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A survey of the coastal vegetation near Port Alfred, eastern Cape

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ABSTRACT

Detailed information on the colonization and succession of the sand dunes, dune slacks and rocky outcrops along the coast between the Riet and Kleinemonde Rivers is provided. The main reasons for the paucity of plants on the vast dune system are the movement of sand by wind and the inconsistent rainfall. Zonation of species along a dune transect is not particularly marked although a greater diversity of species is found in the dune slacks where an increased amount of seepage moisture occurs. Reclamation practices in blow-out areas have resulted in a pioneer cover of indigenous plants which should provide dense coastal scrub if the introduced *Acacia cyclops* is kept under control. Establishment of plants on the rocky promontories has occurred over a very long time and well developed communities and soils have formed. Salt spray and high winds are major controlling factors in the zonation of species along a gradient in this area.

RÉSUMÉ

UN RELEVÉ DE LA VÉGÉTATION CÔTIÈRE PRÈS DE PORT ALFRED, EST DE LA PROVINCE DU CAP

Une information détaillée sur la colonisation et la succession des dunes de sable, dépressions des dunes et affleurements rocheux le long de la côte entre les rivières Riet et Kleinemonde est donnée. Les principales raisons de la rareté des plantes sur le vaste système de dunes sont le mouvement du sable causé par le vent et les chutes de pluie irrégulières. La zonation des espèces le long d'un transect de dune n'est pas particulièrement marquée bien qu'une plus grande diversité d'espèces soit trouvée dans les dépressions des dunes où une quantité accrue d'humidité d'infiltration se produit. Des pratiques de restauration des sols dans les régions dégarnies par les vents ont résulté en une couverture pionnière de plantes indigènes qui devraient donner lieu à une formation côtière broussailleuse dense si on lutte contre l'envahissement de l'espèce introduite Acacia cyclops. *L'établissement de plantes sur les promontoires rocheux s'est produit au cours d'une très longue période et des formations végétales ainsi que des sols bien développés se sont formés. Les vents violents et la vaporisation de sel sont les principaux facteurs limitants dans la zonation des espèces le long de la côte dans cette région.*

INTRODUCTION

Apart from general descriptions of the coastal vegetation by Dyer (1937) and Comins (1962) very little has been written on the eastern Cape coastal vegetation. Unlike the coast of Natal and Zululand (Moll & White, 1978), the extensive dune systems along this coast are almost completely lacking in vegetation and do not show marked successional changes. The potential and real threat of these shifting dunes to surrounding farm and inhabitable land has lead to extensive reclamation programmes by the Department of Forestry (Keet, 1936; King, 1939; Walsh, 1968; Stehle, 1980).

It is important that more information on the extent and nature of the vegetation that becomes established naturally on the exposed dunes and rocky promontories is accumulated, before reclamation practices change the whole environment. This paper aims to provide some information about the vegetation along one section of the coast and explain the major role of the climate in modifying the environment. Changes in the soil and man-induced changes in the coastal ecosystem are also assessed.

The study area

The coastal strip between the Kleinemonde and Riet Rivers, about 12 km east of Port Alfred, is 4 km long and covers an area of approximately 350 ha. This portion of the 1820 Settler farm, Tharfield (Thorpe, 1972) bounded by the Port Alfred/East London road in the north and the sea in the south has been proclaimed a private nature reserve (Fig. 1).

The beach consists of about 100 ha of shifting sand dunes reaching approximately 50 m above sea level. The dune and dune slacks are sparsely vegetated in parts and the permanent vegetation begins with coastal scrub from 100 to 700 m from the shore. In protected areas the scrub becomes well established coastal forest with trees up to 10 m or more tall. In exposed areas the scrub has receded with the development of blow-outs (Oosting & Billings, 1942) which project often as far as 600 m into the scrub vegetation. In order to re-establish scrub in these blow-out areas the owner of the farm, Mr T. Webb, has followed the practice of the Department of Forestry of cutting bush clumps from other areas of the farm land used for grazing and using the cuttings to cover over the exposed sands (Fig. 2). This tends to stabilize the sand and provide a protective mulch for the germination and establishment of seedlings.

Parts of the shoreline are rocky with three striking promontories, called the Three Sisters, which project into the sea. These rocky buttresses vary slightly in size and form and rise up to 20 m from the wave-cut platform at sea level. Each has a steep cliff face on the seaward side, is flattened on top and then slopes towards the beach in the north (Fig. 3). Drift sands overlie the rocks on the beach side of the First and to a lesser extent to the Second Sister but the Third Sister in the east consists almost wholly of aeolianitic rock. This dune-rock is calcareous

