*Journal of Ecology* (1988), **76,** 744–758

# STRUCTURE AND FUNCTION OF THE NAMIB DUNE GRASSLANDS: CHARACTERISTICS OF THE ENVIRONMENTAL GRADIENTS AND SPECIES DISTRIBUTIONS

R. I. YEATON*

*Desert Ecological Research Unit, P.O. Box 1592, Swakopmund 9000, South West Africa/Namibia*

## SUMMARY

(1) Associations of perennial grasses on dune slopes in the Namib Desert were studied across a complex environmental gradient from the Atlantic Ocean (west) to the base of the Great Escarpment of Africa (east).

(2) The number of storms with measurable precipitation increased from the sea inland. In contrast, the rate of sand movement decreased from the west to the east.

(3) The standing crop of the perennial grasses and the rate at which *Stipagrostis sabulicola*, a species found across the dune fields, recharged its xylem water potentials increased inland as a result of the former gradient of increasing rainfall.

(4) Complex environmental gradients also occurred over each dune slope. The rate of sand movement increased from the edge of the inter-dune valley to the top of the dune. However, the moisture gradient was more complex and is poorly understood. There appears to be interflow of soil moisture within the dune such that the upper dune is drier than the mid-dune. At the base of the dune, there is a reduction of soil moisture due either to increased compaction of the sand and subsequent increased surface run-off or, as a result of the closeness of the hard inter-dune substratum, to a smaller sand volume from which roots can extract water.

(5) In consequence, the average standing crops for perennial grasses are greatest in the central portions of the dune slope across the dune fields.

(6) These geographical and local environmental gradients influence the number of species of perennial grasses found forming associations across the dune fields as well as their growth strategies and distributions over a dune slope.

(7) The number of perennial grass species forming associations increases from a single species in the western dunes to four species in the east. Species establishing predominantly from rhizomes are found where rates of sand movement are highest (i.e. in the western dunes and on the upper sections of the dune slope). In contrast, species establishing predominantly from seed are found in the easternmost dunes and at the bases of the dune slopes.

(8) There is an inverse correlation between density of the vegetation and the rate of sand movement. Thus, the ultimate factor controlling the stabilization of these dunes and the dynamics of these grasslands is the amount of rainfall which, in turn, determines the establishment of new individuals from seed.

## INTRODUCTION

The sand dunes of the Namib Desert support from one to several species of perennial grasses. The most diverse and dense coverage of these grasses occurs on the sides of dunes in the easternmost section of the dune fields where rainfall is relatively high. Towards the

* Present address: Department of Botany, University of Venda, P/Bag X2220, Sibasa, Venda, South Africa.

# DEMOGRAPHICS NAME & ADDRESS LIST (COLUMN)

**Combating Desertification**

Printed on Wed 10 April 02 at 14:29:21

---

**ABISOYE, Dr V.**

Tropical Forest Network
P.O. Box 38471
Dugbe
IBADAN 20001
NIGERIA
Telephone (Work): 09234712628
Fax: 092348109051
E-Mail: tfnnigeria95@yahoo.co.uk

**ABRAHAMS, Miss Natasha**

Student
University Of Western Cape
Botany Department
Private Bag X17
BELLVILLE 7535
Telephone (Work): 9593783
Fax: 9592266
E-Mail: nabrahams@uwc.ac.za

**ADESANYA, Mr Adekunle**

Alaaka Community Development Association
P O Box 27040
Agodi Post Office
IBADAN 200003
NIGERIA
Telephone (Work): 0923422410842
Fax: 0923422318400
E-Mail: prince2002t@onebox.com

**ADEYEMI, Prince**

Alaaka Community Development Association
P O Box 27040
Agodi Post Office
IBADAN 200003
NIGERIA
Telephone (Work): 0923422410842
Fax: 0923422318400
E-Mail: prince2002t@onebox.com

**ADISA-BALOGUN, Mrs I. A.**

Tropical Forest Network
P.O. Box 38471
Dugbe
IBADAN 20001
NIGERIA
Telephone (Work): 09234712628
Fax: 092348109051
E-Mail: tfnnigeria95@yahoo.co.uk

**AHMADI, Dr Hassan**

University Of Tehran / Iran Desert Research Center
P O Box 14185/354
TEHRAN 37585-4314
IRAN
Telephone (Work): 09982612223044
Fax: 09982612227765
E-Mail: ghzehtab@chamran.ut.ac.ir

**AJARU, Mr Ali Alias**

Mili Mil Paresh
Kuja
Amuria Country
KATAKWI DISTRIK
UGANDA
Telephone (Work): 092564132004
Fax: 0925641321010
E-Mail: smuwaya@yahoo.com

**ALEX, Mr Lwakuba**

M A A I F
P O Box 102
ENTEBBE
UGANDA
Telephone (Work): 0925641320004
Fax: 0925641321010
E-Mail: smuwaya@yahoo.com

**ALLSOPP, Dr Nickey**

University Of The Western Cape / Botany Department
ARC - Range & Forage Department
Private Bag X17
BELLVILLE 7535
Telephone (Work): 9593373
Fax: 9591376
E-Mail: nallsopp@uwc.ac.za

**ALOJO, Mr Lawrence**

Alaaka Community Development Association
P O Box 27040
Agodi Post Office
IBADAN 200003
NIGERIA
Telephone (Work): 0923422410842
Fax: 0923422318400
E-Mail: prince2002t@onebox.com

**AMAAMBO, Otillie**

D R F N
P O Box 1228
Ondangwa
OSHANA REGION
NAMIBIA
Telephone (Work): 0926465221854

**AMOS, Mr D.G.**

Tropical Forest Network
P.O. Box 38471
Dugbe
IBADAN 20001
NIGERIA
Telephone (Work): 09234712628
Fax: 092348109051
E-Mail: tfnnigeria95@yahoo.co.uk

lower rainfall areas in the west, the grasses decrease rapidly in their densities and species composition. The grasses constituting these assemblages are indigenous species, which have had the opportunity to interact with each other and evolve as natural associations, unlike species in many present-day grasslands (Biswell 1956; Fowler & Antonovics 1981). In addition, these grasslands are relatively simple in structure. Low rainfall restricts the successional patterns normally associated with sand dunes (Cowles 1899; Salisbury 1952; Moll 1972; Weisser 1978) to the grass stages only, so that the effects of woody plants on grasses is rarely a problem (Gause 1934; Ward & Cleghorn 1964; Strang 1969; Tiedemann & Klemmedson 1973). Furthermore, because the Namib dune fields are so great in area, extending as much as 140 km inland, sea spray and its accompanying salt and nutrient inputs, which often affect the germination and establishment of many coastal dune species (Oosting & Billings 1942; Ranwell 1958; Seneca 1972) are also not important in the organization of these grasslands. Finally, the huge extent of the Namib Desert dune fields covers a long, complex environmental gradient in comparison with inland dune systems much smaller in area (Chadwick & Dalke 1965; Wood *et al.* 1978; Barnes & Harrison 1982). Thus, several different combinations of perennial grasses may be found forming associations in the Namib Desert over such environmental gradients, and comparison of these associations can elucidate the factors affecting the structure and dynamics of grasslands generally.

This study describes the general characteristics of local and geographical environmental gradients and the structure of four perennial grassland associations occurring on the sides of dunes over the east–west rainfall gradient in the south-central Namib Desert.

## STUDY AREAS

Four primary study areas and one subsidiary study area were established on the west-facing sides of linear sand dunes in the south-central Namib Desert. The primary study areas were located at Nara Valley (23° 35′ S, 15° 00′ E), 48 km from the sea; at Noctivaga (23° 39′ S, 15° 9′ E), 75 km inland; at Bushman's Circles (23° 45′ S, 15° 30′ E) 88 km inland; and at the Far East Dune (23° 45′ S, 15° 30′ E), 128 km inland at the base of the Great Escarpment. The subsidiary study area is located at Visitor's Dune, adjacent to Gobabeb (23° 34′ S, 15° 03′ E) and 58 km inland on the Kuiseb River. These five sites were used to characterize abiotic factors and their changes across the east–west environmental gradient.

General characteristics of this section of the Namib Desert and of a sand dune are given in Seely (1978a) and Robinson & Seely (1980). Few weather records exist for four of these five study areas. Visitor's Dune is adjacent to Gobabeb, which is the site of a weather station, and for which some records exist and are summarized (Seely & Stuart 1976). Annual precipitation for selected sites are 13 mm for Swakopmund on the coast, 25 mm for Gobabeb, 58 km inland, and 87 mm for Ganab, 112 km inland and near the base of the Great Escarpment (Nieman, Heyns & Seely 1978; Lancaster, Lancaster & Seely 1984). These records are based on the period 1967–74 for Swakopmund, 1962–81 for Gobabeb, and 1967–81 for Ganab.

