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# Some characteristics of the plant communities of three dunes situated across a climatic gradient in the Namib Desert

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ABSTRACT

Plant species diversity, plant cover and plant density are reported for three dunes situated across a climatic gradient in the Namib Desert. Substrate penetrability, dune slope and dune aspect, parameters of importance to the plant community characteristics, are also reported. The central site, Bushman's Circle, had the greatest plant species diversity with four perennial species having more than 0,5% crown cover values. The eastern site, Far East, had two such species, while Nara Valley, the western site, had one. Each plant community contained several other species with cover values of less than 0,5%. Plant crown cover on the dune areas of Far East and Bushman's Circle was about 7,5%. Nara Valley had a considerably lower cover value of about 1,5%. The cover values of the interdune plains at Far East was about 5,0%, while the interdune plains at Bushman's Circle and Nara Valley were virtually unvegetated. Far East had the most compacted substrates. This site did not have a true 'dune crest' zone. At the other sites substrate compaction was highest on the interdune plains and lowest at the dune crests. Plant species diversity and cover values were highest on the dune base and plinth zones of all three dunes. The lowest values of these parameters were recorded on the dune crest and interdune plains zones.

## INTRODUCTION

The Namib is a cool, coastal desert with a steep climatic gradient from the extremely arid coastal belt in the west to the summer rainfall region 140 km inland (Besler 1972; Lancaster *et al.* 1984). Conversely, fog-water precipitation occurs on a decreasing gradient from over 50 mm/annum in the west to a negligable amount in the east.

Most previous studies on plant community characteristics of the central Namib dunes have concentrated on the central region of linear dunes, particularly in the vicinity of Gobabeb, 50 km from the coast (*e.g.* Robinson 1976; Robinson & Seely 1980; Seely & Louw 1980; Seely *et al.* 1977), although mention of the communities to the east (Nel 1983) and the west (Nott 1985) have been made.

Yeaton (1988) described some of the physical characteristics associated with the development of plant communities and the control of species turnover rates, both within and between dunes, of the communities described in this paper. These characteristics included sand movement, sand compactness, rainfall and soil moisture gradients.

The aim of this paper is to present a detailed description of the biotic characteristics of plant communities of several dunes along the east-west climatic gradient of the Namib. Several important physical characteristics of the substrate; surface and sub-surface sand compaction, slope and aspect are also discussed, thus providing baseline data for other ecological studies in these areas and, together with Yeaton's (1988) paper, for more detailed plant community studies.

The plant communities occur in a gradation of species on each dune. The base is relatively well vegetated with species requiring a stable substrate, whereas at the crest primary colonisers cannot become established due to strong winds producing a highly mobile substrate (Yeaton 1988). This has resulted in a series of well-defined zones, each being relatively homogenous in plant community characteristics and some physical aspects (Robinson & Seely 1980; Yeaton 1988). These different zones are described, starting at the compacted interdune plain, and continuing up the dune to the crest. They are similar to the biotic communities described by Holm and Scholtz (1980) and Robinson and Seely (1980) and for conformity a similar nomenclature was adopted. Plant species diversity, plant density, plant crown cover and some related substrate characteristics are reported for each zone.

At all sites the vegetation was relatively sparse compared to more mesic systems and most species were graminiferous. There was a large diversity in individual plant size ranging from less than 0,001 m in crown diameter to over 10 m. Standard sampling methods were adapted to obtain data representative of the plant communities.

## METHODS

### Sampling techniques

Data were collected from December 1984 to May 1985 at three sites; Far East (23°47'S, 15°48'E) which is 128 km from the coast and near to the eastern edge of the desert, Bushman's Circle (23°42'S, 15°21'E), 75 km inland, and Nara Valley (23°37'S, 14°59'E) the western site being 48 km inland (Figure 1). These sites were selected so that all of the main plant associations of the central Namib dunes were represented. Yeaton (1988) has subsequently confirmed that the selection of these three sites achieved this aim.

coast inland

W E

Nara Valley Bush O Far East

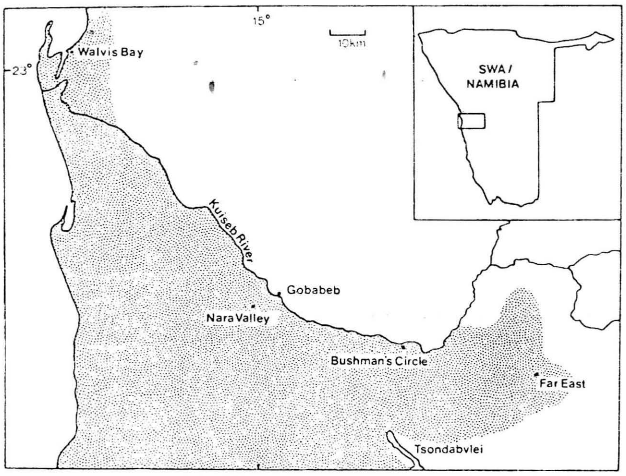



FIGURE 1: Map of the central Namib dunes indicating the three study sites.