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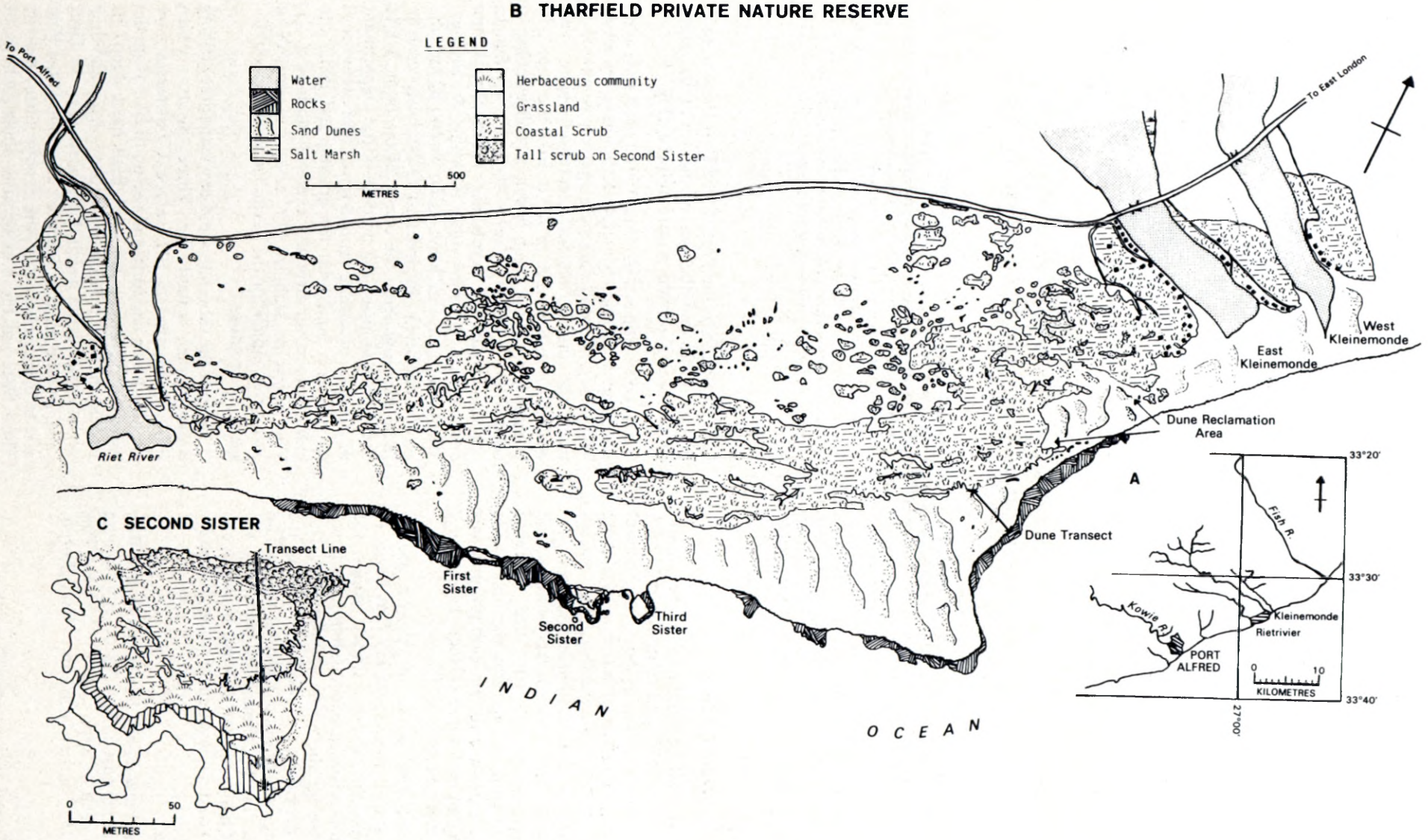

FIG 1.—The study area. A, Location of the Riet and Kleinemonde Rivers; B. Tharfield Private Nature Reserve as interpreted from air photos; C, A detailed map of the Second Sister.

FIG 2.—Dune reclamation of a blow-out in the coastal scrub. Sand stabilizing plants are emerging through the bush cuttings which were placed over the dunes two years previously.

sandstone (Mountain, 1937) formed by lime cementation of ancient sand dunes, which on weathering forms variously shaped pinnacles, holes and small pockets. The dune-rock creates an attractive broken landscape along much of the coast east towards the Fish River and East London and west towards the Bushmans River and Woody Cape.

METHODS

Study sites were selected on the dunes and dune slacks (Fig. 1) wherever vegetation occurred. The foredunes studied were the only ones colonized along this stretch of coastline (Fig. 4). Fifty $1m^2$ quadrats were randomly sampled on the foredunes and 68 in the dune slacks. The number of rooted shoots and percentage aerial cover of each species were recorded. A one metre wide belt transect was taken from the high water mark across the foredunes and dune slack up to the margin of the coastal scrub. (Fig. 5).

The reclamation area in the coastal scrub was divided into five regions on the basis of aspect and one m^2 quadrats were randomly sampled in each region, totalling 43 quadrats in all. The number of rooted shoots and percentage aerial cover of each species was recorded.

The rocky promontory chosen for study was the Second or middle Sister, because it showed a greater diversity of vegetation than the Third Sister and was more isolated from the dunes than the First Sister. Therefore the vegetation of this rocky promontory is not as disturbed and is more representative than that of the other two. A one m^2 belt transect was taken from the point first colonized by plants on the rocky cliff face to the dunes on the north side. An Abney level was used to measure the slope along the transect lines.

FIG 3.—View from the Second Sister looking west towards the First Sister. The herbaceous community is evident in the left foreground, grading into the low scrub community on the right.