One or more species of perennial grasses were present at each of these study areas. *Stipagrostis sabulicola* Pilg., a large mound-building species with a multiple branched and vigorous rhizome, is the only perennial grass species present at Nara Valley and at Visitor's Dune on the dune slopes. This species also occurs on the upper dune slopes of all the other study areas to the east. Towards the east, two species are added at the Noctivaga

**WARD, Viv**
D R F N
NAMIBIA

**WEIK, Mr Jörg**
G T Z
P. O Box
AMMAN 11118
JORDAN
Telephone (Work): 092625359726
Fax: 096265156457
E-Mail: jweik@go.com.jo

**WEISS, Mr Eckehard**
G T Z
P O Box 5180
ESCHBORN 65726
GERMANY
Telephone (Work): 09496196791912
E-Mail: eckehard.weiss@gtz.de

**WERNER, Wolfgang**
D R F N
NAMIBIA

**WILCKE, Mrs Angelika**
Entwicklung And Laendlicher Raum/Agriculture And Rural
Eschborner Landstrasse 122
FRANKFURT 60489
GERMANY
Telephone (Work): 09496924788465
Fax: 09496924788481
E-Mail: A.Wilcke@DLG-Frankfurt.de

**WOEHL, Dr Helmut**
D R F N
GERMANY

**WOLF, Katherine**
D R F N
NAMIBIA
E-Mail: katherinew@drfn.org.na

**ZEHTABIAN, Dr Gholam Reza**
Associate Professor
University Of Tehran
P O Box 14185/354
Natural Resources College Of Tehran University
KARAJ 31585/4314
IRAN
Telephone (Work): 0998261222044
Fax: 0998261222765
E-Mail: ghzehtab@chamran.ut.ac.ir

**ZVINGADZA, Mr Sherpard**
Zero Regional Environment Organization
P O Box 5338
HARARE
ZIMBABWE
Telephone (Work): 09263791333
Fax: 09263791333
E-Mail: zero@mweb.co.zw

study area, *Stipagrostis* cf. *namaquensis* (Nees) Trin. & Rupr., a shrubby species with a long, creeping rhizome, and *Centropodium glaucum* Nees, a tufted grass with a stout, woody rhizome. These three species plus *Stipagrostis lutescens* (Nees) Trin. & Rupr. comprise the association over the dune slope at Bushman's Circles. The latter species is similar in growth form to *S. sabulicola* and *S.* cf. *namaquensis* but is more compact. Four species comprise the perennial grassland association on the Far East Dune as well. However, some major changes in species composition are observed. *Stipagrostis sabulicola* and *S. lutescens* are present still but *S.* cf. *namaquensis* and *C. glauca* are replaced by *Cladoraphia spinosa* (L.f.) Trin., a species with hard, spiny, bushy tufts, and *Stipagrostis ciliata* Desf., a densely tufted grass which covers the inter-dune valleys in this area and extends far up the dune slope as well. Some woody plant species are also found on these dune slopes, but usually at very low densities. These are notably *Trianthema hereroensis* Schinz in the western dunes and *Hermannia minimifolia* M. Holzhammer and *Kohautia ramosissima* Bremek. in the wetter eastern dunes. Finally, after relatively heavy rains, annual species of grasses and forbs are found on the dune slopes, increasing in their species richness from the western to the eastern dunes.

## METHODS

### *Measurement of local and geographic environmental gradients*

Several factors which might affect the west-facing slopes of sand dunes were studied directly or indirectly over the east–west environmental gradient. These factors are rainfall, the pattern of soil moisture distribution over a dune slope after rain, the rate of sand movement and the compactness of the sand. In addition, biotic assays of local and geographic patterns in soil moisture were obtained.

The gradient for rainfall was inferred by regressing the number of storms with measurable precipitation ($>2$ mm) recorded during 1980–82 against the distances that the rain gauges were located from the sea inland to the base of the Great Escarpment (data from Lancaster, Lancaster & Seely 1984).

Soil moisture availability over the Far East dune slope was measured on 20 April 1983, ten days after rains had passed over the area. Five small pits, spaced 1 m apart along the contour of the dune slope, were dug at 30-m intervals up the dune slope and the depth to the wet sand zone measured. These measurements were repeated on 22 April 1983 and 13 May 1983. Mean values and their standard errors were calculated for each zone on the dune slope and for each day that data were collected. In addition, sand samples were taken on 21 April 1983 from the 30-m and 120-m levels on the dune slope for gravimetric determination of water content. Ten replicate samples, at 2 cm below the surface, in the upper, middle and lower portions of the wet sand, and at a point below the wet sand, were taken in each of these two zones. Student's $t$-tests, using arcsin transformations (Steel & Torrie 1960), were used to determine differences in soil-water content within and between sand-levels in these two zones of the dune slope.

The slope angles for a series of 30-m contiguous line transects, from the edge of the inter-dune valley to the top of the dune, were measured with an inclinometer and then plotted to determine the shape of each dune. Rates of sand movement were measured at monthly intervals from October 1983 to June 1984 for five dunes over the geographic gradient. On each dune five sets of ten poles each were placed in the sand. The sets of poles were not located randomly but were placed at the slipface, in the major vegetation zones down the dune slope, and on the fringing edge of the inter-dune valley. The poles in each set were placed in two rows of five, the rows 5 m apart and the poles in each row at 5-m intervals as well. Sand movement for a pole was measured as the distance from the top of the pole to the sand level at its base and relative to that from the measurements made in the previous month. The absolute rate of sand movement (i.e. sign of difference ignored) was calculated for each set of poles on the dune slope. Poles that were lost by either burial or sand deflation were replaced and new baseline measurements made. Hence, in some months fewer than ten poles were included in the average. As a result the rates of sand movement are underestimated for the upper sets of poles where sand instability is the greatest. Mean values and their standard errors for the eight months in which measurements were taken were calculated for each set of poles on each dune. Comparisons of sand movement between the base and top of each dune and within these zones between adjacent study areas over the east–west gradient were made. A $t$-test was applied to a logarithmic transformation of the average daily rate of sand movement recorded over the eight-month period for each of the ten poles in a set.

Soil compactness was measured at Nara Valley and Far East Dunes using a hand penetrometer modified for use in sand by the addition of a disc, 10 mm in diameter, at its point. The measurements were taken at 30-m intervals from the edge of the inter-dune valley to the top of the dune. Means and standard errors were obtained for each set of measurements made over the dune slope. These data were treated statistically with a Mann–Whitney $U$-test (Siegel 1956). Points at the base of the dune (0 m) were compared with the middle (150 m) and the middle with the top (300 m) over a dune and for similar points between the two dunes.

To characterize further the east–west environmental gradient and the local environmental gradient occurring over the dune slope, several biotic assays were made. Daily patterns of xylem water potentials were measured for *Stipagrostis sabulicola* at Nara Valley, Noctivaga and Far East Dunes in the same one-week period (11–18 April, 1984) using a Scholander-type pressure chamber (Ritchie & Hinckley 1975). At each site the xylem water potentials for one stem from each of five individuals were measured hourly over the daylight hours and until midnight. Thereafter, samples were taken at 02.00 h and the sequence begun again at 06.00 h. Due to logistic problems the full 24-hour series could not be obtained at Noctivaga Dune; however, the important inflection points of the daily pattern were monitored. Measurements were also made of ambient air temperatures at the same time. These values were then regressed against xylem water potentials. A strong negative linear relationship was observed between temperature and mean xylem water potential. As a result, the regression coefficients for these relationships were compared statistically between adjacent study areas over the east–west gradient. These measurements yield a bioassay of the east–west environmental gradient as a function of moisture availability in the dune. On a local scale, xylem water potentials for *S.* cf. *namaquensis*, a species with a wide distribution over the dune slope, were measured at the upper and lower parts of its range at Bushman's Circles Dune. The latter bioassay gives an indication of soil-moisture availability in the mid-dune slope region. *Stipagrostis ciliata* at the Far East Dune was studied to determine the pattern of soil moisture availability on the lower dune slope. This species ranges from the mid-dune slope area into the inter-dune valley. One hundred individuals each in the upper, middle and lower portions of its range over the dune slope were selected randomly and the number of individuals with green stems recorded. Results were treated in a $2\times3$ contingency table.

