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Grassland Productivity: The Desert End of the Curve

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Following an unusually heavy rainfall the standing crop of an ungrazed central Namib Desert grassland was measured and related to rainfall. Values ranged from 0 to 49.9 g m^{-2} *for rainfall varying from 11 to 96 mm. Linear regression gave a zero-yield intercept of 20.6 mm. Grass growth occurred in one instance after precipitation of 17 mm. An average of 0.5 mg dry matter g*$^{-1}$ *water was produced. Comparison of the regression lines from these data with those of Walter from a nearby grassland experiencing greater annual precipitation and of Rosenzweig from numerous sources of varied rainfall regimes indicates that the slopes are significantly different.*

Na 'n ongewone swaar reënval is die staande oes van 'n onbewiede grasveld in die sentrale Namib-woestyn gemeet en met die reënval in verband gebring. Die waardes het van 0.0 tot 49.9 g/m^2 *gewissel vir reënval tussen 11 en 96 mm. Lineêre regressie gee vir 'n nul-opbrengs die afsynpunt by 20.6 mm. In een geval het gras by 'n neerslag van 17 mm gegroei. Die gemiddelde opbrengs van droë materiaal was 0.5 mg per gram water. Uit 'n vergelyking tussen die regressielyne uit hierdie gegewens, dié van Walter vir 'n nabygeleë grasveld met 'n hoër jaarlikse neerslag en dié van Rosenzweig ten opsigte van 'n hele aantal bronne met wisselende reënvalregimes blyk dit dat die hellings betekenisvol verskil.*

Quantitative relationships between rainfall and plant production in arid areas have been measured in South West Africa,[1,2] Australia[3] and Tunisia[4] and have been reviewed by Walter and Stadelmann.[5] Studies to date have been carried out in areas where the average annual precipitation ranged from 100 to 1500 mm. In the central Namib Desert on the south-western coast of Africa, precipitation of less than 100 mm produces an intermittent grassland which varies in amount each year according to rainfall. This rainfall may be entirely absent for years, during which time vegetation on the gravel plains is restricted to a few hardy perennial plants in the shallow, dry water courses. In 1973–74 the opportunity arose of measuring grass growth in an area devoid of surface evidence of previous cover. The rainfall decreased towards the west and the actual boundary zone between the grassland and the bare gravel plain was fortuitously included in the study area, affording the unusual opportunity of determining the lower limits for growth in this area. As with the rainfall, this grassland boundary is very mobile.[6] While this plant cover is termed a grassland and the community is dominated by Gramineae, other ephemeral dicotyledonous plant species occur. The purpose of this paper is to describe the relationship between precipitation and above-ground plant production in this extremely low-rainfall regime and to compare this relationship with that of other desert areas.

The study area

Although late summer rainfall predominates in the Namib,[7,8] the central area in the vicinity of 23°S, 15°E is situated at the northern extremity of the Cape winter rainfall region. Rain has been recorded during every month of the year. Precipitation occurs in the central Namib both as fog and rain.[8–10] Fog is used by certain specialised desert plant species[11–14] but only rain is significant for the growth of the grasses of the central Namib plain. Annual rainfall varies from an average of 15 mm on the coast to 65 mm on the 1000 m contour 110 km to the east (Fig. 1). The study transect was located on the central Namib Desert plain extending from Gobabeb, at an elevation of 400 m, to 44 km east at 750 m. This area is subjected to minimal grazing and is free from human activity, an advantage in such studies if valid comparisons of the rainfall response to various rainfall regimes are to be made.[5] The area has a uniform climate covering a similar geological formation consisting of alluvial fans surrounding an inselberg grading into quartz gravel-covered plains underlain by calcrete.[9,10] The soil is calcareous gypsum on a compact gypsum crust (west) or calcrete layer (east). It is covered with a layer of limestone and quartz gravel as a result of deflation. The soils have pH values between 7.4 and 8.3 (in KCl). The cation exchange capacity seldom reaches 10 meq/100 g because of the low clay content. Organic matter averages 0.5% by mass, while the presence of gravel may amount to as much as 90% by volume.[15] In addition, it supports a vegetation cover of approximately uniform species composition. Although smaller-scale edaphic changes no doubt alter above-ground production, sampling an area as large as this one probably provides an integrated estimate of vegetation responses to rainfall.

