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The structure and function of the Namib Dune grasslands: species interactions

R. I. Yeaton*

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This paper describes interactions between species of perennial grasses occupying the sides of sand dunes on the eastern edge of the south-central Namib Desert. Nearest-neighbour analysis indicate that strong competitive interactions are occurring between these grasses, both intraspecifically within a vegetation zone and interspecifically where one species replaces another over the dune slope. Ratios of the diameter of the smaller individual to the distance from its neighbour showed that, for individuals of the same size, interspecific nearest-neighbours are located closer to each other on the upper dune slope than are intraspecific nearest-neighbours. Generally, species lower on the dune slope show no significant differences in these ratios unless the species are different in growth form. Irrigation resulted in changes of xylem water potentials which indicate differences in rates of water uptake, particularly between species on the upper dune slope. It is suggested that *Stipagrostis subulicola* stabilizes the shifting sand of the upper dune slope through a process of mound-building and is replaced over time by *S.* (cf.) *namaquensis*. The process is a cyclical succession as strong winds bury the mid-dune species, causing its eventual death. On the more stable sands of the lower dune slope, morphologically similar species coexist by habitat partitioning resulting in strong zonation patterns while morphologically dissimilar species coexist as a result of root zonation and differences in seasonal patterns of soil water utilization.

Introduction

One to several species of perennial grasses occur on the sides of sand dunes in the Namib Desert, with a maximum of four species forming associations in the eastern regions of the dune fields (Yeaton, 1988). The species forming these grasslands occur in relatively distinct zones. One species is associated with the unstabilized sands of the upper dune, a second with the mid-dune area where sand movement is reduced and soil moisture level higher, and a third and fourth species with the zone at the base of the dune. Here moisture availability is potentially the greatest but the subsurface sand volume from which to extract water is limited.

The objective of this paper is to describe the interactions that occur between the members of the grass community in this area and the mechanisms through which their distributional patterns are attained. Abiotic factors are important in the distribution of at least one of these species over the dune slope. *Stipagrostis sabulicola*, a large, mound-building species, can escape burial by rapid, vegetative growth in the shifting sands of the upper dune slope (Yeaton, 1988). However, where the sands are more stabilized, either due to the mound-building activities of the latter species or to slower rates of sand

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*Department of Botany and UN-FRD Unit for Plant Growth and Development, University of Natal, Pietermaritzburg 3200, South Africa.

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movement lower on the dune slope, biotic factors, such as competition and herbivory, appear to become important in the development of the zonation patterns observed. Competitive interactions may be occurring between plant species. This results in either resource partitioning, in which each species utilizes a particular zone on the dune slope more effectively than other species, or as a successional replacement of species with one species modifying the local environment and facilitating the establishment of a second species better adapted to the changed environmental conditions.

Study areas and methods

The study was conducted at two of the four primary study areas in the south-central Namib Desert described in Yeaton (1988)—Far East and Bushman's Circles dunes—and at a subsidiary site, Mniszechi's Vlei (23° 40′ S, 15° 30′ E), located 21 km east of the latter primary site in an area of star-shaped dunes. The two primary study areas each support three to four common species of perennial grasses. *Stipagrostis sabulicola* Pilg. occurs on the upper dune slopes, *Cladoraphia spinosa* (L.f.) Trin. (Far East Dune) or *S.* (cf.) *namaquensis* (Nees) Trin. & Rupr. (Bushman's Circles Dune) at midslope, and *S. ciliata* Desf. (Far East Dune) or *S. lutescens* (Nees) Trin. & Rupr. (Bushman's Circles Dune) at the dune base (Yeaton, 1988). Overlapping the distribution of *S. lutescens* at Bushman's Circles is a fourth species, *Centropodium glaucum* Nees. *Stipagrostis lutescens* is also found sporadically at Far East Dune mingled with *S. ciliata* and *Cladoraphia spinosa*. The study area at Mniszechi's Vlei is equivalent in species composition and distribution pattern to the Bushman's Circles site, but due to the heterogeneity of star-shaped dunes (Bagnold, 1954), provided multiple replications of the plant distributions found at the Bushman's Circles dune.