The sample plot of each site was 600 m long and 100 m wide, with the long axis of this area at right angles to the length of the dune (Figure 2). All linear and area measurements refer to the surface measurement and were not projected to the horizontal.

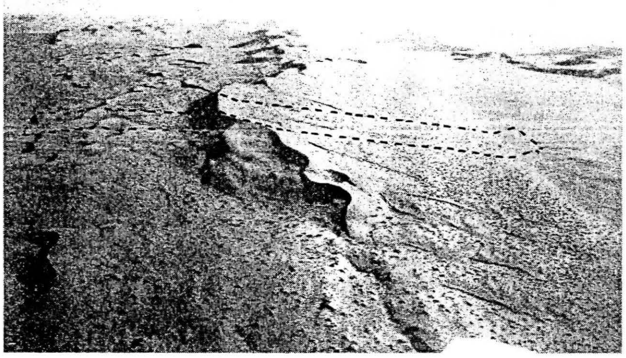


FIGURE 2: Aerial photograph of linear dunes at Bushman's Circle with an outline of the study area superimposed.

At Bushman's Circle and Nara Valley the sample plots commenced on the interdune plain, 60 m west of the dune base, continued over the entire western dune slope to the dune crest and down the eastern slope until a total distance of 600 m was covered. At Nara Valley the end of the plot was approximately 150 m below the dune crest, whereas at Bushman's Circle, due to the smaller dune size, it extended 200 m down from the crest to the interface with the eastern interdune plain. Owing to the relatively higher plant densities found in the interdune area at Far East compared with Bushman's Circle and Nara Valley, sampling started farther west of the dune base (260 m), and continued for 200 m up the western slope to the dune crest. 140 m of the eastern slope was included in this plot to give a total of 600 m.

### Line transects

A series of 30 sets of transects were placed at 20 m intervals starting on the interdune plain, and continuing over the dune (Figure 2). Each set consisted of two lines intercepting each other at right angles; one line of 20 m placed up the slope of the dune, and the other of 10 m, parallel to the base of the dune. A second series of identical transects was placed 80 m farther along the dune, with a third series between these two, *i.e.* each series was located at 40 m intervals. For the third series, both lines were 10 m in length. Due to the sparse plant cover at Nara Valley the sampling intensity was increased to yield a large enough sample for an accurate description of this habitat to be made. The transects were again placed at 20 m intervals over the dune, but in this case five series of transects were used, at distances of 20 m along the dune, with each set consisting of two 20 m lines.

### Quadrats

Two series of sixty contiguous quadrats, stretching the entire length of the sample plots were used. Each quadrat measured 10 m by 10 m. These quadrats were placed over the dune in the same position as the two peripheral line-intercept transects described above.

Due to the low plant densities at Nara Valley three series of contiguous quadrats were used. Each series was 40 m from the next and contained sixty 20 m by 10 m quadrats.

### Stratified random sampling

A total of 60 points, 30 on each side of the central line of each sample plot, were selected at 20 m intervals using a stratified random sampling technique. Each point could be a maximum of 50 m from the centre of the sample plot.

## Collection and analysis of data

### Species diversity

Perennial plant species present at each site and within each zone were recorded and Hill's $N_2$ species diversity index (Hill 1973; Peet 1974) was calculated. ???

Crown cover was used as the measure of frequency of occurrence of each species. This measurement was used because there was a large variation in plant size, both between and within species, which would bias any index using simple counts towards the more numerous, and often smaller and less significant, species. In addition, several of the species encountered formed sprawling mounds of vegetation and it was often difficult to determine whether such a mound contained one or many plants. Use of cover, rather than plant counts, as the measure of frequency removed this uncertainty.

### Plant crown cover

Plant crown cover was determined by the line intercept method (Greig-Smith 1983).

All standing plant material, dead or alive, was recorded as 'cover'. This was applied so that perennial ephemeroids, which are able to cease all above ground photosynthetic activity until they appear to be dead (Noy-Meir 1973), were included. Several of the species occurring in the study areas appeared to be perennial ephemeroids; *e.g.* the grasses *Centropodia glauca* (Nees) Nevski, *Stipagrostis ciliata* (Desf.) de Winter and *S. lutescens* (Nees) de Winter, and the herbs *Hermannia minimifolia* M. Holzhammer and *Kohautia ramosissima* Bremek. Wind-blown detritus, which can range from microscopic particles to entire plants, was not included.