**PAXTON, Ms Midori**
U N D P
WINDHOEK
NAMIBIA
Telephone (Work): 09264612046232
Fax: 09264612046203
E-Mail: midori.paxton@undp.org

**PELLANT, Mr Mike**
Bureau Of Land Management
1687 S. Vinnell Way
Boise
IDAHO 83709
USA
Telephone (Work): 0912083733823
Fax: 0912083733805
E-Mail: mike_pellant@blm.gov

**PENNY, Ms Roben**
D R F N
Woodbine
Essex Road
KALK BAY
Telephone (Work): 7881285
E-Mail: robenpen@jaywalk.com

**PHILANDER, Angy**
D R F N

**PRINZ, Aubrey**
D R F N
NAMIBIA

**RAJI, Dr B. A.**
Ahmadu Bello University
Department Of Soil Science
Faculty Of Agriculture/Institute For Agricultural Research
P.M.B. 1044
ZARIA 0023469
NIGERIA
Telephone (Work): 0923469551607
E-Mail: cndciar@inet-global.com

**RETHMAN, Dr Norman**
University Of Pretoria
Department Of Plant Production And Soil Sciences
PRETORIA 0002
Telephone (Work): 0124203225
Fax: 0124204120
E-Mail: nrethman@postino.up.ac.za

**ROGGE, Jo**
D R F N
NAMIBIA

**SAIDE, Mr Eusebio**
Coterra
Rua Henrique De Sousa
No 45.
MOPUTO
MOZAMBIQUE
Telephone (Work): 092581308866
Fax: 092581308866
E-Mail: eusibio2001@yahoo.com

**SALOMO, Mr C A**
D R F N

**SASS, Ms M**
D R F N

**SCHLYTER, Dr Peter**
Stockholm University
Se-10691
STOCKHOLM
SWEDEN
Telephone (Work): 094686747822
E-Mail: peter.schlyter@natueo.su.se

**SECK, Dr Emmanuel**
Endatm
B P 3370, 54 Rue Carnot Dakar
DAKAR
SENEGAL
Telephone (Work): 092218222496
Fax: 092218217495
E-Mail: energy2@enda.sn

**SEELY, Dr Mary**
D R F N
P O BOX 20232
WINDHOEK
NAMIBIA
Telephone (Work): 0926461229855
Fax: 0926461230172
E-Mail: mseely@drfn.org.na

**SHIKONGO, Mr Sem**
No Info At This Stage
NAMIBIA

**SHOKO, Mr Mzondiwa**
P O Box Cy385
Causeway
HARARA
ZIMBABWE
Telephone (Work): 092634705671
Fax: 092634793123
E-Mail: zpn143@mweb.co.zw

### *Measurement of species distributions*

The distribution of each species over a dune slope was measured in a series of quadrats positioned along the contours of the dune. Ten quadrats were measured in each zone, beginning along the contour 10 m from the apex and proceeding at 20-m intervals along the contours down the dune slope to the inter-dune valley. Quadrat size varied depending on the size and abundance of the perennial species present. The large but low density individuals of *Stipagrostis sabulicola* were measured in 10 m × 10 m quadrats, while the more abundant large individuals of *S. lutescens*, *S.* c.f. *namaquensis* and *Cladoraphia spinosa* were measured in 2 m × 10 m quadrats. The very abundant, small species, *S. ciliata* and *Centropodium glaucum*, were measured in 1 m × 1 m quadrats. Each individual plant covered a roughly circular area and its size was measured as the diameter of that area. When individuals were noticeably elliptical in the area covered, the long axis of the ellipse and the axis at right angles to it were measured and the average of the two taken as the size of the individual. A series of at least twenty-five individuals of each species with different diameters were harvested at sand level and their standing crops determined. Power curves were fitted to these data and the biomass of each individual present in a quadrat extrapolated from these curves. Then for each species the total biomass present in a quadrat was summed and averaged over the ten quadrats sampled at that level on the dune slope. These data were obtained for each of the four primary study areas. Species distributions over a dune slope were represented by the proportional occurrence of each species over the dune slope.

The diameters of all plants found within the area delineated by each set of poles, used to measure rate of sand movement at various points on each dune, were also obtained and converted to basal area. The basal areas were summed and the total basal area per 100 $m^2$ calculated. These values were then plotted against the average monthly rate of sand movement for that set of poles to determine if density of vegetation has any effect on rates of sand movement or vice versa.

## RESULTS

### *Local and geographic environmental gradients*

The number of storms per year with measurable precipitation increases with increasing distance from the sea (Fig. 1, $r^2=0{\cdot}69$, $P<0{\cdot}01$). The total amount of precipitation measured during the two-year period does not show any significant correlation with increasing distance from the sea.

Approximately ten days after a rainfall of unknown amount at Far East Dune, the top of the wet sand layer was very close to the surface in the upper and central sections of the duneslope and much deeper in the lower section close to the inter-dune valley (Fig. 2). Two days later the top of the wet sand layer was very close to the surface over the entire dune slope. Progressively the wet sand layer was located at greater depths over the entire dune slope, with no wet sand layer present in the uppermost section of the dune. Measurement of the water content of this wet sand layer at 30 m (lower dune slope) and at 120 m (centre of dune slope) distance from the inter-dune valley gave values ranging from 1·5% to 2·6% in contrast to the 0·4% to 0·9% range measured for the dry sand immediately above and below this zone. The distribution of this water content varied significantly along the slope with the 120 m site having significantly more moisture present in the upper portion of the wet sand layer than the centre and lower portions (upper



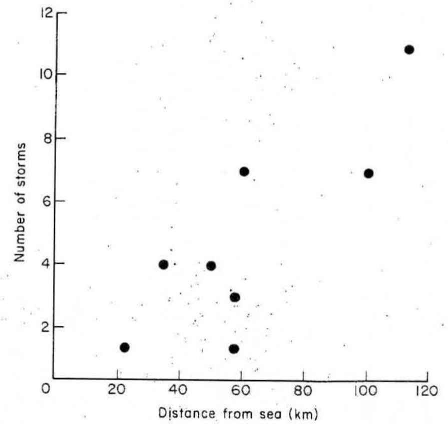


FIG. 1. Relationship between the number of storms with measurable precipitation (>2 mm) recorded during 1980–82 and the distance a rain gauge was located from the sea.

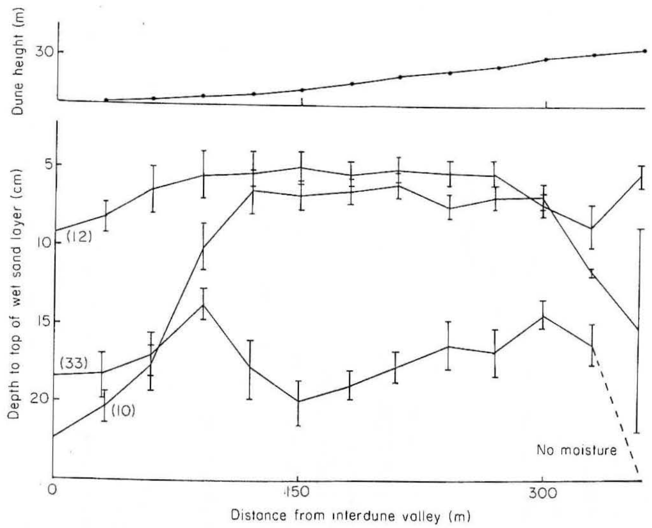


FIG. 2. Dune shape and the mean depth ($\pm 2$ S.E., $n=10$) to the top of the wet sand layer measured at intervals over the Far East dune slope, Namib Desert following the rains of 9–10 April 1983. Number in parentheses denotes days passed since rain.

**NZABONIMPA, Abdallah**
Channel Africa Radio
P O Box 91313
AUCKLAND PARK
Telephone (Work): 0117144198
Fax: 0117142424
E-Mail: nzabonimpaa@sabc.co.za

**O' FARRELL, Mr Patrick**
University Of Cape Town
24 The Avenue
WOODSTOCK 7925
Telephone (Work): 4483675
E-Mail: ofarrell@nbict.nbi.ac.za

**ODADA, Ms Catherine**
U N D P
WINDHOEK
NAMIBIA
Telephone (Work): 09264612046232
Fax: 09264612046203
E-Mail: catherine.odada@undp.org

**OETTLE, Noel**
E M G
P O Box 13378
Mowbray
CAPE TOWN 8001
Telephone (Work): 4882881
E-Mail: dryland@global.co.za

**OGUNLOLU, Mr Olufemi Adebayo**
F R S C Kwara
P O Box 2068
Sapon
ABEOKUTA OGUN 110221
NIGERIA
Telephone (Work): 0923208023076889
E-Mail: femog2001@yahoo.com

**OKPARA, Mrs C. N.**
Nigerian Concerned Group For Environment, Popuation And
57 Njiribeako Street
P O Box 3122
OWERRI
NIGERIA
Fax: 09234012610310
E-Mail: n_cogep_d@usa.net

**OKPARA, Prof Enoch**
Nigerian Environmental Study / Action Team
1 Oluokun Street
Off Awolowo Avenue
U I P O Box 22025
IBADAN
NIGERIA
E-Mail: nestnig@nest.org.ng