Stipagrostis sabulicola is a large, mound-building grass, an individual of which may occupy an area of 40–50 m^2. It has a much-branched and vigorous rhizome and usually colonizes open sites by vegetative growth. *Stipagrostis namaquensis* and *S. lutescens* are also large in size (1–3 m in diameter) and are similar in growth form to *S. sabulicola* but have less vigorous rhizomes. *Cladoraphia spinosa* replaces *S. namaquensis* to the east. The largest individuals of *C. spinosa* are similar in size and growth form to *S. namaquensis*. However, most reproduction in *C. spinosa* is from seed and not by vegetative propagation as in *S. namaquensis*. The other two species in this study, *S. ciliata* and *C. glaucum* are smaller grasses that rarely grow larger than 1 m in diameter. They are found on the lower sections of the dune slope and reproduce predominantly from seed.

Nearest-neighbour analysis

Interactions within and between the perennial grass species at the Far East and Bushman's Circles dunes were studied using nearest-neighbour analysis (Pielou, 1962). To select individuals for measurement a point on the horizon was chosen and walked towards. The size of each individual intersected during the walk was measured and its identity recorded. Most individuals covered a roughly circular area and their size was measured as the diameter of that area. When individuals were noticeably eliptical in the area covered, the long axis of the elipse and the axis at right angles to it were measured and the average of the two taken as the size of the individual. In addition, the identity and size of its nearest-neighbour and the distance between the centres of the two plants was determined. This selection process was repeated until at least 50 nearest-neighbour pairs for every possible intra- and interspecific combination were obtained. Not all combinations of species present on a dune are possible due to the abrupt replacement patterns of one species by another over the dune slope (Yeaton, 1988). The distances between nearest-neighbour individuals were regressed against the sum of the sizes of the two neighbours with a positive, linear correlation between the two variables and a slope significantly different from zero suggesting a competitive interaction (Pielou, 1962). The tolerance of one species towards another was studied using a method in which the larger of the two individuals in a nearest-neighbour pair is regarded as determining the size of the other (Yeaton & Cody, 1976). Ratios of the size of the smaller individual to the distance from its neighbour were calculated for each pair of species replacing or associating with one another over the dune slope. Each intraspecific pairing was compared with the interspecific pairing in which that species was the larger individual. Statistical comparisons of these ratios was accomplished by applying Student's *t*-test to a logarithmic transformation of these values (Steel & Torrie, 1960).

Watering experiments

Xylem water potentials were measured using a Scholander-type pressure chamber following the methodology of Ritchie & Hinckley (1975). After an initial determination of a species' xylem water potential in the heat of the day, individuals were watered with the equivalent of a 10 mm rainstorm over a 1 m^2 quadrat centred over each individual. Xylem water potentials were re-measured 1·5 h after watering and, in most cases, again the next mid-day. In some instances, where an increase (less negative) in xylem water potentials appeared to be occurring, a further series of measurements was made 2·5–3 h after watering. The basic experimental design was to water large adjacent individuals of different species in their zone of replacement over the dune slope. This design had to be modified depending on the species and the number of green tillers available for use in the pressure chamber. In each zone at Bushman's Circles one individual of *S. namaquensis* was compared with an adjacent individual of *S. sabulicola* or *S. lutescens*. Initially, the xylem water potentials for five tillers taken from each individual were measured. 1·5 h after watering, the xylem water potentials were determined for another 10 tillers from each individual. A similar experimental design was used at Far East Dune for *S. sabulicola* and *Cladoraphia spinosa*, except that 10 tillers were measured prior to watering. Two different designs were used for the smaller species of perennial grasses, *Centropodium glaucum* and *S. ciliata*, which had too few green tillers per individual for statistical comparisons within the plant over time. The xylem water potential for one tiller from each of 10 individuals of *C. glaucum* at Bushman's Circles was measured and these same 10 plants were re-measured 1·5 h and 2·5 h after watering. This procedure was varied for *S. ciliata* at Far East Dune which had even fewer green tillers per individual than *C. glaucum*. Ten individuals were watered there. Then the xylem water potentials for these 10 individuals and for 10 unwatered individuals were determined 1·5 h afterwards. Ambient air temperatures at 1 m height above the sand were recorded at the time of each measurement of xylem water potentials. All comparisons of xylem water potentials were made using Student's *t*-test.