Plant cover was reported as a percentage of the total surface area. Coefficients of variation (C.V.s) were presented to give an indication of the homogeneity of cover of the various species within each area. Percentage cover was arcsine transformed for calculation of C.V.s. (Zar 1984).

To enable comparisons to be made between sites and with similar studies in other deserts, average plant cover was reported for the entire area of each of the two substrates (*i.e.* dune and interdune plain at each site) and for each zone.

### Plant density

Density (number of plants per unit area) of perennial plants was estimated by counting the total number of plants of each species using a series of quadrats. Plants which occurred on the edge of quadrats were recorded only if more than half of the crown area was within the quadrat. The mean density per species in each quadrat was calculated.

Several plant species encountered, all grasses, appeared to reproduce vegetatively using rhizomes. These were *Cladoraphis spinosa* (L. fil.) Thunb., *S.* c.f. *namaquensis* (Nees) de Winter and *S. sabulicola* Pilg. de Winter. Such plants were only considered as separate entities if the various parts were separated by bare sand or another species of plant (see also species diversity calculations). Again, owing to the occurrence of perennial ephemeroids, all plants whether appearing dead or alive were included.

### Substrate compactness

Substrate compactness, or penetrability, was measured using a soil penetrometer, employing a stratified random sampling technique. The penetrometer gave a graph of soil resistance as a 1,5 cm diameter pointed probe was pushed into the substrate.

Substrate compactness was tested at each sample point, and at the four ordinal points 2 m away from the sample point, giving 10 data points at each 20 m interval. If a sample point coincided with vegetation the nearest point of bare sand not occurring beneath the plant canopy was sampled. Compaction values were averaged within 20 m intervals at depths of 5 cm and 10 cm, and in areas of low compaction, at 15 cm and 20 cm. Because of mechanical problems, it was only possible to obtain data for the 5 cm, 10 cm and 15 cm soil depths at Nara Valley.

### Slope

Dune slope was measured, using an inclinometer (Suunto Optical Reading Clinometer), at 20 m intervals over the entire dune. At each interval three readings were taken, at distances of 40 m along a line parallel to the base of the dune, each reading coinciding with the intercept points of the line transects. The mean of these angles was taken as the dune slope at that interval.

### Zonation of the study sites

The criteria used for delineation of zones were changes of plant species rank order and amount of cover.

The cover value of each species, within 20 m intervals, was used to determine species rank order. Adjacent 20 m interval blocks were classed as being within the same zone unless the species rank orders were different, or the plant cover values were markedly different. If either were so, then the blocks were deemed as being in different zones.

Following the delineation of zones the average plant cover, plant density and sand compactness were calculated for each zone.

## RESULTS

### General description of the study sites

The plant species present at the three sites, their percentage cover and homogeneity of cover are shown in Tables 1, 2 and 3.

TABLE 1: Percentage cover of each plant species on the dunes and the interdune plains at Far East. Coefficients of variation (CV) indicate the degree of homogeneity of distribution of each species. Mean total cover for each substrate type is also indicated.

| Species | Dunes | | Interdune plains | |
|---|---|---|---|---|
| | Cover % | CV % | Cover % | CV % |
| *Cladoraphis spinosa* | 5,15 | 55 | 0,02 | 360 |
| *Stipagrostis ciliata* | 1,54 | 53 | 4,47 | 21 |
| *S. lutescens* | 0,01 | 412 | | |
| *S. sabulicola* | 0,33 | 174 | | |
| *Hermannia minimifolia* | Trace | | | |
| *Kohautia ramossisima* | 0,32 | 120 | 0,03 | 360 |
| Total | 7,39 | | 4,52 | |

TABLE 2: Percentage cover of each plant species on the dunes and the interdune plains of Bushman's Circle. Coefficients of variation (CV) indicate the degree of homogeneity of distribution of each species. Mean total cover for each substrate type is also indicated.

| Species | Dune | | Interdune plain | |
|---|---|---|---|---|
| | Cover % | CV % | Cover % | CV % |
| *Centropodia glauca* | 1,55 | 104 | 0,15 | 173 |
| *Stipagrostis ciliata* | Trace | | 0,61 | 54 |
| *S. lutescens* | 0,95 | 176 | 0,26 | 173 |
| *S.* c.f. *namaquensis* | 3,44 | 56 | | |
| *S. sabulicola* | 1,74 | 155 | | |
| *Kohautia ramossisima* | Trace | | | |
| Total | 7,70 | | 1,02 | |