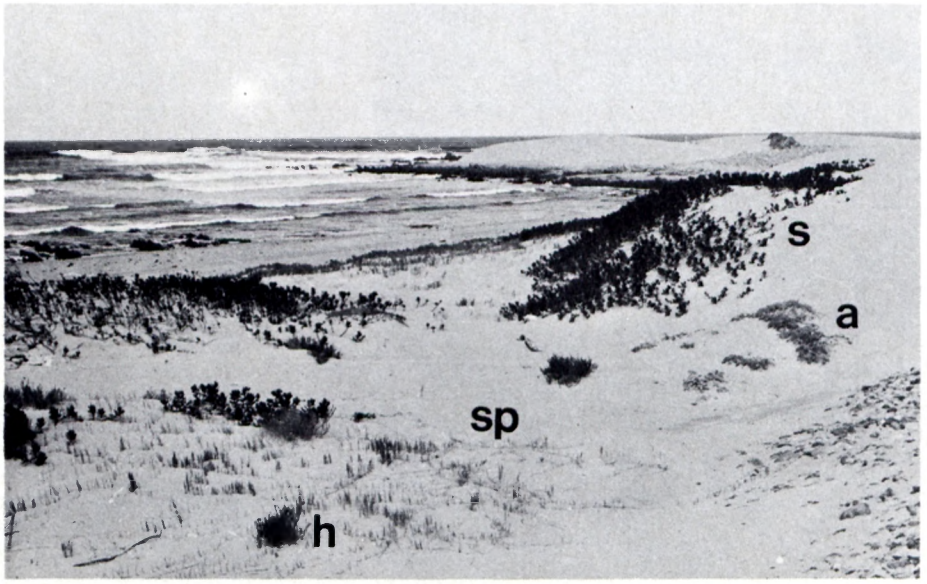

FIG 4.—The foredunes colonized by *Scaevola thunbergii* (sc), *Arctotheca populifolia* (a), *Sporobolus virginicus* (sp) and *Hebenstreitia cordata* (h).

FIG 5.—Line of the belt transect taken through the foredunes up to the coastal scrub in the distance.

Soil samples were taken from the surface 10 cm of a number of random quadrats in the dune slacks and in the reclamation area. Similar samples were taken at intervals from the quadrats along the transects. The moisture content was determined for each sample by oven drying at 80–100°C. An estimate of organic content was obtained by combustion of oven dried soil in a muffle furnace at 400°C (Huntley & Birks, 1979). The pH was measured of each sample in water using a Metrohm pH meter and the conductivity of a 1 : 5 soil/water suspension was measured on an Electronic Switchgear conductivity meter.

RESULTS

The vegetation and floristic relationships.

Dyer (1937) gives a brief account of the species colonizing sand dunes and rocky cliffs in the Bathurst district. The general trend for both subtropical and Cape floristic elements to occur in the plant communities of the eastern Cape is also evident in this environment. *Scaevola thunbergii*, the abundant pioneer of tropical and subtropical foredunes occurs less frequently, its role being taken by other species such as *Arctotheca populifolia* or *Sporobolus virginicus* (Fig. 4), which are more frequent along the eastern Cape coast. *Myrica cordifolia, Metalasia muricata* and *Stoebe plumosa* are Cape species which very often supplant *Passerina rigida*, the dominant shrub colonizing the dunes behind the *Scaevola thunbergii* zone in Natal and Zululand (Moll & White, 1978; Ward, 1980).

Colonization of foredunes and dune slacks

The flora of the shifting sand dunes is poor and colonization of the extensive dune systems is sporadic. Where plants do occur they never cover areas of more than 50–100 m^2. Twenty species were recorded in the study area and the abundance of the 14 species which occurred in the quadrats sampled is given in Table 1. The distribution of species from the high water mark up to the coastal scrub is shown in Fig. 6.

Scaevola thunbergii is the primary colonizer of the fore dunes on the more sheltered eastern section of this coastline. *Sporobolus virginicus*, although occurring more frequently in the dune slacks, is abundant on the fore dunes as well (Fig. 4). In patches the introduced *Acacia cyclops* has become established as a low-growing creeping bush and may oust the indigenous vegetation even in this harsh