**OLIVER, Mrs Ian**
Karoo Desert N B G
P O Box 152
WORCESTER
Telephone (Work): 0233470785
Fax: 0233428719
E-Mail: karroid@intekom.ca.za

**ORLALE, Mr Martin**
Practical Skills Training Institute
P.O. Box 57729
NAIROBI 00100
KENYA
Telephone (Work): 09254272772360
E-Mail: pinstitute@pinfosol.com

**OUESSAR, Mr Mohamed**
Researcher
Institut Des Régions Arides (IRA)
Ira, Route De Jorf Km22.5
MÉDENINE 4119
TUNISIA
Telephone (Work): 0926165633005
Fax: 0921675633006
E-Mail: Ouessar.Mohamed@ira.rnrt.tn

**OYEBODE-ADESINA, Mr Adewale**
Timmey Nig.Ltd
P O Box 28241
IBADAN 200003
NIGERIA
Telephone (Work): 09232716548
Fax: 09232413988
E-Mail: shinedude2@yahoo.com

**PALMER, Anthony**
A R C - Range And Forest Institute
P.O. Box 101
GRAHAMSTOWN 6140
Telephone (Work): 0466222638
Fax: 0466222638
E-Mail: t.palmer@ru.ac.za

**PANDO-MORENO, Ms Marisela**
Lecturer
Universidad Autonoma De Nuevo Leon
P O Box 41
LINARES 67700
MEXICO
Telephone (Work): 095282124895
Fax: 095282124251
E-Mail: mpando55@hotmail.com

**PAUDYAL, Prof Dhanpati**
Inshured
10 New Ban Pb6218
KATHMANDU 6218
NEPAL
Telephone (Work): 099771487376
Fax: 099771487376
E-Mail: inshured@hotmail.com

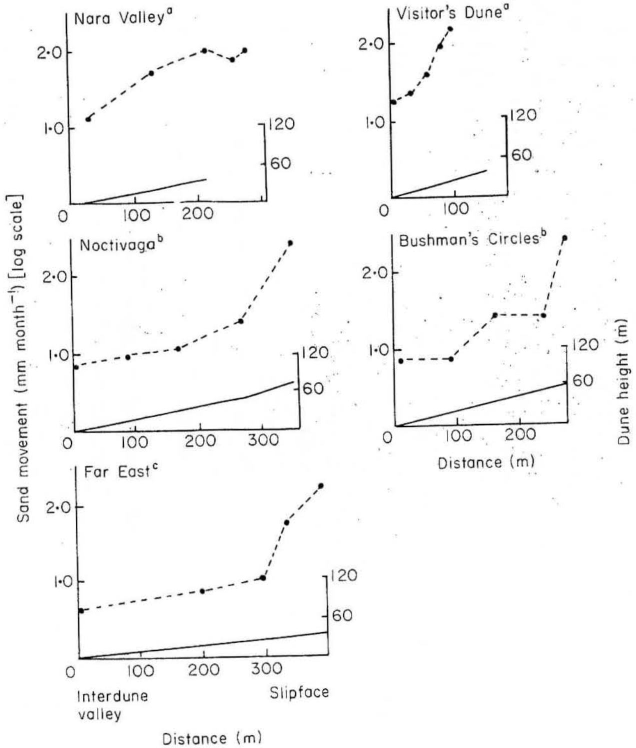


FIG. 3. Dune shape and rates of monthly sand movement over the dune slope at five study sites located along an east–west environmental gradient in the Namib Desert. Dissimilar superscripts indicate significant differences ($P<0.05$) in the rates of sand movement between dunes. Symbols: (- - - - -) rate of sand movement; (——) shape of dune.

portion of wet sand layer versus centre, $t=2.45$, d.f. $=18$, $P<0.05$; upper portion versus lower, $t=6.01$, d.f. $=18$, $P<0.001$), while the site 30 m up the dune slope from the interdune valley had significantly more moisture in the centre portion of the wet sand layer than in the upper and lower portions of this band (centre portion versus upper, $t=2.77$, d.f. $=18$, $P<0.02$; centre versus lower, $t=3.76$, d.f. $=17$, $P<0.01$). Comparison of the sand moisture content between the 120 m and 30 m sites yielded significantly more moisture in the centre and lower portions of the wet sand layer at the 30 m site (centre, $t=4.11$, d.f. $=18$, $P<0.001$; lower, $t=3.00$, d.f. $=17$, $P<0.01$) while no significant difference was found in the upper portions.

The rates of sand movement as well as the shapes of each dune are given in Fig. 3. The five dunes can be divided into three groups based on analysis of the daily rates of sand movement for each post at the base and at the top of the dune. Nara Valley and Vistor's Dune are similar in their rate of sand movement at the base and top of the dune, while



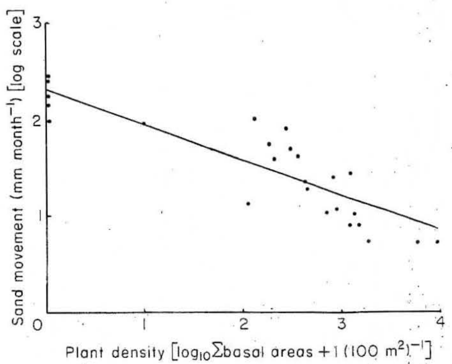


FIG. 4. Relationship between plant density and the monthly rates of sand movement along an east–west environmental gradient in the Namib Desert.

Noctivaga and Bushman's Circles are also similar but with lower rates of sand movement at the base than Nara Valley and Visitor's Dune. Far East Dune has the lowest rates of sand movement of all the sites, both at the base of the dune and at its top. A significant negative logarithmic relationship between the basal area per 100 $m^2$ of the vegetation located within each set of ten poles and the rate of sand movement was also noted (Fig. 4; $r=0.79$, $P<0.01$).

The compactness of the sand increased gradually upslope at the Far East Dune (Mann–Whitney *U*-tests, bottom versus middle, $P<0.002$; middle versus top, $P<0.002$). In contrast, sands of the middle section of the Nara Valley dune are more compacted than those at its base or at its top ($P<0.002$ for both cases). Comparisons between the Far East and Nara Valley dunes at the bottom, middle and top show no significant differences in sand compaction in the middle of the dunes but significantly greater compaction at the Far East Dune at its base and top than at Nara Valley ($P<0.002$ for both cases).

Biotic assays of the east–west environmental gradient demonstrate access to more subsurface water at sites progressively inland from Nara Valley (Fig. 5). The pattern of daily xylem water potentials for individuals of *Stipagrostis sabulicola* located in the upper sections of the dune slope across the dune fields shows more rapid recharging of the plants at the Far East Dune after sunset than is found at Nara Valley. In addition, xylem water potentials reach their lowest values at Nara Valley. Noctivaga Dune is intermediate, in its daily pattern of xylem water potentials, between Nara Valley and Far East Dune. There is a significant negative linear correlation between temperature and xylem water potential ($r$ ranges from 0·92 to 0·94, $P<0.001$) at each of the three sites (Fig. 6). Comparison among the regression coefficients shows significantly greater slopes from west to east across the dune fields (Nara Valley versus Noctivaga, $t=2.33$, d.f. $=35$, $P<0.05$; Noctivaga versus Far East, $t=3.71$, d.f. $=33$, $P<0.001$) indicating the more rapid recharging of the plants to the east. Local measurements of xylem water potentials during the heat of the day over a dune slope were made for *S.* cf. *namaquensis* in the upper and lower portions of its range at Bushman's Circles. Xylem water potentials were $-2.11$ MPa in the upper part of the dune and $-1.17$ MPa in the lower ($t=4.11$, d.f. $=8$, $P<0.01$). Finally, on the long, low-angled Far East Dune, the number of *S. ciliata* individuals with photosynthetically active

**MUSONDA, Mr Thomson C**
No Info At This Stage
LUSAKA
ZAMBIA

**MUTAMBA, Mr Emmanuel**
Team Director
Green Living Movement
P O Box 38254
LUSAKA 10101
ZAMBIA
Telephone (Work): 0926096760966
E-Mail: emutamba@yahoo.com

**MUWAYA, Mr Stephen**
M A A I F
P O Box 102
ENTEBBE
UGANDA
Telephone (Work): 0925641343696
Fax: 0925641321255
E-Mail: ccdnap@infocom.co.ug

**MWANZA, Regina**
P O Box 50266
LUSAKA
ZAMBIA

**NAKALE, Tufikifa**
D R F N
NAMIBIA

**NANGOMA, Everhart**
No Info At This Stage
BLANTYRE
MALAWI
Telephone (Work): 09266621348
Fax: 09266621022
E-Mail: umoyo@malawi.net