TABLE 3: Percentage cover of each plant species on the dunes and the interdune plains at Nara Valley. Coefficients of variation (CV) indicate the degree of homogeneity of distribution of each species. Mean total cover for each substrate type is also indicated.

| Species | Dune | | Interdune plain | |
|---|---|---|---|---|
| | Cover % | CV % | Cover % | CV % |
| *Stipagrostis ciliata* | 0,04 | 195 | 0,01 | 173 |
| *S. sabulicola* | 1,12 | 86 | | |
| *Trianthema hereroensis* | 0,37 | 127 | | |
| Total | 1,53 | | 0,01 | |

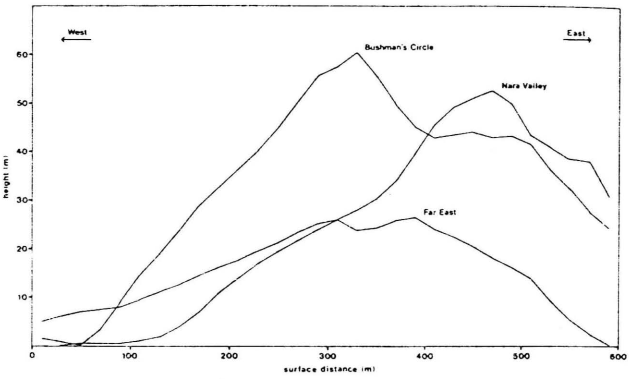



FIGURE 3: A cross-sectional diagram of three dunes in the central Namib. The horizontal axis represents distance as measured on the surface and is not projected to the horizontal.

### Dune area

The dune area of Far East had two dominant species, *C. spinosa* and *S. ciliata*. These were uniformly distributed over the dune, with C.V.s of about 50%. *H. minimifolia* also occurred at Far East, but it was uncommon and despite the intensive sampling regime it was not sampled.

At Bushman's Circle there were four plant species present on the dunes with crown cover values of more than 0,5%. *S.* c.f. *namaquensis* had the greatest extent of cover and the most even distribution. *K. ramosissima* occurred at this site, but it was uncommon, with a clumped distribution, and was not sampled.

Nara Valley had one dominant species, *S. sabulicola*, although *Trianthema hereroensis* Schinz constituted a quarter of the total plant cover at this site.

The total plant cover of the dunes at Far East and Bushman's Circle was similar. Nara Valley was more sparsely vegetated with a plant cover value of only one fifth of the two eastern sites.

### Interdune plains area

*S. ciliata* was the main plant species on the interdune plains. Its cover decreased over four hundredfold from Far East to Nara Valley. At Far East and Bushman's Circle this species was evenly distributed, but at Nara Valley it had a patchy distribution.

## Characteristics of zones

The vegetation zones at Bushman's Circle and Nara Valley are described together as these dunes are of a similar physical form. Both dunes are within the linear dune system (Barnard 1973), but are complex in character, Nara Valley having a single main ridge with several sub ridges, while Bushman's Circle has multifaceted crests (Lancaster 1983). The dunes are about 60 m high with relatively steep slopes (Figure 3). Far East dune is within the star dune system (Barnard 1973), although the basic linear dune format is still evident, the dune ridges tend to be a chain of interconnecting multifaceted dunes (Lancaster 1983). Far East dune is less than 30 m high and its slopes have a shallow gradient. Each site is discussed beginning at the western interdune plain.

### Far East

The substrate of the western interdune plain at Far East was more compacted than the other zones (Figure 4) and had a dense monospecific stand of *S. ciliata* (Table 4). The western dune plinth was also densely vegetated, with *C. spinosa* as the dominant species (Figure 7). On the dune crest vegetation was sparser and the sand less compacted. This area was also dominated by *C. spinosa*, but species diversity was greater than on the dune plinth, despite fewer species occurring in this zone. This was a result of a greater heterogeneity of the cover values of each species present. The western dune plinth and crest zones had a number of small depressions, where the substrate was more compacted, in which *S. ciliata* was the dominant species. The eastern zone was similar to the western interdune plain, but the vegetation was sparser. Due to the local topography this area was surrounded on three sides by dunes and therefore could not be considered part of the interdune plain to the east of the dune, but rather a large *S. ciliata* covered depression within the dune complex.

### Bushman's Circle and Nara Valley

At Bushman's Circle and Nara Valley the interdune plain was sparsely vegetated with *S. ciliata* (Figures 8 & 9; Tables 5 & 6). At Bushman's Circle a species diversity figure of 1,46 was calculated for this zone, although this was likely to be an inflated value due to an 'edge effect', or slow transition of vegetation types from the interdune plain zone to the dune base zone. At both sites the slope of this zone was negligible and the substrate was very compact (Figures 4 & 5).