Results

Nearest-neighbour analysis

All intra- and interspecific nearest-neighbour pairings show significant positive linear correlations between nearest-neighbour distance and the sum of sizes of the two neighbours, and in all cases the slopes of the regression lines are significantly greater than zero (Table 1). The tolerance of an individual for a member of its own species or for an individual of a second species that replaces or co-occurs with it over the dune slope varies (Table 2). On the upper sections of the slope, in the area of relatively unstabilized sand, *Stipagrostis sabulicola* tolerated *Cladoraphia spinosa* and *S. namaquensis* closer to itself than it did an individual of the same size of its own species. For example, if the smaller

Table 1. *The relationship between nearest-neighbour distance and the sum of plant diameters for intraspecific and interspecific pairs of perennial grass species on the slopes of dunes in the Namib Desert*

Intraspecific pairs	*n*	*b*	*r*
Stipagrostis sabulicola	66	0·70	+0·83
S. namaquensis	63	0·72	+0·91
S. lutescens	80	0·84	+0·94
Centropodium glaucum	78	0·84	+0·90
S. ciliata	113	0·67	+0·78
Cladoraphia spinosa	74	0·67	+0·68
Interspecific pairs	*n*	*b*	*r*
S. sabulicola versus *S. namaquensis*	76	0·61	+0·72
S. namaquensis versus *S. lutescens*	75	0·78	+0·94
S. lutescens versus *Centropodium glaucum*	95	1·11	+0·77
S. sabulicola versus *Cladoraphia spinosa*	75	1·26	+0·89
C. spinosa versus *S. ciliata*	102	0·84	+0·81

n = number of pairs sampled; b = the slope of the regression line; r = the correlation coefficient. All slopes are significantly greater than zero at $p < 0{\cdot}05$ and all correlation coefficients are significant at $p < 0{\cdot}01$.

Table 2. *Average distance between nearest-neighbour pairs when the diameter of the smaller individual is fixed at 1 m*

Far East Dune

Intraspecific	Distance (m)*	Interspecific	Distance (m)	*p*
Ss versus Ss	3·33	Ss versus Cs	1·96	<0·001
Cs versus Cs	3·23	Cs versus Ss	1·47	<0·001
Cs versus Cs	3·23	Cs versus Sc	3·33	ns
Sc versus Sc	2·63	Sc versus Cs	2·78	ns

Bushman's Circles Dune

Intraspecific	Distance (m)*	Interspecific	Distance (m)	*p*
Ss versus Ss	3·33	Ss versus Sn	2·17	<0·001
Sn versus Sn	3·13	Sn versus Ss	2·33	<0·01
Sn versus Sn	3·13	Sn versus Sl	2·56	<0·001
Sl versus Sl	2·63	Sl versus Sn	2·63	ns
Sl versus Sl	2·63	Sl versus Cg	3·13	ns
Cg versus Cg	2·70	Cg versus Sl	1·85	<0·01

* Larger individual is listed first.

ns = not significant, Ss = *Stipagrostis sabulicola*, Cs = *Cladoraphia spinosa*, Sc = *S. ciliata*, Sn = *S. namaquensis*, Sl = *S. lutescens*, Cg = *Centropodium glaucum*.

individual is 1 m in diameter, the distance between individuals of *S. sabulicola* is 3·33 m while the distances between *S. sabulicola* and smaller individuals of *C. spinosa* and *S. namaquensis* are 1·96 m and 2·17 m (Table 2). A similar pattern is observed for the converse situation in which *S. sabulicola* is the smaller of the two nearest-neighbour individuals. Lower on the dune slope, where the sands are more stabilized, the tolerances of the species are more complicated. *Cladoraphia spinosa* and *S. ciliata* at Far East Dune interact with each other as if they are members of the same species. No significant differences between the ratios for the size of the smaller over the nearest-neighbour distance could be detected (Table 2). At Bushman's Circles similar results were obtained only in the cases where *S. lutescens* is the larger of the two nearest-neighbours.

