: The environment along the Dune-hollow transect.

cushionfield from the adjoining hollow-grassland (Fig. 4). Sodium levels in the rear dune did not match the peak in conductivity there (Table 1), suggesting that the latter also reflects nutrient enrichment, possibly from the adjacent fields. Calcium was low throughout the dunes, except adjacent to the pasture, where there may have been agricultural influence. In the cushionfield (Fig. 4), Ca was lower than in the adjoining hollow-grassland ($P = 0.011$ by analysis of variance), Mg higher ($P = 0.00057$) and the Mg:Ca ratio therefore more than double ($P = 0.0015$).

Within the cushionfield, a higher Mg:Ca ratio was seen below the surface (i.e. at 5-15 cm; $P = 0.000078$ for difference between depths by analysis of variance after log transformation; Fig. 5).

Wind

Wind speed at 10 cm above the ground, averaged over the measurement occasions (Fig. 3), was high

on the front dune. It was equally high in the cushion area, and higher there than in the adjacent hollow-grassland ($P = 0.0022$ by analysis of variance; Fig. 4). Wind speed was lower in the rear dune. Wind at 1 m above ground was little different between areas.

Sand movement

Sand accumulated in the traps at 5 m from high tide at an average rate of 5.6 g day^{-1} in the period Nov 6 - Dec 1, and 11.0 g day^{-1} in Dec 1 - Dec 19. No sand appeared in any traps further inland.

Discussion

Dune physiognomy

Movement of sand occurs on the front dune ridge, but there seems to be no net change in sand surface elevation, i.e. the dunes are 'fixed' (Steers, 1946). Salt is apparently an important factor on the front dunes: *Ammophila arenaria*, *Senecio elegans* and *Pseudognaphalium luteoalbum*, which occur here, are tolerant of salt spray and of salt in the substrate (Sykes and Wilson, 1988).

The hollow between the front and rear dunes is not a slack, for there is no standing water, even in winter, nor is there any sign of the organic-matter buildup typical of slacks. Species typical of slacks in the region (Roxburgh *et al.*, 1994) are absent. The most appropriate term in the literature for such a hollow is a 'low' (Chapman, 1960; Salisbury, 1952).

Switches and the cushion community

The existence of the cushion community in patches at Chrystalls beach is initially a puzzle. How could such short vegetation resist the invasion of taller species from the Hollow-grassland community-type, especially *Lupinus arboreus* during those years when it was dominant? Several environmental factors offer some explanation, many of them exacerbated by the vegetation, suggesting the presence of a positive-feedback switch, in which the vegetation modifies its environment, and that modified environment favours continued tenure of that type of vegetation (Wilson and Agnew, 1992). The sharpness of the cushion / hollow-grassland boundary also suggests that a switch may be operating, for switches tend to sharpen boundaries (Wilson and Agnew, 1992).

The short stature of the vegetation permits high wind; at the surface of bare dunes, wind speed may be 50% of that 60 cm above, whereas with even sparse (but tall) *Ammophila arenaria* wind speed at the dune surface may be only 25% of that at 60 cm (Chapman, 1964). This in turn can inhibit the growth

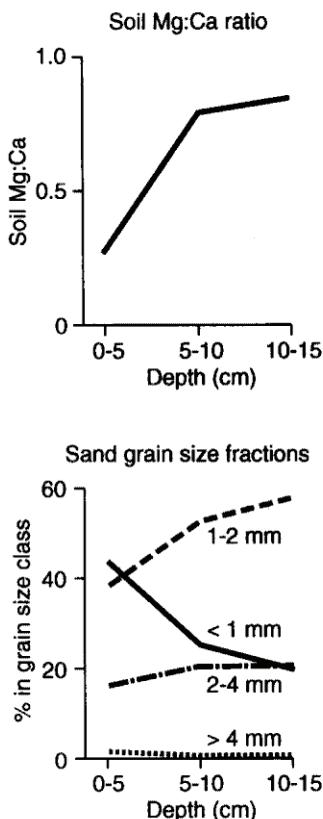


Figure 5: Differences in soil properties in the cushionfield with depth.

of taller species, completing a wind switch, in that the short vegetation allows high wind speeds, and the high wind speed may inhibit the invasion of taller mid-dune species (Wilson and Agnew, 1992).