**NANTANGA, Komeini**
D R F N
NAMIBIA

**NAWASEB, Gabes**
D R F N
NAMIBIA

**NDITEZEUA, Mina**
D R F N
NAMIBIA

**NDJITEZEUA, Asser**
Khoadi Llhôas Conservatory
P. O Box 119
KAMANJAB
NAMIBIA
Telephone (Work): 0926467333017
Fax: 0926467333020

**NDLELA, Elmon**
Brot Für Die Welt / UNCCD Support Programme
A C A T
Eastern Cape
E-Mail: des2002@gliese.de

**NJEAZAEH, Mr Jerome Akaning**
Associated Country Women Of The World (Acww)
P. O. Box 446
BUEA 0144
CAMEROON
Telephone (Work): 092377523264
Fax: 092377523264
E-Mail: nnangela@yahoo.com

**NOMTSHONGWANA, Mr Ngcali**
D E A T
JOHANNESBURG

**NTANDO, Mr Simanga**
Yonge Nawe
Covetry Cresent
Jenden Building Office 13
MBABANE
SWAZILAND
Telephone (Work): 092684041394
Fax: 092684047710
E-Mail: btmakama@yongenawe.rg.sz

**NUPPENAU, Prof Ernst-August**
Justus-Liebig-University
Institut Fuer Agrarpolitik
Senckenbergstrasse 3
GIESSEN 35390
GERMANY
Telephone (Work): 09496419937022
Fax: 09496419937029
E-Mail: Ernst-August.Nuppenau@agrar.uni-giessen.

**NYIKA, Walter Mugove**
Zimbabwe Institute Of Permaculture - S C O P E
P O Box CY301
Causeway
HARARE
ZIMBABWE
Telephone (Work): 092634333812
Fax: 092634333811
E-Mail: scope@africaonline.co.zw

**NYIKAYARAMBA, Mr Charles Marcos**
Department Of Natural Resources
P O Box 585
MUTARE
ZIMBABWE
Telephone (Work): 092632062509
Fax: 092632067098

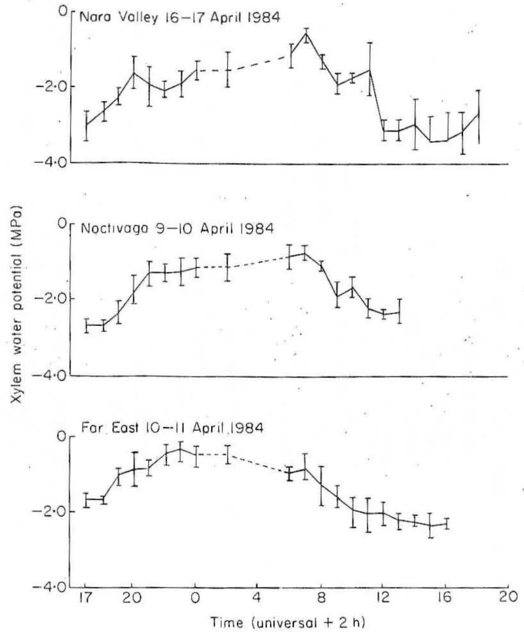


FIG. 5. The daily course of change in xylem water potentials for *Stipagrostis sabulicola* at the Far East, Noctivaga and Nara Valley dunes in the Namib Desert. Error bars indicate ±2 S.E., $n=5$.

tillers decreased from the upper portion of its range to a point adjacent to the inter-dune valley (Table 1, $\chi^2=32{\cdot}3$, $P<0{\cdot}001$).

### *Species distributions*

Allometric growth curves for the six species of grasses fitted power curves in which a constant value was multiplied by approximately the square of the plant diameter. Based upon these data the average biomass for perennial grasses was found to decrease from the eastern to the western study area (Table 2). The study areas are again grouped, as in the case of rates of sand movement, into Nara Valley and Visitor's Dunes, Noctivaga and Bushman's Circles, and the distinctive Far East Dune. Over the Far East Dune slope, the area with the greatest standing crop, above-ground biomass is low at the top of the dune, increases gradually to relatively high values at mid-dune and then decreases downslope to the inter-dune valley (Fig. 7).

The species distributions across the dune fields show an increase from one species on the westernmost dune to a maximum of four species on the two easternmost dunes (Fig. 8). *Stipagrositis sabulicola* is the only species present on the dune slope at Nara Valley and, as species are added to the associations to the east, is restricted to the upper zones of the dune slope where the rates of sand movement are greatest. The three species present at Noctivaga Dune are clearly zoned over the dune slope (Fig. 8b) with *Centropodium glaucum* at the base of the dune replaced upslope by *S.* cf. *namaquensis* at mid-dune and



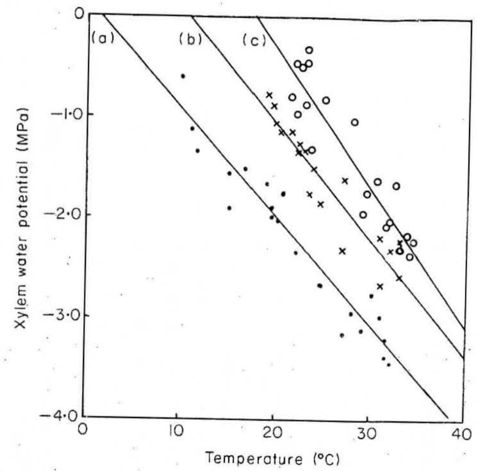


FIG. 6. Relationship between ambient temperature and xylem water potentials at (a) Nara Valley (westernmost dune studied), (b) Noctivaga (central study area) and (c) the Far East Dune (easternmost dune studied) in the Namib Desert. Symbols: ●, Nara Valley; x, Noctivaga; ○, Far East Dune.

TABLE 1. The number of individuals of *Stipagrostis ciliata* with green tillers at a point just below the *Cladoraphia spinosa* zone (upper) in the middle of the zone of distribution of *S. ciliata* (middle) and at the lower edge of the latter's distribution next to the inter-dune valley (lower) on the Far East Dune, Namib Desert.

| Zone of distribution of *S. ciliata* | Number of individuals at Far East Dune with Green tillers | No green tillers |
|---|---|---|
| Upper | 42 | 58 |
| Middle | 17 | 83 |
| Lower | 0 | 100 |

TABLE 2. Average biomass of perennial grasses occurring at a series of dune sites in the Namib Desert. The number of storms represents an extrapolation of the data from Fig. 1 for the number of storms with measurable precipitation recorded during 1980–82. $n=$ the number of zones sampled at 20-m intervals down the dune slope.

| Dune | Number of storms 1980–82 | Average biomass (g m$^{-2}$) | Standard error | $n$ |
|---|---|---|---|---|
| Nara Valley | 3·6 | 10·1 | 3·4 | 14 |
| Visitor's Dune | 4·4 | 14·9 | 5·8 | 6 |
| Noctivaga | 5·8 | 54·4 | 9·3 | 14 |
| Bushman's Circles | 6·8 | 72·9 | 9·8 | 11 |
| Far East Dune | 10·0 | 448·9 | 64·6 | 14 |

**MANSUR, Prof Shaban**
TRIPOLI
LIBYA

**MCCLURE, Mr Beaumont**
Bureau Of Land Management
222 N. Central Avenue
Phoenix
ARIZONA 85004
USA
Telephone (Work): 091602419430
Fax: 091602417998
E-Mail: beau_mcclure@blm.gov

**MHLANGA, Rose M**
No Info At This Stage
ZAMBIA

**MITCHELL, Dr David**
Wolverhampton University
School Of Applied Sciences
WOLVERHAMPTON WV11SB
UK
Telephone (Work): 091441902322173
Fax: 091441902322680
E-Mail: d.mitchell@wlv.ac.uk

**MITEMBE, William**
No Info At This Stage
LILONGWE
MALAWI
Telephone (Work): 09265771000
Fax: 09265784268
E-Mail: sadcfstu@malawi.net

**MODISAOTSILE, Mr Modisaotsile K C**
Ministry Of Agriculture
Private Bag 003
GABORONE
BOTSWANA
Telephone (Work): 0926735510
Fax: 09267307057
E-Mail: mmodisoatsile@gov.bw

**MOLAPO, Mr Jobo**
Director
S A D C Elms
MASERU
SWAZILAND

**MONTOIRO, Mr Marcos**
Associate External Relations Officer
U N C C D Secretariat
Martin Luther King Street 8
BONN
GERMANY
Telephone (Work): 09492288152806
Fax: 09492288152899
E-Mail: mmontoiro@unccd.int

**MOORE, Mr Franklin**
U S A I D
WASHINGTON
USA
Telephone (Work): 092027121863
E-Mail: fmoore@usaid.gov

**MOSER, Petra**
D R F N
NAMIBIA

**MOUAT, Dr David**
Division Of Earth And Ecosystem Sciences
Desert Research Institute
2215 Raggio Parkway
RENO NEVADA 89512
USA
Telephone (Work): 097756737042
Fax: 097756747557
E-Mail: dmouat@dri.edu