Materials and methods

During the 1973–74 summer, simple rainfall gauges were erected at 2-km intervals extending 44 km ENE from Gobabeb along a transect intersecting the area where the western boundary of the grass cover may occur. The gauges consisted of

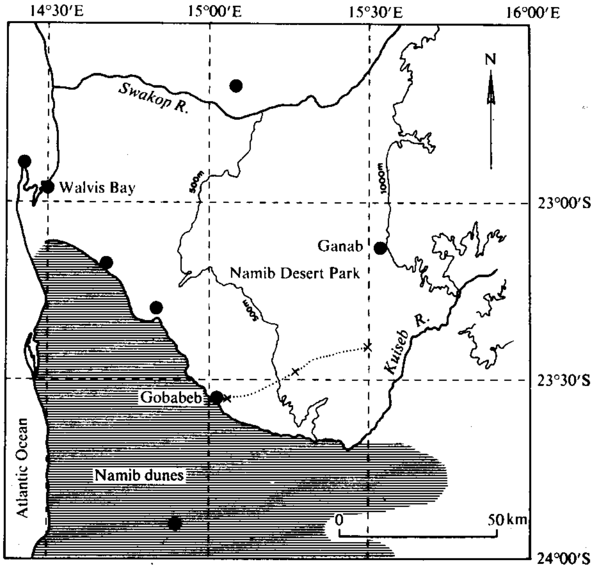

Fig. 1. Map of the central Namib Desert showing the location of meteorological stations (●) and temporary rain gauges along the transect (×).

funnels inserted into collection bottles erected 1.5 m above the ground. Soft plastic funnels with broad rims were employed, introducing some error of measurement (~10%). Total precipitation collected was measured the same day or the day following each rainfall event.

In March 1974, when all the grass had set seed and that towards the west was beginning to dry out, five quadrats of one square metre were clipped at ground level near each rain gauge along the transect. The sites were randomly selected on the level gravel plain and thus quadrats devoid of vegetation were included; runoff concentrations were avoided. These samples were sorted to species and dry masses determined. As none of the area had supported a grass cover the previous year, there was no contribution of biomass either as standing dead material or litter from previous growing seasons. All samples were obtained using a square wooden frame. The sparse nature of the plant cover allowed the frame to be inserted easily to ground level. In agreement with general practice, grass species together with annual dicotyledons are included in this study.[16]

Results and discussion

Throughout the transect *Stipagrostis ciliata* predominated, comprising from 80.6 to 100% of the dry matter of each set of clippings, except at kilometer 12 where *S. subacaulis* made up 87.9% of the total. Other species occurring on the transect are listed in Table 1. The relationship of the number of species present to rainfall suggests an increased number of species with increasing precipitation. That the reduced number of species is an indirect result of rainfall, and not seed availability, has been confirmed by the unusually heavy rains of the 1975–76 season. Many species not normally seen are now growing in the study area west of Gobabeb, which had an unprecedented 98 mm of rain in January to March 1976 alone. These species occurred only east of the 24 km rain gauge in 1974 (35 mm minimum). The rainfall intensity during a single event may also have an influence on total production as well as species composition.

Table 1. Standing crop on the central Namib transect of *Stipagrostis ciliata* (Desf.) De Winter (*S. c.*), *S. obtusa* (Delile) Nees ex Kunth (*S. o.*), *S. subacaulis* (Nees) De Winter (*S. s.*), *Triraphis pumilio* R. Br. (*T. p.*), *Trianthema triquetra* Willd. (*T. t.*), *Tephrosia dregeana* E. Meyer (*T. d.*), *Monechma desertorum* (Engler) C. B. Clarke (*M. d.*).

km	Productivity ($g\,m^{-2}$)	Percent of total dry mass by species						
		S.c.	*S.o.*	*S.s.*	*T.p.*	*T.t.*	*T.d.*	*M.d.*
6	1.74	100						
8	0.75	100						
10	1.16	100						
12	1.08	12.1		87.9				
14	0.97	100						
16	0.79	100						
18	0.81	100						
20	1.73	100						
22	6.37	100						
24	4.09	100						
26	7.63	93.1					6.9	
28	14.22	100						
30	15.19	80.6	19.3					0.1
32	22.47	93.9		5.9			0.2	
34	41.62	99.1					0.2	0.7
36	32.06	100						
38	24.89	94.2			0.6		0.1	5.1
40	37.54	100						
42	27.50	91.8			0.6	7.6		
44	49.92	99.6			0.2	0.2		