Higher Mg:Ca ratios, as in Community-type C, might inhibit the growth of some species (Lee and Reeves, 1989; Tibbetts and Smith, 1992), by causing a deficiency of calcium via Mg:Ca antagonism, by inhibiting potassium uptake, and by raising pH (Proctor and Nagy, 1992; Diem and Godbold, 1993). Indeed, pH is highest in the cushionfield. Mineral content will vary with time, but the highest Mg:Ca ratios were found in the slightly deeper layers, in which there is probably less variation. It is not known whether the vegetation itself may affect Mg:Ca ratios, which would comprise a switch. Conductivity is low in the cushionfield, suggesting nutrient deficiency. Lack of direct seawater influence is attested to by the low sodium levels at the time of sampling, and also by the presence of *Colobanthus muelleri* (Sykes and Wilson, 1989) which is intolerant of salt in the rooting-medium, and of the relatively saltspray-intolerant *Hydrocotyle novae-zelandiae* (Sykes and Wilson, 1988).

The rather coarse substrate, especially below the surface, probably leads to water deficit, explaining the presence of the apparently drought-tolerant *Colobanthus muelleri*, *Scleranthus uniflorus* and *Raoulia australis* (Wardle, 1991). Wind may exacerbate the water stress, directly by increasing evapotranspiration, and indirectly by removing finer sand particles (there are pebbles on the surface) and hence keeping the water-holding capacity of the soil low. The low stature and hence probably low litter production, combined with the high wind, will inhibit the buildup of organic matter in the soil, again exacerbating the water stress, and forming a switch mechanism.

The sand surface is probably very stable, in spite of the high wind, as evidenced by the lack of sand appearing in sand traps. Indeed, *Colobanthus muelleri* and *Geranium sessiliflorum*, which occur in the cushion community, are intolerant of burial (Sykes and Wilson, 1990). The pebbles of the cushionfield are similar in size, colour and consistency to those in the intertidal zone of Chrystalls Beach. The rather coarse sand texture is seen more clearly below the surface, suggesting it is an older feature, and not due to current processes of deposition or erosion. The dune hollow may be a relict beach from before the foredune had built up, though the existence of a vegetation/environment switch in current conditions is independent of such an interpretation.

We conclude that the cushion area represents an area of beach with coarse sand and surface pebbles,

which was cut off by the formation of the present front dune ridge. The cushionfield does not differ significantly from the hollow-grassland alongside in particle-size distribution, suggesting that the dune hollow was originally close to uniform, and that small initial differences were amplified and are maintained by a switch involving soil organic content, water supply, wind and Mg:Ca ratio. This implies that the cushionfields were probably distinct from other dune hollow areas before European interference, and will have some resistance to invasion by taller species.

History and conservation

Originally, *Desmoschoenus spiralis*, the endemic dune-building cyperad, must have dominated the front dunes. It now occurs only as a few scattered patches. *D. spiralis* often disappears when *Ammophila arenaria* invades, perhaps because of competition for water, and stabilisation of the sand (Partridge, 1992b).

An early photograph to the north of Cooks Head shows tall graminoids (probably *Poa cita*, but just possibly *Isolepis nodosa* or *Ammophila arenaria*), apparently with cushion plants between (at least *Raoulia* spp.) (Anon, 1905). Probably cushion plants were once more widespread, but there is no evidence for a greater extent of the pure cushion community. The area of the photograph may have originally been covered by coastal scrub, removed by 1905 by burning and grazing (a sheep is visible in the photograph), though somewhat regenerated since.

The cushionfield is probably an ancient feature. It is unlikely that the characteristic species have immigrated recently. In spite of some evidence for displacement of cushion species by *Lupinus arboreus*, the cushion community itself has been demonstrably resistant to invasion, we suggest because of the organic/water/wind/Mg switch, giving the rather sharp boundary between communities C and HG, a characteristic outcome of a switch (Wilson and Agnew, 1992).

Dune cushion communities apparently occur elsewhere in New Zealand, though none has yet been described, but there seem to be no others in southern N.Z. The area is therefore well deserving of conservation, though there appear to be no immediate threats to the integrity of the habitat and community.