**MSANGI, Prof Josephine**
Professor And Head Of Department
University Of Namibia
Private Bag 13301
WINDHOEK 264
NAMIBIA
Telephone (Work): 0926412063383
Fax: 0926412063424
E-Mail: jpmsangi@unam.na

**MTHETHWA, Mr Doctor**
No Info At This Stage

**MUGUTI, Mr Edward Chege**
Trace(K) Network
P.O. Box 525
EMBU 254(0)161
KENYA
Telephone (Work): 0925416120120
Fax: 0925416130165
E-Mail: chegeh@yahoo.co.uk

**MUKUTE, Mutizwa**
Brot Für Die Welt / U N C C D Support Programme
PELUM
ZIMBABWE
E-Mail: des2002@gliese.de

**MULINDWA, Miss Aisha**
Rwanda Desert Awareness Organisation
B.P. 6215
KIGALI 250
RWANDA
Telephone (Work): 0925074506
Fax: 09250570188
E-Mail: aishamulinda@yahoo.com

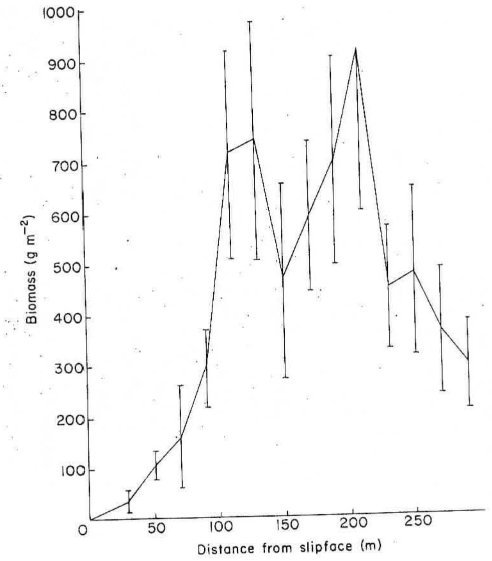


FIG. 7. Distribution of average biomass (±2 S.E., $n = 10$) over the Far East Dune slope.

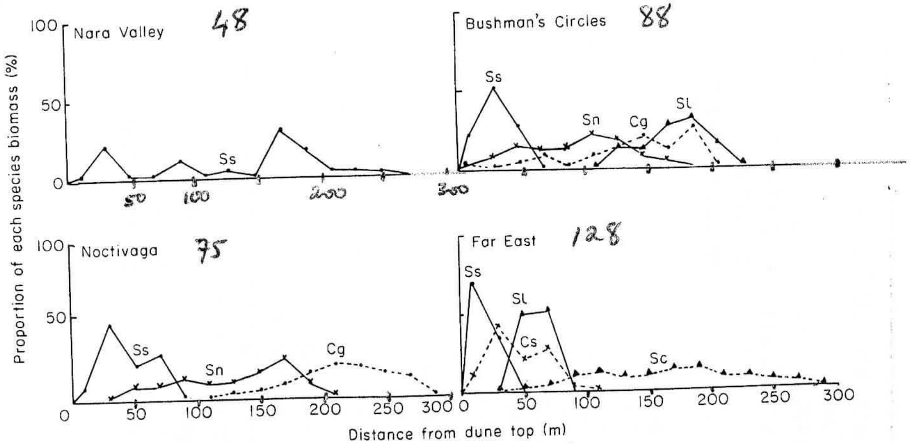


FIG. 8. Distribution of the relative biomass for each species over the dune slope at four sites in the Namib Desert. Symbols: Ss, *Stipagrostis sabulicola*; Sn, *S.* cf. *namaquensis*; Cg, *Centropodium glaucum*; Sl, *S. lutescens*; Cs, *Cladoraphia spinosa*; Sc, *S. ciliata*.



the latter replaced by *S. sabulicola* at the top. At Bushman's Circles a fourth species, *S. lutescens*, is added to the association at the base of the dune and overlaps extensively with the distribution of *C. glaucum*. Finally, *S. ciliata* covers an extensive portion of the lower and middle dune slopes at the Far East Dune, intruding from the inter-dune valley (Fig. 8d). The presence of this species compresses the distributions of the other three species forming the association to the uppermost sections of the dune where *S. lutescens* is replaced upslope by *Cladoraphia spinosa* and the latter replaced by the ubiquitous *S. sabulicola* at the very top of the dune.

## DISCUSSION

Rainfall in this region of the Namib Desert is very low (Seely 1978b) but increases towards the Great Escarpment. Due to the sporadic nature of desert rainstorms, records for precipitation show no clear pattern of increasing rainfall with increasing distance from the sea (Lancaster, Lancaster & Seely 1984). This failure is primarily due to the short period over which records have been maintained. Because a storm may pass either directly over a rain gauge or only fringe it, widely disproportionate amounts of precipitation may be recorded. This factor, coupled with the low frequency of storms in desert areas generally, will influence greatly the yearly averages obtained at a site such that they may only be representative of the actual rainfall when very long-term records are available. Thus, to illustrate this potential gradient for the Namib Desert, it was necessary to correlate the number of storms with measurable precipitation recorded over two years with distance from the sea at which the rain gauge was located, and assume that the number of storms directly reflected the amount of rain received at a site over the long term. The pattern of increasing number of storms with increasing distance from the sea, coupled with long-term data for sites on the coast and inland, indicate that a gradient of rainfall does exist. This inference is confirmed by the xylem water potentials of *Stipagrostis sabulicola* at the tops of dunes across the dune fields. These plants can recharge their tissues each night on the soil moisture stored deep within each dune. Griffin (1973) suggests that water potentials higher than −0·6 MPa indicate that oaks in the foothills of the Sierra Nevada of central California are rooted in the water table. *Stipagrotis sabulicola* has values much greater than this. Furthermore, the rate of recharge is greatest at the Far East Dune where rainfall is presumed higher and lowest at Nara Valley, the westernmost dune studied. In addition, each population monitored maintained itself at a higher water potential from west to east across the dune fields. It has been suggested that rainfall is accumulated and stored better within sand dunes than in the more compacted soils of inter-dune valleys (Chadwick & Dalke 1965; Pavlik 1980). Finally, the standing crops measured across the dune fields increase towards the east demonstrating again more establishment and growth over time from west to east as a result of increasing rainfall.

There also is a decreasing gradient in soil moisture availability on a local scale over a dune slope, at least from the middle of the dune to the top. It appears that there is redistribution of water down the dune slope after rain, even though the water content of the sand was below field capacity, a situation which Bagnold (1954) considered unlikely. In any event, the uppermost section of the dune is drier than those sections downslope. A comparison of the xylem water potentials for *S.* cf. *namaquensis* shows that water potentials are significantly lower during the heat of the day in the upper section of this species' range on the dune slope at Bushman's Circles than it is in the lower section.

**KELLNER, Prof Klaus**
Potchefstroom University For C H E
School Of Environmental Sciences And Development
POTCHEFSTROOM 2520
Telephone (Work): 0182992510
Fax: 0182992370
E-Mail: plbkk@puknet.puk.ac.za

**KHUMALO, Mr Luyanda T.**
No Info At This Stage
MBABANE
SWAZILAND
Telephone (Work): 092684043858
Fax: 092684044700
E-Mail: lups@realnet.co.sz

**KIHAULE, Mr Joseph**
No Info At This Stage
DAR ES SALAAM
TANZANIA

**KLINTENBERG, Patrik**
D R F N
NAMIBIA

**KOELLE, Ms Bettina**
Social Geographer
Indigo Development Change
P O Box 350
NIEUWOUDTVILLE 8180
Telephone (Work): 0272181148
Fax: 0272181148
E-Mail: bettina@indigo-dc.org

**KOMATI, Justine**
D R F N
NAMIBIA

**KOOTJIE, Albertus**
D R F N
NAMIBIA

**KRUGER, Bertus**
D R F N
NAMIBIA

**KRÜGER, Prof Gert**
Potchefstroom University For C H E
School Of Environmental Sciences And Development
POTCHEFSTROOM 2520
Telephone (Work): 0182992520
Fax: 0182992503
E-Mail: plbghik@puknet.puk.ac.za

**LANCASTER, Ms Judith**
Division Of Earth And Ecosystem Sciences
Desert Research Institute
2215 Raggio Parkway
RENO NEVADA 89512
USA
Telephone (Work): 097756737300
Fax: 097756747557
E-Mail: judith@dri.edu

**LERATA, Mr Thabiso**
Ministry Of Environmental, Gender And Youth Affairs (E M P R
MASERU
LESOTHO
Telephone (Work): 09266314763
Fax: 09266310506
E-Mail: natenv@ilesotho.com