Watering experiments

Watering experiments at Bushman's Circles Dune showed rapid uptake of soil water by the uppermost species, *S. sabulicola*, in comparison with the mid-dune species, *S. namaquensis*. During the 1·5 h after irrigation, the average water potential of 10 tillers of *S. sabulicola* had increased from −2·5 MPa to −1·7 MPa, while 10 tillers of *S. namaquensis* decreased from −2·1 MPa to −2·3 MPa ($t = 2{\cdot}94$, df. = 18, $p < 0{\cdot}01$). Only at mid-day, the next day, could a significant difference in water potential be detected for *S. namaquensis*. The average xylem water potentials increased from −2·3 MPa to −1·2 MPa during this period ($t = 3{\cdot}04$, df. = 18, $p < 0{\cdot}01$). Ambient air temperatures were 33°C at the time of xylem water potential measurement on both days. A similar experiment for *S. namaquensis* and the species which replaces it downslope, *S. lutescens*, showed no significant differences in the rates of water uptake, although both had higher xylem water potentials the next day, significantly so in the case of *S. lutescens* ($t = 2{\cdot}59$, df. = 18, $p < 0{\cdot}02$). *Centropodium glaucum*, a species at the lower edge of the dune slope and overlapping the distributioin of *S. lutescens*, also responded rapidly to irrigation. Average xylem water potentials for 20 plants increased from −1·52 MPa to −0·93 MPa during the 1·5 h period after irrigation ($t = 3{\cdot}33$, df. = 18, $p < 0{\cdot}01$). Similar results were obtained for plants from the Far East Dune. *Stipagrostis sabulicola* utilized the additional water more rapidly than did its downslope replacement, *C. spinosa*. The average xylem water potential for 10 tillers of *S. sabulicola* increased from −1·2 MPa to −0·5 MPa during the 2·5 h period after irrigation ($t = 2{\cdot}65$, df. = 18, $p < 0{\cdot}02$), while *S. ciliata*, a species ranging from the inter-dune valley onto the dune slope, had significantly higher xylem water potentials 1·5 h after watering ($t = 5{\cdot}13$, df. = 18, $p < 0{\cdot}01$).

Discussion

Nearest-neighbour analysis is an inferential technique. However, many researchers have utilized this technique in other arid-zone plant associations and then demonstrated experimentally that competition for soil moisture within and between species is occurring (Fonteyn & Mahall, 1978; Robberecht, Mahall & Nobel, 1983; Ehleringer, 1984; Nobel & Franco, 1986). The results of nearest-neighbour analyses in this study reveal that strong competitive interactions are occurring between adjacent individuals. Such competitive interactions, presumably for soil moisture, may be responsible for the zonation patterns of different species observed over the dune slope (Yeaton, 1988). However, these competitive interactions, by themselves, do not explain whether the replacement of species over a dune slope is due to the partitioning of resources leading to ecological differentiation and coexistence, or part of a successional process in which species are retained in the association as part of disturbance. A species tolerance of an individual of a second species closer to itself than a similar-sized individual of its own species also does not distinguish between the two functional mechanisms through which potentially competing species may coexist.

Such tolerances do, however, focus attention on the fact that the species are not equivalent ecologically if two different species maintain smaller nearest-neighbour distances than similar-sized individuals of the same species (Yeaton & Cody, 1976; Yeaton *et al.*, 1985). Similarly, when these distances are the same for similar-sized interspecific and intraspecific pairings, they suggest that the species are interacting with one another as if they are members of the same species.