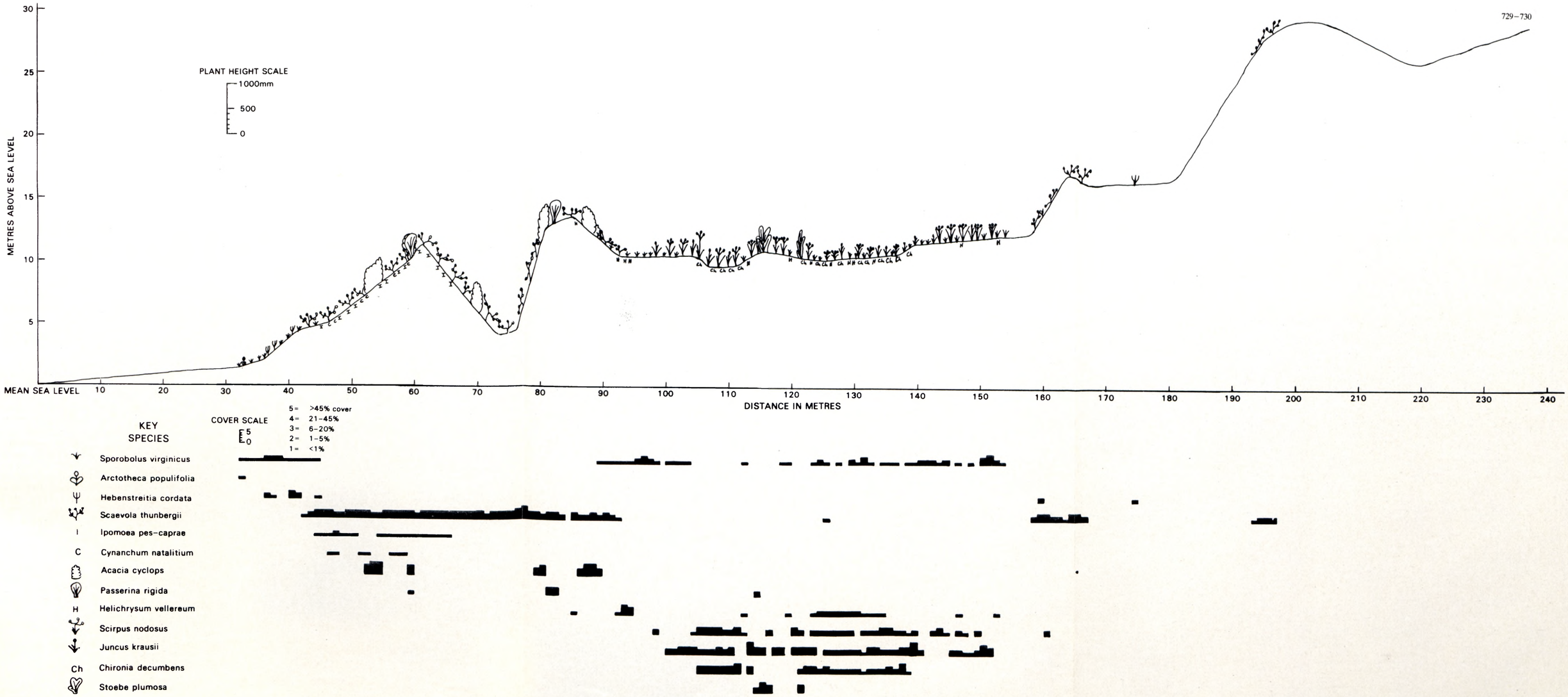

FIG 6.—Profile diagram of the vegetation on the dunes and dune slack near Kleinemonde. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1m² quadrat along the transect.

TABLE 1. — Percentage frequency, aerial cover and density of species colonizing fore dunes and dune slacks

Species	% Frequency		% Aerial Cover		Density (plants m^{-2})	
	Dunes	Dune slacks	Dunes	Dune slacks	Dunes	Dune slacks
Exclusive to foredunes:						
Scaevola thunbergii	58	—	6,4	—	5,4	—
Acacia cyclops	2	—	1,8	—	0,02	—
Ipomoea brasiliensis	2	—	0,06	—	0,06	—
Tetragonia decumbens	2	—	0,2	—	0,2	—
Gladiolus gueinzii	2	—	0,01	—	0,02	—
Occurring in both habitats:						
Sporobolus virginicus	30	44,1	3,12	3,58	3,12	3,75
Arctotheca populifolia	8	22,05	1,0	1,23	0,62	1,04
Hebenstreitia cordata	6	1,47	0,44	0,01	1,01	0,11
Exclusive to dune slacks:						
Juncus kraussii	—	22,53	—	1,16	—	0,77
Scirpus nodosus	—	17,64	—	0,94	—	1,55
Helichrysum praecinctum	—	10,29	—	0,04	—	0,42
Chironia decumbens	—	7,35	—	0,51	—	0,52
Senecio elegans	—	1,47	—	0,01	—	0,01
Zalusianskya maritima	—	1,47	—	0,01	—	0,01

Additional species not recorded in quadrats: *Chrysanthemoides monilifera*, *Cynanchum natalitium*, *Mariscus congestus*, *Passerina rigida*, *Rhus crenata* and *Stoebe plumosa*.

environment. Although not abundant on the dune illustrated, in some areas *Ipomoea brasiliensis (=I. pes-caprae)* and *Arctotheca populifolia* become important pioneers, especially on the flattened dunes near estuaries.

In the dune slacks *Sporobolus virginicus* and *Arctotheca populifolia* are abundant in the drier areas and *Juncus kraussii* and *Scirpus nodosus* more frequent in wetter sand. Many more species appear in the dune slacks, often abundant in one particular dune slack but localized in extent. The transect (Fig. 6) traverses a rather moist luxuriant dune slack with many individuals and a greater diversity of species than most of the dune slacks that were sampled (Fig. 7).

Coastal scrub reclamation

The area in the coastal scrub which has been covered with brush to stabilize the sand occupies an area of about 7,9 ha. Of this area an estimated 5,2% has been colonized by *Acacia cyclops*. This *Acacia cyclops* thicket occurs in one region and was not sampled. The abundance of the species in the total area is indicated in Table 2. A total of 48 species were recorded, although 13 of these occur infrequently or in localized areas and were not recorded in quadrats. This is a large number of species to occur on unstabilized dunes and is due to the introduction of seeds of many coastal scrub species with the brush wood.

The protection and stabilizing effect offered by the branches (Fig. 2) allows for the germination of many species that normally would not occur on

FIG 7.—Looking SE in the direction of the line transect. The moist dune slack in the centre of the photograph is dominated by *Juncus kraussii* and *Scirpus nodosus* with *Sporobolus virginicus* abundant in the drier areas.