Several plant species were represented in only one plot or were present but not measurable (+): *Lotononis platycarpa* (Viv.) Pic. Ser. 0.1% at km 43; *Limeum argute–carinatum* Wawra and Peyr. (+) km 38, (+) km 42.

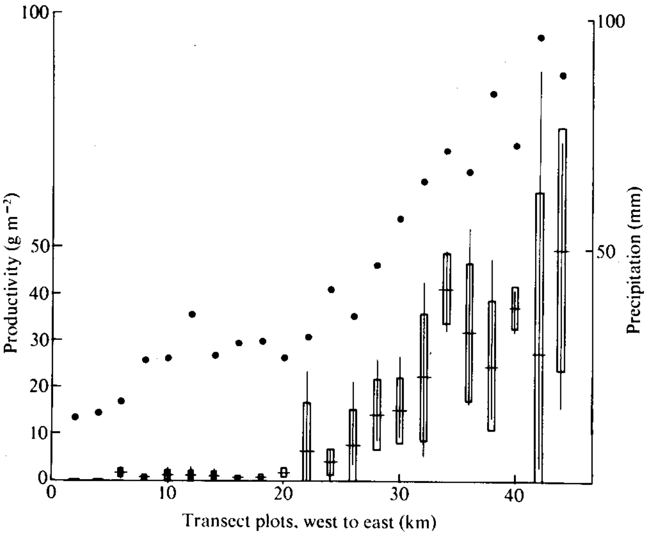

Fig. 2. Rainfall (●) and grass productivity along the 44-km transect extending eastward from Gobabeb. The range of productivity is indicated by the vertical lines, average productivity by the longer horizontal lines, and one standard deviation by the enclosed areas.

Data from various arid regions show that the average annual above-ground production varies between 30 and 200 $g\,m^{-2}$.[17] In this study (Fig. 2) the average biomass value was 14.6 $g\,m^{-2}$ Thus, above-ground production in the central Namib is at the lower extreme of reported values for desert vegetation. Inspection before collection indicated that none of the recently germinated material had yet died. Thus the values obtained represented the production during the current growth season only. Productivity may be calculated as 0.25 $g\,m^{-2}$ per day for the period between the first precipitation inducing germination and harvesting. After harvesting, growth continued on the eastern portion of the transect although it had ceased towards the west. Dead leaves had appeared on the still-growing plants in the east one month after harvest. Thus the values presented represent the maximum growth before any death occurred rather than the maximum production for the season.

Productivity in arid ecosystems is highly correlated with rainfall.[17] This relationship may be expressed as $Y = b(P - a)$, where Y = productivity and P = precipitation. The term a has been called 'ineffective precipitation' or 'water losses (evaporation and runoff)', but it may represent the genetically and environmentally determined minimal rainfall required for germination. This will be especially true where runoff is insignificant, as in this study. The coefficient b represents efficiency in mg dry matter per g water.

Published values for the zero-yield intercept a range between 25 and 75 mm/year.[17] From regression analysis of the Namib transect data, this value for a is 20.6 mm. In one instance vegetative growth occurred with only 17 mm of precipitation. This value was obtained in an area where runoff did not occur and may represent the minimal precipitation required for germination. Noy-Meir[17] indicates that values of b range from 0.5 to 2.0 mg dry matter per g water. When calculated from these Namib data, $b = 0.5\ mg\,g^{-1}$. From these data it would appear that the linear relationship between precipitation and grass production holds at the lower extremes of precipitation.