The western dune base was an area of relatively high plant diversity and cover with three species forming important components of the plant community at both sites. The western plinth occupied the bulk of the western side of these two dunes. Vegetation cover was again fairly high, but monospecific: *S.* c.f. *namaquensis* at Bushman's Circle and *S. sabulicola* at Nara Valley. The slipface area was characterised by a lack of vegetation and low compaction values. The eastern

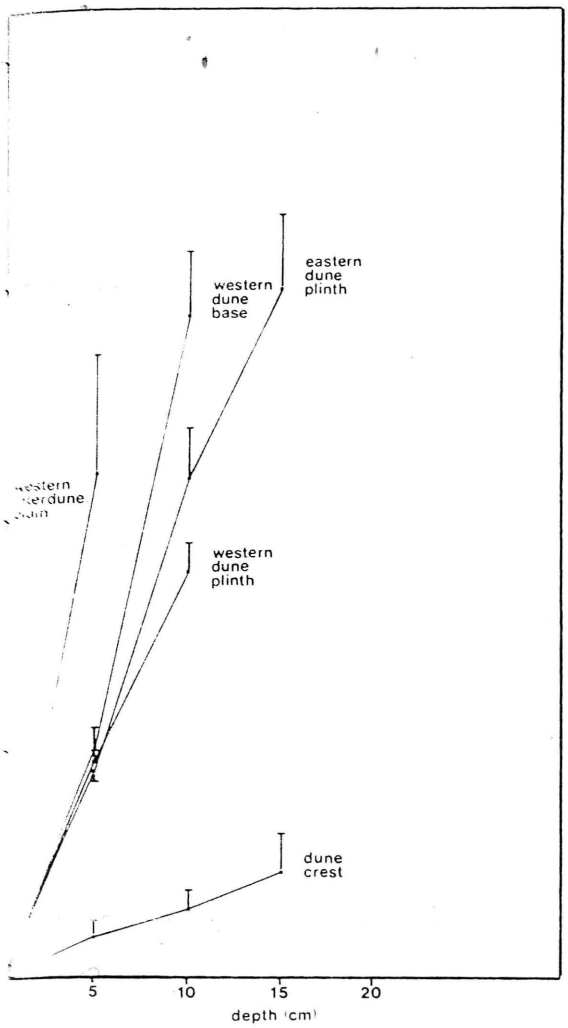
TABLE 4: Plant density, cover and coefficient of variation of cover (CV) of zones at Far East.

| Zone | Plant species present | Species Diversity | Density No./ha | Cover % | CV % |
|---|---|---|---|---|---|
| Western interdune plain | *Stipagrostis ciliata* | | 50 275 | 4,5 | 21 |
| | Total | 1,00 | | 4,5 | |
| Western dune plinth | *Cladoraphis spinosa* | | 1 831 | 9,0 | 9 |
| | *S. ciliata* | | 1 916 | 1,4 | 63 |
| | *S. lutescens* | | 53 | Trace | 282 |
| | *S. sabulicola* | | 19 | 0,5 | 154 |
| | *Kohautia ramossisima* | | 288 | 0,5 | 361 |
| | Total | 1,55 | | 11,3 | |
| Dune crest | *C. spinosa* | | 560 | 2,4 | 33 |
| | *S. ciliata* | | 3 855 | 1,3 | 63 |
| | *S. sabulicola* | | 45 | 0,3 | 223 |
| | *K. ramossisima* | | 120 | 0,3 | 103 |
| | Total | 2,42 | | 4,3 | |
| Eastern plinth/depression | *C. spinosa* | | 138 | 1,3 | 118 |
| | *S. ciliata* | | 36 750 | 2,1 | 28 |
| | *S. sabulicola* | | | 0,1 | 200 |
| | *K. ramossisima* | | | 0,2 | |
| | Total | 2,03 | | 3,5 | |

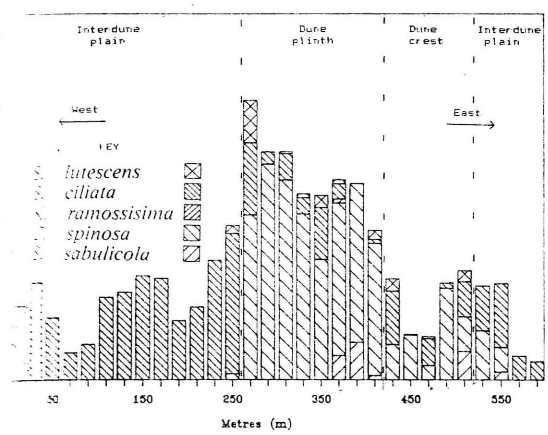
TABLE 5: Plant density, cover and coefficient of variation of cover (CV) of zones at Bushman's Circle.