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References

- Anon 1905. *The cyclopedia of New Zealand*, Vol 4, Otago and Southland Provincial Districts. Cyclopedia Company, Christchurch, N.Z. 1115 pp.
- Beever, J.E.; Allison, K.W.; Child, J. 1992. *The mosses of New Zealand*, edn 2. University of Otago Press, Dunedin, N.Z. 214 pp.
- Brown, E.A. 1978. Vegetation patterns across the Farewell Spit dune system. *Tane* 24: 9-20.
- Chapman, V.J. 1960. The plant ecology of Scolt Head Island. In: Steers, J.A. (Editor), *Scolt Head Island, revised edn*, pp. 85-158. Heffer, Cambridge, U.K. 269 pp.
- Chapman, V.J. 1964. *Coastal vegetation*. Pergamon, Oxford, U.K. 245 pp.
- Clifford, H.T.; Stephenson, W. 1975. *An introduction to numerical classification*. Academic Press, New York, U.S.A. 229 pp.
- Connor, H.E.; Edgar, E. 1987. Name changes in the indigenous New Zealand Flora, 1960-1986 and *Nomina Nova* IV, 1983-1986. *New Zealand Journal of Botany* 25: 115-170.
- Diem, B.; Godbold, D.L. 1993. Potassium, calcium and magnesium antagonism in clones of *Populus trichocarpa*. *Plant and Soil* 155/156: 411-414.
- Johnson, P.N. 1992. *The sand dune and beach vegetation inventory of New Zealand*. II: South Island and Stewart Island. DSIR Land Resources Scientific Report No. 16, DSIR Land Resources, Christchurch, N.Z. 278 pp.
- Lee, W.G.; Reeves, R.D. 1989. Growth and chemical composition of *Celmisia spedenii*, an ultramafic endemic, and *Celmisia markii* on ultramafic soil and garden loam. *New Zealand Journal of Botany* 27: 595-598.
- Oyama, M., Takehara, H. 1970. *Revised standard soil color charts*. Japan Colour Research Institute, Tokyo, Japan. 14 pp.
- Partridge, T.R. 1992a. *The sand dune and beach vegetation inventory of New Zealand*. I: North Island. DSIR Land Resources Scientific Report No. 15, DSIR Land Resources, Christchurch, N.Z. 253 pp.
- Partridge, T.R. 1992b. Vegetation recovery following sand mining on coastal dunes at Kaitorete Spit, Canterbury, New Zealand. *Biological Conservation* 61: 59-71.
- Patrick, B. 1992. Moths of Chrystalls Beach. *The Weta* 15: 35-38.
- Proctor, J.; Nagy, L. 1992. Ultramafic rocks and their vegetation: an overview. In: Baker, A.J.M.; Proctor, J.; Reeves, R.D. (Editors), *The vegetation of ultramafic (serpentine) soils*, pp. 469-494. Intercept, Andover, U.K. 509 pp.
- Roxburgh, S.H.; Wilson, J.B.; Gitay, H.; King, W. McG. 1994. Dune slack vegetation in southern New Zealand. *New Zealand Journal of Ecology* 18: 51-64.
- Salisbury, E.J. 1952. *Downs and dunes: their plant life and its environment*. Bell, London, U.K. 328 pp.
- Stace, C.A. 1991. *New flora of the British Isles*. Cambridge University Press, Cambridge, U.K. 1226 pp.
- Steers, J.A. 1946. *The coastline of England and Wales*, edn 2. Cambridge University Press, Cambridge, U.K. 750 pp.
- Sykes, M.T.; Wilson, J.B. 1988. An experimental investigation into the response of some New Zealand sand dune species to salt spray. *Annals of Botany* 62: 159-166.
- Sykes, M.T.; Wilson, J.B. 1989. The effect of salinity on the growth of some New Zealand sand dune species. *Acta Botanica Neerlandica* 38: 173-182.
- Sykes, M.T.; Wilson, J.B. 1990. An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand. *Acta Botanica Neerlandica* 39: 171-181.
- Sykes, M.T.; Wilson, J.B. 1991. Vegetation of a coastal sand dune system in southern New Zealand. *Journal of Vegetation Science* 2: 531-538.
- Tibbetts, R.A.; Smith, J.A.C. 1992. Vacuolar accumulation of calcium and its interaction with magnesium availability. In: Baker, A.J.M.; Proctor, J.; Reeves, R.D. (Editors), *The vegetation of ultramafic (serpentine) soils*, pp. 367-373. Intercept, Andover, U.K. 509 pp.
- Tucker, M.E. 1991. *Sedimentary petrology: An introduction*, edn 2. Blackwell Scientific, Oxford, U.K. 252 pp.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, U.K. 672 pp.
- Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. 1988. *Flora of New Zealand, Vol. IV*. Botany Division, DSIR, Christchurch, N.Z. 1365 pp.
- Wilson, J.B. 1994. Who makes the assembly rules? *Journal of Vegetation Science* 5: 275-278.
- Wilson, J.B.; Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23: 263-336.