For this regression analysis, data from one year only are available for the Namib. Although under constant post-rain growth conditions the amount of above-ground productivity resulting from a given amount of rain would be expected to be similar, very different growth conditions between years may alter the slope of the regression and/or the y-intercept. Other factors affecting these parameters are: intensity of the rainfall, interval between the rainfall events, and time of year of the

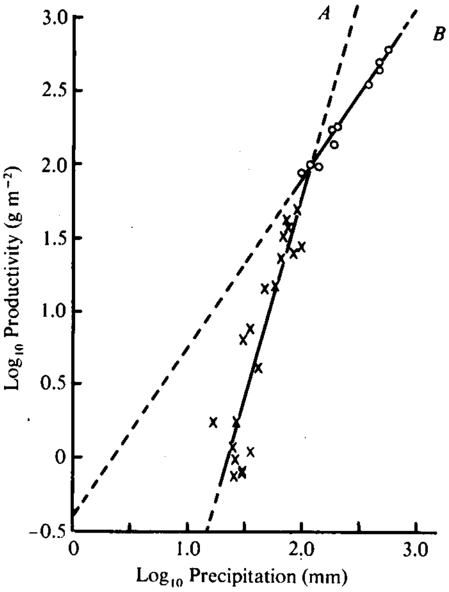

Fig. 3. Relationship of grass productivity to precipitation in the central Namib (*A*) and more mesic South West Africa (*B*) (ref. 1).

rainfall. Thus the relationship of above-ground productivity to rainfall may differ slightly from year to year and these data for the Namib should be viewed in this light.

To compare these data with those obtained in an arid region experiencing much higher rainfall (100–500 mm),[1] the two data sets were converted to a common log scale (Fig. 3). When comparison is made between regression lines representing Walter's[1] data and mine the slopes were found to be significantly different at the 0.5% level. A two-tailed *F*-test based on the residual mean squares was employed. It would appear that extrapolation from higher rainfall conditions to areas with minimal amounts is not a valid approximation. The differences may be explained by the fact that Walter's plots contained only perennial grasses, whereas my plots supported only annual seedlings of, for example, *Stipagrostis ciliata*. Perennial plants use rainfall more efficiently as they have a developed root system. Annual plants must not only germinate but build up new shoots and a root system[3] before maximising growth. In the Namib the annual precipitation and the greater part of the annual growth of all grasses occurs from January to March or April. The greater production of the plants growing in the less arid environment could simply mean that the perennial forms there have a longer growing season.

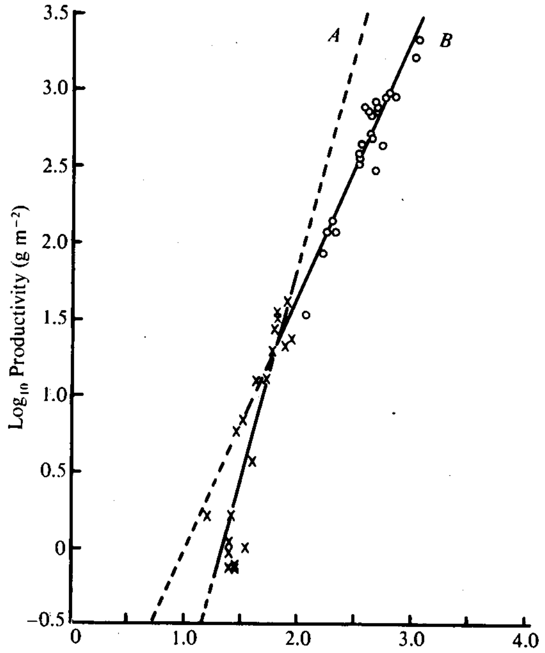

Fig. 4. Relationship of grass productivity to evapotranspiration in the central Namib (*A*) and calculated from literature values from various environments (*B*) (ref. 18).

In arid environments where potential evapotranspiration is greater than precipitation, actual evapotranspiration may be very nearly equal to annual precipitation.[18] Using production data from a variety of environments, Rosenzweig[18] has related production to actual evapotranspiration. By equating actual evapotranspiration with precipitation, these desert data may be compared with those from other environments. Use of actual evapotranspiration would lead to prediction of values significantly different ($P < 0.5\%$) from those measured in the Namib Desert plains. Thus measurements from higher rainfall areas would lead to prediction of higher production values in a low-rainfall desert area than were actually measured. Rainfall may be the limiting factor but soil differences and length of growing season may also be involved. These data from the central Namib provide a measurement of annual growth at the lower extremity of rainfall.

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