TABLE 2. — Percentage frequency, aerial cover and density of species found in the reclamation area of the coastal scrub

Species	Frequency (%)	Density (Plants m^{-2})	Aerial Cover (%)
Ehrhata villosa	50,0	6,59	3,07
Helichrysum praecinctum	25,83	0,95	0,373
Senecio elegans	20,0	0,63	0,112
Senecio litorosus	17,5	0,45	0,051
Felicia echinata	14,17	0,25	0,244
Carpobrotus edulis	9,17	0,092	0,297
Ficinia aphylla	8,33	0,275	0,579
Stoebe plumosa	7,5	0,16	0,633
Polycarena cuneifolia	6,67	0,3	0,035
Brachylaena discolor	6,67	0,067	0,285
Zaluzianskya maritima	5,8	0,13	0,024
Rhus crenata	5,0	0,25	0,192
Passerina rigida	5,0	0,1	0,095
Helichrysum asperum	5,0	0,058	0,172
Pentaschistis heptamera	5,0	0,05	0,005
Anthospermum littoreum	4,17	0,075	0,493
Myrica cordifolia	4,17	0,05	0,243
Acacia cyclops	4,17	0,05	1,103
Eugenia capensis	2,5	0,05	0,005
Felicia capensis	2,5	0,05	0,005
Metalasia muricata	2,5	0,033	0,003
Acacia karroo	1,67	0,025	0,003
Rhoicissus digitata	1,67	0,017	0,083
Stipagrostis zeyheri var. *capensis*	1,67	0,017	0,068
Cynanchum natalitium	1,67	0,017	0,002
Kedrostis nana	0,83	0,017	0,083
Aloe sp.	0,83	0,0083	0,001
Berkheya heterophylla	0,83	0,0083	0,001
Clematis brachiata	0,83	0,0083	0,001
Knowltonia capensis	0,83	0,0083	0,001
Clutia daphnoides	0,83	0,0083	0,001
Helichrysum cymosum	0,83	0,0083	0,001
Heteroptilis suffruticosa	0,83	0,0083	0,001
Maytenus procumbens	0,83	0,0083	0,001
Salvia scabra	0,83	0,0083	0,001

Other species not found in quadrats: *Acacia saligna, Ammophila arenaria, Senecio pterophorus, Bulbine latifolia, Casuarina equisetifolia, Chironia baccifera, Chrysanthemoides monilifera, Dolichos falciformis, Hebenstreitia cordata, Helichrysum teretifolium; Ipomoea brasiliensis, Sarcostemma viminale and Scaevola thunbergii.*

exposed dunes. *Ehrharta villosa, Helichrysum* spp. and *Senecio elegans* were the species found most frequently in the reclamation area. The grass *Ehrharta villosa* becomes extremely abundant and well established in these conditions and although the aerial cover is low it has long rhizomes and plays a major role in dune stabilization. All of the abundant species are primarily secondary colonizers of blow-out areas in coastal scrub and are very different from the primary colonizers of fore dunes (Table 1).

Vegetation of the rocky promontories

The First Sister, that furthest to the west, consists of both herbaceous and low scrub communities, but it is similar in area and has been more disturbed than the Second Sister because it is more accessible to the beach. Of the 36 species recorded on the First Sister some, such as *Scaevola thunbergii* and *Senecio elegans*, are species of the sand dunes, and have not been found on the Second Sister. On the other hand, some of the 35 species of the Second Sister are shrubs not recorded on the First Sister. The Third Sister is much more exposed and consists almost solely of herbaceous plants, because very little sand has been deposited here. Only 16 species were recorded on this rocky buttress.

The Second Sister shows a distinct zonation of herbaceous and scrub communities (Figs. 1c & 3,

Table 3). The profile diagram of the rocky promontory (Fig. 8) shows how the two community types are distributed and how the prevailing winds have affected the growth form of the plants. The dominant species of the herbaceous community are, in decreasing order of frequency: *Limonium scabrum, Plantago carnosa, Sporobolus virginicus, Delosperma littorale, Stenotaphrum secundatum, Aizoon rigidum* and *Gazania rigens* var. *uniflora.* The two grasses are also found in the scrub community although less common there. The dominant species in the scrub are *Maytenus procumbens, Rhoicissus digitata, Haemanthus albiflos* and *Eugenia capensis.* In areas closer to the sea or near to the land other species become locally dominant (Fig. 8).

There is a minimum of sand accumulation on the rocky cliffs and this lack of substrate and the strong winds prevents colonization by other species. Many of the species on the cliffs are halophytes also commonly found in estuaries, because there is an intense accumulation of spray on these rocks, especially during storms and high winds.

ENVIRONMENTAL FACTORS

The severity of the marine climate is the main limiting factor in the establishment of plants on both shifting dune sands and rocky promontories. The Cape is well known for its tempestuous conditions and unpredictable changes in weather.

Temperature

Extremes in temperature are common. In the summer, maximum air temperatures can exceed 40°C and in the winter the maximum temperature falls as low as 2–3°C (Schulze, 1980). Due to the high insolation and high air temperatures, the sandy and rocky substrates exhibit widely fluctuating temperatures. These soils with mainly physical components and low water holding capacity heat up to greater temperatures and fluctuate more markedly than soils with more organic matter and which dry out less rapidly. The soil temperatures may exceed 60°C in summer although this is only on the surface layers, because soil is a poor conductor of heat. At 20 cm depth the soil temperature was found to vary between 18,5–20°C on the dune reclamation site, whereas air temperature over the same 24 hour period in May, 1980 fluctuated from 18,5–29°C. Salisbury (1952) has also measured the moderating effect of depth in the soil on fluctuating temperatures in Britain. Soil temperatures over the 24 hour period were greatest on the fore dunes (22°C) followed by the dune reclamation site (20°C) and then the dune-slack (18°C). The dune-slack soil was also only subject to a 2°C temperature change over the 24 hour period compared with 6°C on the fore dunes. Plants in the sand dune environment must therefore contend with wide diurnal and seasonal fluctuations in temperature and variations in temperature at different depths in the soil.