| Zone | Plant species present | Species Diversity | Density No./ha | Cover % | CV % |
|---|---|---|---|---|---|
| Western interdune plain | *Centropodium glauca* | | 975 | 0,4 | 173 |
| | *Stipagrostis ciliata* | | 17 667 | 0,6 | 51 |
| | *S. lutescens* | | 941 | 0,3 | 173 |
| | Total | 1,00* | | 1,3 | |
| Western dune base | *C. glauca* | | 2 531 | 4,5 | 16 |
| | *S. ciliata* | | 450 | Trace | |
| | *S. lutescens* | | 1 744 | 4,7 | 58 |
| | *S.c.f. namaquensis* | | 306 | 1,5 | 117 |
| | Total | 2,56 | | 10,7 | |
| Western dune plinth | *C. glauca* | | 913 | 0,9 | 64 |
| | *S. lutescens* | | 6 | Trace | 200 |
| | *S.c.f. namaquensis* | | 853 | 5,6 | 8 |
| | *S. sabulicola* | | 9 | Trace | |
| | Total | 1,31 | | 6,5 | |
| Dune crest | *S.* cf. *namaquensis* | | 50 | 0,1 | 200 |
| | *S. sabulicola* | | 25 | 0,1 | 200 |
| | Total | 2,00 | | 0,2 | |
| Eastern dune plinth | *C. glauca* | | 25 | 0,2 | 282 |
| | *S. lutescens* | | 6 | Trace | 282 |
| | *S.c.f. namaquensis* | | 266 | 4,0 | 18 |
| | *S. sabulicola* | | 200 | 5,8 | 36 |
| | Total | 2,02 | | 10,0 | |
| Eastern dune base | *C. glauca* | | 1 442 | 3,6 | 23 |
| | *S. ciliata* | | 4 367 | Trace | 173 |
| | *S. lutescens* | | 450 | 2,1 | 32 |
| | *S.c.f. namaquensis* | | 217 | 3,4 | 43 |
| | *S. sabulicola* | | 8 | 0,2 | 173 |
| | Total | 3,01 | | 9,3 | |

*see text




…: Mean substrate compaction, with standard errors indi- … different depths in five zones at Nara Valley.




…: Crown cover of the perennial plant species in thirty … each 20 m wide, at the Far East study site.

…ad little vegetation at Nara Valley and low …on values. At Bushman's Circle this zone was …mpacted and supported a fairly dense stand of …n consisting of two species. The eastern dune …s not sampled at Nara Valley as the study area … extend this far. At Bushman's Circle this zone …ilar to the western dune base, with high plant … and cover.

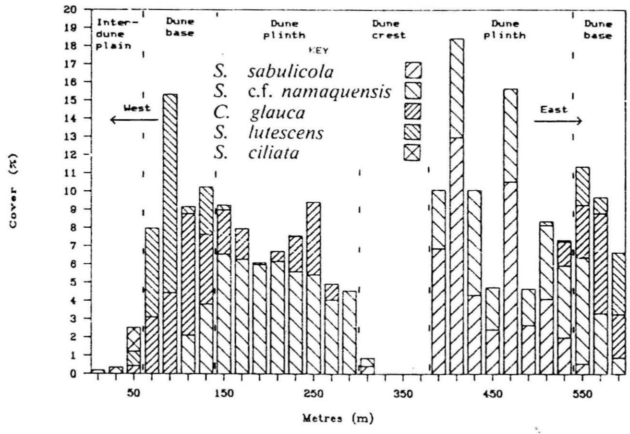



FIGURE 8: Crown cover of the perennial plant species in thirty transects, each 20 m wide, at Bushman's Circle study site.

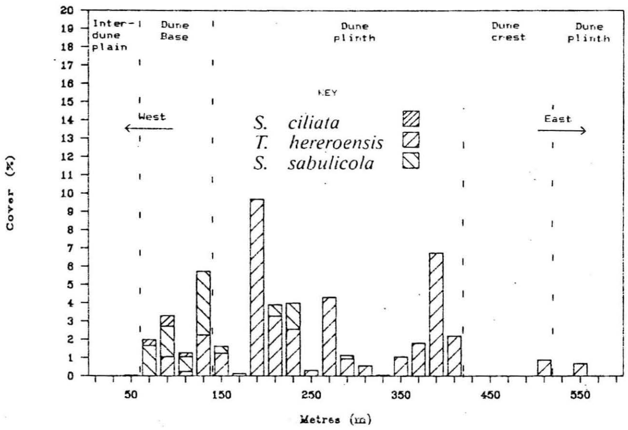



FIGURE 9: Crown cover of the perennial plant species in thirty transects, each 20 m wide, at the Nara Valley study site.