The results of the watering experiments begin to demonstrate some aspects of these ecological differences. *Stipagrostis sabulicola*, an upper-dune, mound-building species, rapidly takes up the experimentally supplemented water, while *S. namaquensis* and *Cladoraphia spinosa*, the mid-dune replacements and frequent colonizers of mounds in the lower portion of the distributional range of *S. sabulicola*, are much slower in the uptake of water. These results suggest that the root systems of the mid-dune species are much deeper than those of the upper-dune *S. sabulicola*, or that differences exist between species in their resistance to water entry or to water transport. Unfortunately, there is no direct evidence to distinguish between these possibilities. Observations of the root systems of these species after wind erosion of the sand on the dune slope, indicate that the roots of *S. sabulicola* are more often exposed than those of the mid-dune species, that they are more superficial and extensive, and that individuals of this species are more likely to be uprooted. In contrast, no such differences were observed in the rates of uptake of water between the mid-dune *S. namaquensis* and the congeneric *S. lutescens* found at the base of the dune slope. These two species are similar in size and, in the case of *S. lutescens* being the larger, interacted as if they were members of the same species.

Yeaton (1988) argues that the lower mid-dune is the most favourable section of the dune slope for deep-rooting grasses. There is more soil moisture available to grasses in this zone due to the subsurface infiltration of water through the dune from the upper slopes. In addition, the subsurface volume of sand from which to extract this water is greater there than lower on the dune slope where the harder substrata are closer to the surface. If rooting depth is important, *S. lutescens* may have relatively more superficial roots than does *S. namaquensis*, and for smaller individuals of the latter to establish the two species must interact as one. With time the roots of *S. namaquensis* might penetrate deeper in the sand, reducing competition with *S. lutescens*, since the former species extracts soil moisture from subsurface zones not utilized by the latter. Only in the lower portion of the distribution of *S. namaquensis*, where it is replaced downslope by *S. lutescens*, does this interaction occur. In contrast, *Centropodium glaucum* extensively overlaps the distributional range of *S. lutescens*. The root system of this small species is very shallow (personal observation and as evidenced by its rapid uptake of water). When it establishes next to an individual of *S. lutescens*, the major interaction occurs in the upper sand layer already occupied by the roots of the latter species. Hence, *S. lutescens* interacts with *C. glaucum* as if it were another *S. lutescens*. In contrast, *S. lutescens*, establishing next to an individual of *C. glaucum*, could avoid the bulk of the latter's root system by placing its roots deeper in the sand and hence, would be tolerated closer to a previously established *C. glaucum*. The cases of *S. namaquensis* and *C. glaucum* interacting with *S. lutescens* suggest that partitioning of resources is the mechanism through which coexistence of these species occurs over the dune slope. In the former case this resource partitioning is spatial and results in the zonation of *S. namaquensis* and *S. lutescens* on the dune slope, while in the latter case the two species have very different rates of water uptake. Segregation of root systems for associated species of grasses has been hypothesized by many authors as a mechanism for coexistence (Coupland & Johnson, 1965; Harris, 1967; Cook & Ratcliff, 1984; Knaap, 1984).

Upslope, the interaction of *S. sabulicola* with *S. namaquensis* is different. Despite the appearance of zonation, many of the mounds built initially by *S. sabulicola* are occupied also by *S. namaquensis*. An experiment, in which *S. namaquensis* was removed from a series of such mounds, demonstrated a significant increase ($p < 0{\cdot}05$) in the number of leaves produced by *S. sabulicola* when compared with a control series of adjacent mounds on which both species were present. The outcome of this experiment was weakened by the low number of replicates at the end of 8 months as a result of the death of several of the experimental and control plants due to burial by the shifting sands. This pattern suggests that a cyclical succession may be occurring on the upper dune slopes. Over time and with the stabilization of the sand by *S. sabulicola*, *S. namaquensis* will invade these mounds and replace the latter, only to be buried later as a result of its inability to grow as rapidly as the upper dune species.

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