Rainfall

The rainfall along this coast is rather eratic as Dyer (1937) has shown. The weather station at Great Fish Point, only a few km to the north east (33°32'S, 27°6'E) is situated just above the dunes at 73 m a.s.l. Over a 42 year period up to 1960, a mean average rainfall of 589,8 mm was recorded of which 60% fell in the summer months (Anon, 1965, Climate of South Africa). The annual rainfall chart shows a bimodal distribution with two maximum periods of March (mean 62,3 mm) and October (mean 69,0 mm) and the minimum rainfall in August (mean 32,1 mm).

Wind and sand movement

The effect of wind and sand movement is probably the major controlling factor in the distribution and establishment of plants in these coastal environments. The nearest weather station where wind records are kept is East London which experiences only about 11% calms in summer months and about 6% in winter months (Schulze, 1980). In the summer the predominant winds are easterlies or north-easterlies, but more intense winds occur in the winter months from the west or south-west. Therefore the sand dunes are orientated in a NW-SE direction and the greater movement of sand is from the west to the east. Blow-out areas in the coastal scrub face towards the beach in the direction from which the majority of prevailing winds arise (Fig. 1). The presence of vegetation on the dunes lowers the wind speed considerably, as does the profile of the dune itself, thus the wind speed in the slacks is considerably lower than on the dune face (Chapman, 1976).

Wind is also one of the major limiting factors in the establishment of vegetation on the cliffs and rocky promontories. The herbaceous plants on the exposed sides of the Three Sisters are able to become established by clinging to crevices and small pockets in the rocks where some sand may also accumulate. The pruning effect of the wind on the shrubs is apparent in the profile diagram across the Second Sister (Fig. 8). Due to increased transpiration and the chilling effect on the shoots and buds in exposed positions, growth is slowed down or stopped resulting in the pruned appearance of the shrubs.

Soil factors

The soil characteristics determined from soil samples taken from random quadrats in the dune slacks, the reclamation area, and along the line transects are listed in Table 4. The initial studies of the vegetation and soils of the different areas were made at different times in 1979 and 1980 but the soils were all re-sampled on 16th July, 1981 and re-analysed to give comparable results.

Soil factors are probably of secondary importance in the ability of plants to become established in coastal habitats, because a variety of dune species show a great range of tolerance to different soil conditions. Dunes usually have a neutral to alkaline pH which becomes more acidic with age (Ranwell, 1972). The pH of the dunes and dune slacks was between 8,00 and 8,2 (Table 4) whereas along the transect on the Second Sister where vegetation has been established for many years the pH drops

TABLE 3. — Percentage frequency of species on the Second Sister and the occurrence of all species on the rocky promontories

Species (in order of occurrence from seaward side of Second Sister)	Percentage Frequency on Second Sister			Occurrence on:	
	Herbaceous community	Scrub community	Total area	First Sister	Third Sister
Chenolea diffusa	23,73	0	11,67	+	+
Disphyma crassifolium	33,9	0	16,67	+	+
Aizoon rigidum	53,9	0	27,50	+	+
Limonium scabrum	94,92	0	46,67	+	+
Gazania rigens var. *uniflora*	62,71	0	30,83	+	+
Sporobolus virginicus	79,66	9,84	44,17	+	+
Plantago carnosa	79,66	0	39,17	+	-
Delosperma litorale	77,97	0	38,33	+	+
Falkia repens	15,25	0	7,5	-	-
Stenotaphrum secundatum	62,71	4,92	33,33	-	+
Mariscus congestus	8,47	11,48	10,00	-	-
Passerina rigida	5,08	9,84	7,5	+	+
Anthosperum littoreum	0	47,54	24,17	+	-
Carpobrotus edulis	0	31,15	15,83	+	+
Helichrysum teretifolium	0	16,39	8,33	+	+
Rhoicissus digitata	0	79,69	40,0	-	-
Euclea racemosa	0	32,79	16,67	+	-
Rhus crenata	0	9,84	5,0	+	-
Maytenus procumbens	0	83,61	42,5	+	-
Eugenia capensis	0	67,21	34,17	+	+
Haemanthus albiflos	0	68,85	35,0	+	+
Rhoiacarpos capensis	0	18,03	9,17	-	-
Cassine sphaerophylla	0	14,75	7,5	-	+
Rhus undulata	0	3,28	1,67	-	-
Euclea natalensis	0	1,64	0,83	-	-
Cynachum natalitium	0	9,84	5,0	+	-
Pavetta capensis	0	3,28	1,67	-	-
Secamone alpini	0	11,48	5,83	+	-
Sideroxylon inerme	0	6,56	3,33	+	+
Crassula nudicaulis var. *nudicaulis*	0	16,39	8,33	+	-
Chironia baccifera	0	6,56	3,33	-	-
Ficinia aphylla	0	3,28	1,67	+	-
Mimusops caffra	0	8,20	4,17	+	-
Chrysanthemoides monilifera	0	6,56	3,33	+	-
Maerua cafra			+	-	-
Solanum quadrangulare			-	-	+
Senecio elegans			-	+	-
Gladiolus guenzii			-	+	-
Scaevola thunbergii			-	+	-
Myrica cordifolia			-	+	-
Helichrysum argenteum			-	+	-
Senecio litorosus			-	+	-
Crassula expansa var. *filicaulis*			-	+	-
Scirpus nodosus			-	+	-
Lycium cf. L. campanulatum			-	+	-
Drosanthemum ambiguum			-	+	-
Acacia cyclops			-	+	-
Cassine maritima			-	+	-
Total number of species			35	36	16