**LUNGU, Bazak Zakeyo**
Brot Für Die Welt / U N C C D Support Programme
ZAMBIA
E-Mail: des2002@gliese.de

**MACHARIA, Mr Peter**
Senior Research Officer
Kenya Agricultural Research Institute / Kenya Soil Survey
P.O. Box 14733
NAIROBI
KENYA
Telephone (Work): 092542440903
Fax: 092542443376
E-Mail: kss@iconnect.co.ke

**MAJUVA, Rosaldina A C**
No Info At This Stage
DAR ES SALAAM
TANZANIA
Telephone (Work): 0925522218005
Fax: 0925522182240
E-Mail: jet@africaonline.co.tz

**MANDAKH, Miss Nyamtseren**
Institute Of Geoecology Mongolian Academy Of Sciences
Ulaanbaatar.Bruun Selbe - 13.
ULAANBAATAR
MONGOLIA
Telephone (Work): 0997697411326620
E-Mail: maaggi@yahoo.com

**MANGANDA, Ernest**
Focal Point
CONGO
E-Mail: Une adresse@yahoo.fr gratuite et en

Ambient temperatures would be strongly correlated with the saturation deficit of the air and consequently the transpiration rate. This effect is most likely the cause of the low water potentials recorded at high ambient temperatures for *S.* cf. *namaquensis* and *S. sabulicola*. In contrast, moving downslope to the inter-dune valley at the Far East dune, the population of *S. ciliata* has progressively fewer individuals with photosynthetically active tillers. The root systems of *S. ciliata* are very shallow and take up water rapidly when the upper layers of the sand are irrigated (unpublished data). Soil compactness may be important here as surface run-off is greater and infiltration lower in more compact soils (Etherington 1982). *Stipagrostis ciliata* may have less access to subsurface moisture downslope under such circumstances.

Alternatively, *S. cilata* may have a longer period over which to grow at points in its upper range when interflow is occurring from the upper dune to lower levels. Unlike the distribution of standing crop across the dune fields this variable up a dune slope is confounded by differences in growth forms between species. The only notable difference in standing crop over the Far East Dune is a reduction in the biomasses in the areas adjacent to the inter-dune valleys. Here, the volume of sand in which each grass individual can root is reduced because of the proximity of solid substrata beneath. The growth forms of grasses are restricted to those perennial species with small canopies and shallow root systems or to annual species. Furthermore, proximity of these solid substrata to the dune's surface may lead to a more rapid drainage of subsurface soil moisture (Spalding 1909) making the lower sections of dunes, with long gentle slopes and compacted sands at their base, drier towards the inter-dune valley.

The negative relationship between density of plants and rates of sand movement across the dune fields suggest that rate of sand movement is only a proximate factor in the determination of the species composition of these associations. Windspeeds are very similar across the dune fields (N. Lancaster, personal communication). Wind speeds are greatest at the tops of dunes (Salisbury 1952). As a result, species found where rates of sand movement are high are restricted to those that are best able to produce seed before burial. Because seeds are rapidly buried in areas where sand is moving rapidly (Maun 1981; Hewett 1970), these species persist in such sites by growing predominantly vegetatively (e.g. *Stipagrostis sabulicola* and *S.* cf. *namaquensis*) or by acting as an annual or biennial and reaching reproductive age rapidly. The former case is more frequently observed. Plants with rhizomatous growth are more successful at establishing in moving sands (Olson 1958; Malakouti, Lewis & Stubbendieck 1978) and their vegetative growth may be stimulated by sand deposition (Wagner 1964). Plants reproducing from seed in areas of rapidly moving sand can only do so when rainfall events are frequent. Hence, the ultimate factor in the determination of the species composition of these associations is rainfall. Persistence of species in these dune fields, particularly where rate of sand movement is low, is dependent upon the establishment of new individuals from seed. All species in this grassland produce viable seed even if they persist by vegetative growth in areas of rapidly moving sand. A single rainfall of at least 10 mm is necessary for germination of this seed (Seely 1978b). Establishment of individuals and their subsequent growth initiates a process of stablization of the dune. Mound-building by species such as *S. sabulicola* is the first step in this process. Such mound-building serves to slow the rates of sand movement as sand accumulates at the base of each individual (Grieg-Smith, Gemmell & Gimingham 1947; Willis *et al.* 1959; Gibbens *et al.* 1983). In areas of higher rainfall, such as the Far East Dune, the rate of sand movement is reduced by the frequency at which *S. ciliata* and *Cladoraphia spinosa* establish from seed on the dune slope. More sand movement on the lower slopes is recorded for those dunes to the west as a result of reduced rainfall and subsequently lower rates of seed germination and establishment. Only *Centropodium glaucum* reproduces predominantly from seed at the base of Bushman's Circles and Noctivaga dunes. Further west, at Nara Valley, most establishment of new individuals of *S. sabulicola* is by vegetative propagation as it is throughout the dune fields. The replacement of *C. spinosa* by *S.* cf. *namaquensis*, a species occupying a similar position on the dune slope below *S. sabulicola*, on Bushman's Circles Dune may be due to the lower levels of rainfall there, which limit the germination and establishment of the former species from seed and favour the establishment of *S.* cf. *namaquensis* by vegetative propagation.



## ACKNOWLEDGMENTS

I thank J. Balfour-Cunningham, S. Clark, A. Fleming, L. Fielden, E. Huebner, M. James, T. Massey, C. Vingewold and J. Waggoner for their assistance at various times in the field and M. K. Seeley for sharing her knowledge of the Namib Desert with me. Financial and administrative support were provided by the Council for Scientific and Industrial Research and by the Tranvaal Museum. Facilities and permission to work in the Namib–Naukluft Park were granted by the Division of Nature Conservation and Tourism, S.W.A.A.

## REFERENCES

**Bagnold, R. A. (1954).** *The Physics of Blown Sand and Desert Dunes.* Methuen, London.

**Barnes, P. W. & Harrison, A. T. (1982).** Species distributions and community organization in a Nebraska sandhills mixed prairie as influenced by plant/soil water relationships. *Oecologia*, **52**, 192–201.

**Biswell, H. H. (1956).** Ecology of California grasslands. *Journal of Range Management*, **9**, 19–24.

**Chadwick, H. W. & Dalke, P. (1965).** Plant succession on dune sands in Fremont County, Idaho. *Ecology*, **46**, 765–780.

**Cowles, H. C. (1899).** The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette*, **27**, 95–117.

**Etherington, J. R. (1982).** *Environment and Plant Ecology.* Wiley, Chichester.

**Fowler, N. & Antonovics, J. (1981).** Competition and coexistence in a North Carolina grassland. I. Patterns in undisturbed vegetation. *Journal of Ecology*, **69**, 825–841.

**Gause, G. F. (1934).** *The Struggle for Existence.* Williams & Wilkins, Baltimore.

**Gibbens, R. P., Tromble, J. M., Hennesay, J. T. & Cardenas, M. (1983).** Soil movement in mesquite dunelands and former grasslands of southern New Mexico from 1973 to 1980. *Journal of Range Management*, **36**, 145–148.

**Grieg-Smith, P., Gemmell, A. R. & Gimingham, C. H. (1947).** Tussock formation in *Ammophila arenaria* (L.) Link.. *New Phytologist*, **46**, 262–268.

**Griffin, J. R. (1973).** Xylem sap tension in three woodland oaks of central California. *Ecology*, **54**, 152–159.

**Hewett, D. G. (970).** The colonization of sand dunes after stabilization with marram grass (*Ammophila arenaria*). *Journal of Ecology*, **58**, 657–668.

**Lancaster, J., Lancaster, N. & Seely, M. K. (1984).** Climate of the central Namib Desert. *Madoqua*, **14**, 5–61.

**Malakouti, M. J., Lewis, D. T. & Stubbendieck, J. (1978).** Effect of grasses and soil properties on wind erosion in sand blowouts. *Journal of Range Management*, **31**, 417–420.

**Maun, M. A. (1981).** Seed germination and seedling establishment of *Calamovilfa longifolia* on Lake Huron sand dunes. *Canadian Journal of Botany*, **59**, 460–469.

**Moll, E. J. (1972).** A preliminary account of the dune communities at Pennington Park, Mtuzini, Natal. *Bothalia*, **10**, 615–626.

**Nieman, W. A., Heyns, C. & Seely, M. K. (1978).** A note on precipitation at Swakopmund. *Madoqua*, **11**, 69–73.

**Olson, J. S. (1958).** Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette*, **119**, 125–170.

**Oostins, H. J. & Billings, D. W. (1942).** Factors affecting vegetational zonation of coastal dunes. *Ecology*, **23**, 131–142.