## DISCUSSION

Robinson (1976) and Yeaton (1988) made the generalization that plant species diversity and density increase from west to east in the Namib. Intuitively this seems reasonable and as the eastern most site, Far East, falls within a higher rainfall isohyet than Bushman's Circle and Nara Valley, Far East should have the highest plant species diversity and cover values. However, the plant community at Bushman's Circle had the highest species diversity index of the three sites, although the ?? total number of species occurring at Far East was greater than at the other sites. The plant cover values of Far East and Bushman's Circle were similar. The higher diversity index at Bushman's Circle may be a result of the reduced number of habitat types at Far East, where the dunes are smaller, and the upper and lower habitat zones, the dune slipface and the dune bases, are reduced or absent. Yeaton (1988) suggests that *S. ciliata* occupies a broader niche at Far East than at the other sites, thus compressing the species of the middle and upper dune into the upper dune zones.

Several authors have indicated a similarity of biota on each side of linear dunes, both in the Namib (Robinson & Seely 1980) and other deserts (Leistner 1967; Zohary 1973). The quantitative measurements of the present study show that although many of the zones

TABLE 6: Plant density, cover, coefficient of variation of cover (CV) and biomass of zones at Nara Valley.

| Zone | Plant species present | Species Diversity | Density No./ha | Cover % | CV % |
|---|---|---|---|---|---|
| Western interdune plain | *Stipagrostis ciliata* | | 139 | Trace | 173 |
| | Total | 1,00 | | Trace | |
| Western dune base | *S. ciliata* | | 675 | 0,3 | 71 |
| | *S. sabulicola* | | 46 | 0,9 | 86 |
| | *Trianthema hereroensis* | | 92 | 1,9 | 30 |
| | Total | 2,11 | | 3,1 | |
| Western dune plinth | *S. sabulicola* | | 121 | 2,5 | 61 |
| | *T. hereroensis* | | 14 | 0,2 | 179 |
| | Total | 1,15 | | 2,7 | |
| Dune crest | *S. sabulicola* | | 8 | 0,2 | 223 |
| | Total | 1,00 | | 0,2 | |
| Eastern dune plinth | *S. sabulicola* | | 29 | 0,2 | 200 |
| | Total | 1,00 | | 0,2 | |

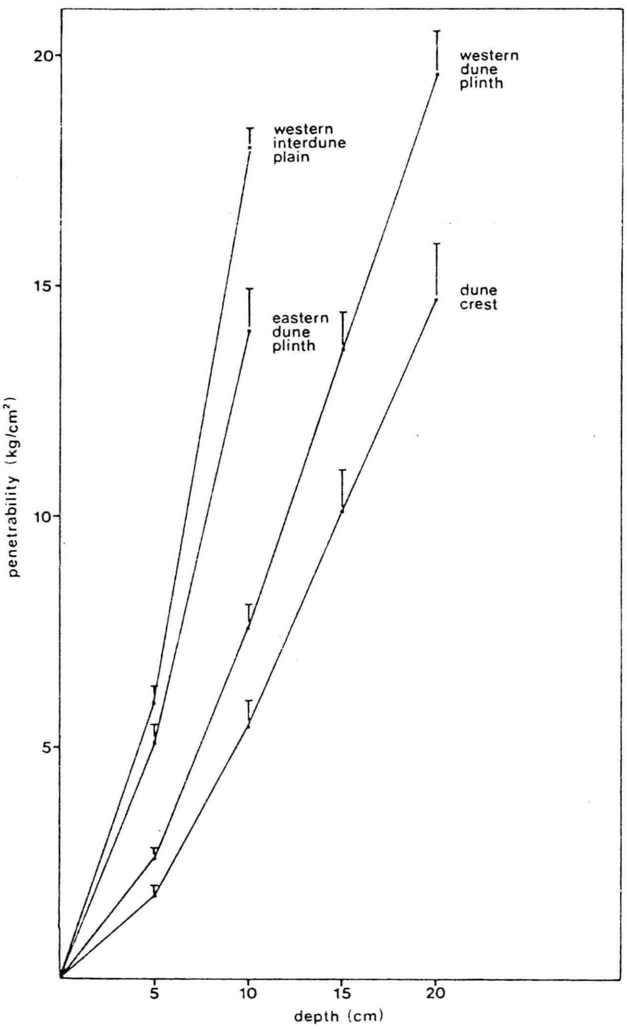



FIGURE 4: Mean substrate compaction, with standard errors indicated, at different depths in four zones at Far East.