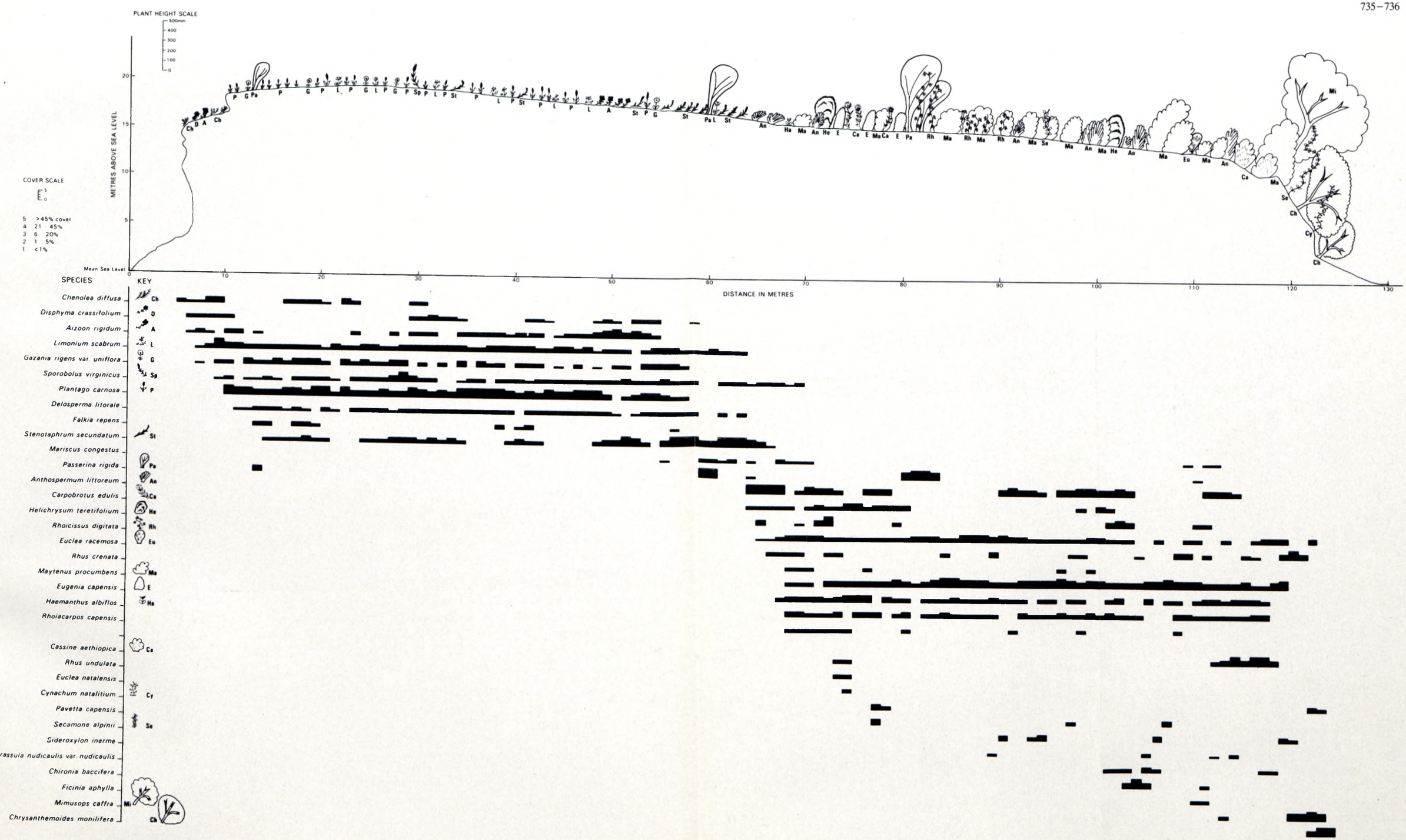

FIG 8.—Profile diagram of the vegetation across the Second Sister. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1m² quadrat along the transect.