**GUSTAFSSON, Sigi**
D R F N
NAMIBIA

**GUSTAVO, Margareth**
D R F N
NAMIBIA
Telephone (Work): 0926461229855
Fax: 0926461230172
E-Mail: margarethg@drfn.org.na

**HASSANE, Mr Moussa**
Researcher In Forestry Agroforestry
P O Box 429
INRAN
NIGER
Telephone (Work): 09227740916

**HAYWARD, Ntsiki**

**HENDRICKS, Howard**
South African National Parks
P O Box 110040
Hadison Park
KIMBERLEY 8306
Telephone (Work): 0538325488
Fax: 0538334543
E-Mail: howardl@parks.sa.za

**HESSELMAN, Mr H**

**HOFFMAN, Prof Timm**
Institute For Plant Conservation
U C T
RONDEBOSCH
Telephone (Work): 6502440
Fax: 6504046
E-Mail: thoffman@botzoo.uct.ac.za

**HUONGO, Mr Abias**
J E A
ANGOLA
Telephone (Work): 0924423969547
E-Mail: jea@angola.com

**JAFARI, Dr Mohammad**
Associate Professor
University Of Tehran
P O Box 14185/354
Natural Resources College Of Tehran University
KARAJ 37585-4314
IRAN
Telephone (Work): 09982612223044
Fax: 09982261227765
E-Mail: mjafari@chamran.ut.ac.ir

**JAIN, Dr Kalpana**
23, Jhiniret Ki Gali
UDAIPUR 313001
INDIA
Telephone (Work): 0991294525593
Fax: 0991294529922
E-Mail: ncjain@bppl.net.in

**JONAS, Miss Zuziwe**
University Of Cape Town
47 Fumana Street Harare
Khayelitsha
CAPE TOWN 8000
E-Mail: zjonas@botzoo

**KALENGA, Mrs Lahja**
D R F N
P. O. Box 175
Oshakati
OSHAKATI 9000
NAMIBIA
Telephone (Work): 0926465221854

**KALENTA,**
D R F N
NAMIBIA

**KALLIPA, Mrs Wandile**
Channel Africa Radio
P O Box 91313
AUCKLAND PARK
Telephone (Work): 0117143759
Fax: 0117144959
E-Mail: kallipaw@channelafrica.org

**KANOUTE, Mr Salif**
S T P / C I G Q E
B P 2357
BAMAKO
MALI
Telephone (Work): 09223231074
Fax: 09223235867

**KARIMPOOR REIHAN, Dr Majid**
Tehran University
Iran Desert Research Center
TEHRAN 31585
IRAN
Telephone (Work): 0998218958448
Fax: 0998218965287
E-Mail: karimpoor@chamran.ut.ac.ir

**KASUSYA, Mr Pius**
Resource Projects Kenya
P O Box 59411
NAIROBI
KENYA
Telephone (Work): 092542890595
Fax: 092542890592
E-Mail: iagi.rp@africaonline.co.ke

**Pavlik, B. M. (1980).** Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. *Oecologia*, **46**, 147–154.

**Ranwell, D. (1958).** Newborough Warren, Anglesey. I. The dune system and dune slack habitat. *Journal of Ecology*, **47**, 571–601.

**Ritchie, G. A. & Hinckley, T. M. (1975).** The pressure chamber as an instrument for ecological research. *Advances in Ecological Research*, **9**, 166–254.

**Robinson, M. D. & Seely, M. K. (1980).** Physical and biotic environments of the southern Namib dune ecosystem. *Journal of Arid Environments*, **3**, 183–203.

**Salisbury, E. J. (1952).** *Downs and Dunes. Their Plant Life and Its Environment*. Bell, London.

**Seely, M. K. (1978a).** The Namib Dune Desert: an unusual ecosystem. *Journal of Arid Environments*, **1**, 117–128.

**Seely, M. K. (1978b).** Grassland productivity: the desert end of the curve. *South African Journal of Science*, **74**, 295–297.

**Seely, M. K. & Stuart, P. (1976).** Namib climate. 2. The climate of Gobabeb; ten year summary 1962–1972. *Namib Bulletin*, **1**, 7–9.

**Seneca, E. D. (1972).** Seedling response to salinity in four dune grasses from the outer banks of North Carolina. *Ecology*, **53**, 465–471.

**Siegel, S. (1956).** *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.

**Spalding, V. M. (1909).** *Distribution and Movements of Desert Plants*. Publication of the Carnegie Institution, **113**. Carnegie Institution, Washington, D.C.

**Steel, R. G. D. & Torrie, J. H. (1960).** *Principles and Procedures of Statistics*. McGraw-Hill, New York.

**Strang, R. M. (1969).** Soil moisture relations under grassveld and under woodland in the Rhodesian highveld. *Commonwealth Forestry Review*, **48**, 26–40.

**Tiedemann, A. R. & Klemmedson, J. O. (1973).** Effect of mesquite on physical and chemical properties of all the soil. *Journal of Range Management*, **26**, 27–29.

**Wagner, R. H. (1964).** The ecology of *Uniola paniculata* in the dune-strand habitat of North Carolina. *Ecological Monographs*, **34**, 79–96.

**Ward, H. F. & Cleghorn, W. B. (1964).** The effects of ring-barking trees in *Brachystegia* woodland on the yield of veld grasses. *Rhodesia Agricultural Journal*, **61**, 98–107.

**Weisser, P. J. (1978).** Changes in area of grasslands on the dunes between Richard's Bay and the Mfolozi River, 1937 to 1974. *Proceedings of the Grassland Society of Southern Africa*, **13**, 95–97.

**Willis, A. J., Folless, B. F., Hope-Simpson, J. F. & Yemm, E. W. (1959).** Braunton Burrows: the dune system and its vegetation. *Journal of Ecology*, **47**, 1–24.

**Wood, M. K., Blackburn, W., Eckert, Jr. R. & Peterson, F. (1978).** Interrelations of the physical properties of coppice dunes and vesicular dune interspace soils with grass seedling emergence. *Journal of Range Management*, **31**, 189–192.

*(Received 24 October 1986; revision received 22 June 1987)*

**DIALLO, Mr Hama Arba**
BURKINA FASO

**ELFADL, Dr Mohamed**
Forestry Research Centre
P.O. Box 7089
Soba
KHARTOUM
SUDAN
Telephone (Work): 0924911787136
E-Mail: mohamed.elfadl@helsinki.fi

**EL GAMRI, Tarig**
Researcher
Environment And Natural Resources Research Institute
P O Box 6096
People Hall
KHARTOUM
SUDAN
Telephone (Work): 0924911475153
Fax: 0924911463416
E-Mail: tarig_ncr@yahoo.com

**ESLER, Dr Karen**
University Of Stellenbosch
Private Bag X1
Matieland
STELLENBOSCH 7603
Telephone (Work): 8083063
Fax: 8083607
E-Mail: kje@sun.ac.za

**ESMAEIL ZADEH, Mr Hamid**
Tehran University
Faculty Of Natural Resources
KARAJ 31585
IRAN
Telephone (Work): 09982662232721
Fax: 09982612227765
E-Mail: hesmaely@yahoo.com

**FITTER, Dr Joern**
G T Z Office
P O Box 8016
WINDHOEK 061
NAMIBIA
Telephone (Work): 096461222447
Fax: 094661222427
E-Mail: fitter@iafrica.com.na

**FOX, Dr Dennis**
Associate Professor
C N R S
U M R Espace 6012 Cnrs
98 Blvd Ed Herriot
NICE 06800
FRANCE
Telephone (Work): 0933493375380
Fax: 0933493375430
E-Mail: fox@unice.fr

**GABES, Arnold**
D R F N
NAMIBIA

**GAMATHAM, Helen**
D R F N
NAMIBIA

**GASEB, Nickey**
D R F N
NAMIBIA

**GAUR, Dr Mahesh**
Head, Department Of Geography
S B K Government College
10/35 Chopasni Housing Board
JODHPUR 342000
INDIA
Telephone (Work): 0991291754406
Fax: 0991291438691
E-Mail: iemsd@satyam.net.in

**GEORGE, Kevin**
F O N S A G
GABORONE
BOTSWANA
Telephone (Work): 09267307506
E-Mail: fonsag@global.bw

**GLIESE, Jürgen**
Brot Für Die Welt / U N C C D Support Programme
Schifferstr 33a
FRANKFURT D-60594
GERMANY
Telephone (Work): 09496961993706
Fax: 09496961993707
E-Mail: des2002@gliese.de

**GOAGOSEB, Gabriel**
D R F N
NAMIBIA

**GOUWS, Ms Sarah**
Landscape Committee
D R F N
Postal Agency
PAULSHOEK 8221
Telephone (Work): 0275411055
Fax: 0276521356

**GURUNG, Mr Kumar**
Inshured
10 New Ban Pb6218
KATHMANDU 6218
NEPAL
Telephone (Work): 099771487376
Fax: 099771487376
E-Mail: inshured@hotmail.com