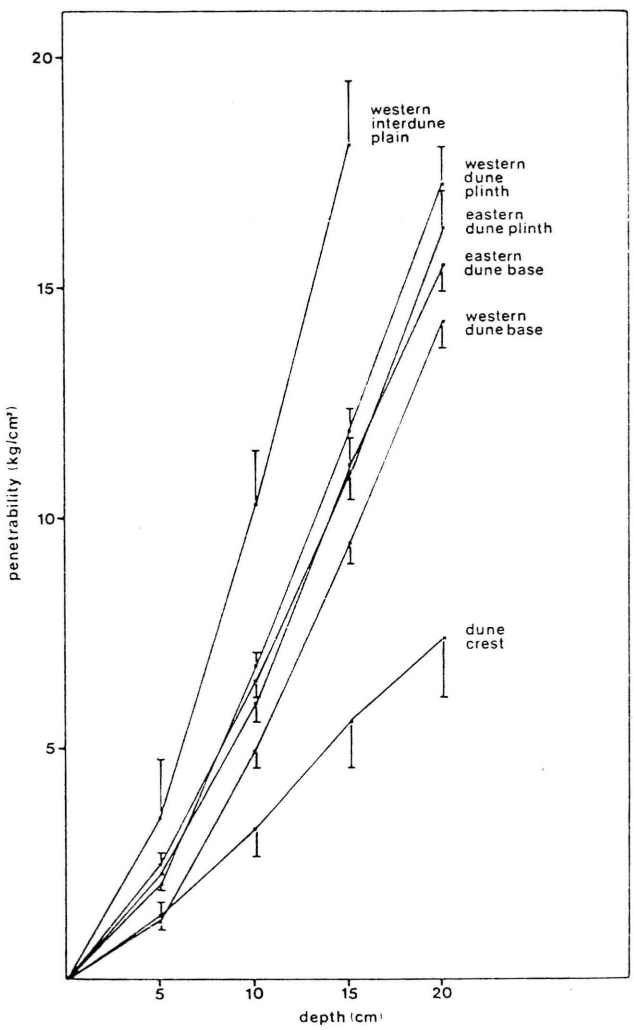



FIGURE 5: Mean substrate compaction, with standard errors indicated, at different depths in six zones at Bushman's Circle. The standard error for the eastern dune base zone at 5 cm depth (omitted from figure) was ± 0,3.

have similar vegetation in the Namib, regardless of whether they are situated on the eastern or western aspect of the dune, they are not the same. They differ, not only in the amount of vegetation, but also in the species which occur there.

The plant communities of dunes near to Gobabeb described by Robinson and Seely (1980) contained most of the species reported in this study (*i.e. C. glauca, S. ciliata, S. lutescens, S. sabulicola,* and *T. hereroensis*). The values reported in the present study confirm Robinson and Seely's (1980) qualitative observations of a vertical stratification of the dune plant community into a series of distinct biotic zones.

Yeaton (1988) has shown a negative logarithmic relationship between sand movement and plant basal cover. Windspeed is correlated to the vertical height of the dune above the surrounding plain (Lancaster 1983), therefore it is not surprising that plant cover is less in the upper zones than in those lower on the dune. Decreasing soil water potential differences in the lower zones may also be important in determining the plant density stratification, as well as species diversity, of the dune (Yeaton 1988).

Sub-surface compaction rates formed a decreasing gradient from the interdune valley to the dune crest at all three sites. Yeaton (1988) reports that surface compaction decreases with dune height at Far East, but is greater in the mid-dune region of Nara Valley than at the dune base. The present study indicates that all dune slope compaction values are similar to a depth of 5 cm at Nara Valley, thereafter the lower zone, the dune base, has greater compaction values than the upper dune zones.

The interdune substrate at Far East had different physical characteristics to that at Bushman's Circle and Nara Valley. The substrate was a compacted, relatively deep (precise depth unknown) layer of coarse sand. At Bushman's Circle and Nara Valley the interdune plains consisted of sandstone with a thin covering of sand and small pebbles (Scholz 1972; pers. obs.). Low rainfall and the lack of a deep 'moisture retaining' substrate on the interdune plains at Bushman's Circle and Nara Valley probably resulted in the vegetationless character of these areas compared to Far East.

Zohary (1973) reported a similar lack of vegetation on the stony substrates of the Middle Eastern deserts for similar amounts of precipitation. He suggested that sand can store water for long periods of time, so ameliorating drought conditions which may restrict or prevent plant growth on other substrates.

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