TABLE 4. — Characteristics of the soils (Mean ± std. error)

Locality	pH	Conductivity (millimhos cm^{-1})	Moisture content (%)	Estimated Organic content (%)
Fore dunes	8,02 (±0,01)	79,15 (±4,18)	1,64 (±0,30)	0,88 (±0,04)
Dune slacks	8,11 (±0,03)	120,54 (±14,16)	12,06 (±2,78)	0,675 (±0,045)
Dune Transect				
Zone I (Beach)*	8,1	290	2,21	1,36
Zone II (Fore dunes)	8,16 (±0,01)	72,76 (±6,02)	1,63 (±0,37)	1,08 (±0,09)
Zone III (Dune slacks)	8,16 (±0,02)	80,93 (±4,00)	11,66 (±4,57)	0,86 (±0,10)
Zone IV (Rear dune)	8,24 (±0,02)	68,05 (±4,72)	1,84 (±0,31)	0,74 (±0,08)
Coastal Scrub Reclamation Area	7,92 (±0,02)	64,53 (±1,40)	1,99 (±0,24)	0,99 (±0,05)
Second Sister				
Zone I (Rocky ledge)	8,20 (±0,20)	1600,0 (±770,0)	13,78 (±5,04)	4,42 (±2,66)
Zone II (Herbaceous exposed)	7,92 (±0,07)	435,0 (±118,57)	3,52 (±0,72)	2,13 (±0,51)
Zone III (Herbaceous)	7,83 (±0,12)	549,0 (±207,34)	9,78 (±2,05)	6,46 (±0,06)
Zone IV (Scrub)	7,96 (±0,05)	188,60 (±7,16)	7,81 (±0,64)	5,59 (±0,78)
Zone V (Tall Scrub)	7,78 (±0,13)	346,67 (±118,37)	5,88 (±2,50)	3,68 (±1,29)

* Not replicated

consistently. Likewise in the coastal scrub reclamation area the pH is slightly lower.

The base exchange capacity in sandy dune soils is low initially, but increases with the accumulation of organic matter. Salisbury (1925) found that the organic matter increased from below 1% to more than 5% after 200 years of vegetation establishment. The calcium carbonate content of these soils decreases correspondingly with age. The estimated organic content of the soils (Table 4) was not corrected for calcium carbonate and the values are probably exaggerated. However, on the young dunes the organic content is invariably less than 1%. On the Second Sister, however, organic matter has been accumulating over a long period and a more complex soil has developed. In the herbaceous community the 6,46% organic matter would represent an accumulation for more than 250 years on the basis of Salisbury's (1925) predictions.

On the mobile dunes accumulation of salts in the soils from sea spray may not be a problem because frequent flushing by rains will remove the salts from the sand. Although the actual salt content was not measured the conductivity gives an indication of salt accumulation in the soil. On the porous loose sands of the dunes the conductivity was generally less than 80 micromhos cm^{-1} but in the dune slacks a mean of 120,54 micromhos cm^{-1} was measured. On the beach (Zone I of the dune transect) and on the rocky ledges on the Second Sister, much higher conductivity readings were recorded. The effects of high tides and sea spray which inundates the rock cliffs is apparent and in the more well developed soil of the Second Sister consistently high readings were obtained because the soil could not be flushed of the salt ions as it is on the sand dunes.

The inconsistent rainfall and high porosity of sand which lacks a fine fraction results in a low availability of water for most of the year. The sand has a low water holding capacity and very low field moisture capacity of only about 7% (Salisbury, 1952). In the young dunes moisture content was generally less than 2%, except in the seepage areas of dune slacks where water accumulates close to the surface (Chapman, 1976), and was generally about 12% of the dry weight of the soil. The water table rises as the dune is built up (Hill & Hanley, 1914), and fluctuates with rainfall as has been reported from England (Willis *et al.*, 1959). On the rocky promontories the increased organic content gives better water retention and moisture content exceeded 10% in some zones of the Second Sister. There is a significant correlation between organic and moisture content of the soil ($r = 0,686$; prob $< 0,01$) in this area.

DISCUSSION

The absence of plants from these extensive dune systems can be explained by the migratory nature of

the sand dunes due to persistent winds during most of the year. The movement of sand from the west to the east in winter and to a lesser extent in the reverse direction in summer, coupled with an inconsistent rainfall and high summer temperatures makes the establishment of plants on the dunes very sporadic, if at all.

The zonation of the plants along the transect can be explained in terms of the slight differences in soil conditions and climatic factors. The increased seepage of moisture, lack of spray and high insolation in the dune slacks allows for the establishment of a great diversity of plant species. Therefore, although no single factor can account for zonation on coastal dunes as has been reported by others (Oosting & Billings, 1942), the combination of environmental factors results in the zonation of species away from the shore. The importance of sea spray in controlling the distribution of species has been stressed (Oosting & Billings, 1942; Pammenter, pers. comm., 1979) and is currently been investigated for *Scirpus nodosus*, one of the dominant species of the dune slacks.

The re-establishment of plants in the reclamation area of the coastal scrub is being successfully achieved by covering the sands with brushwood. Although the microclimate and soil factors are changed only slightly by this action, the stabilization of the sand from further wind movement allows for regrowth of a great variety of coastal scrub and sand dune species. Since this study was carried out, the *Acacia cyclops* thickets have been removed and within the next 10 years a pioneer scrub community should be well established in this blow-out area.

The Three Sisters have well established plant communities which show various stages of plant succession. The high winds and spray are the major factors responsible for the distinct zonation of the plants in the area. The rocky ledge and very exposed herbaceous zones are generally characterized by *Chenolea diffusa*, a plant more common in salt marshes. The presence of halophytes indicates that salt spray is considerable in the region, a fact which is borne out from conductivity studies of the soil. With the accumulation of soil organic matter, which is indicative of the long period of establishment of plants on the rocky promontory, there is a correspondingly higher moisture content and substantial scrub communities have developed.

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