Journal of Arid Environments (1987) 13, 237–243

The origin of vegetation circles on stony soils of the Namib Desert near Gobabeb, South West Africa/Namibia

G. W. Cox*

Accepted 21 October 1985

Circular patches of annual or short-lived perennial grasses, ranging from *c.* 2·3 to 11·4 m in diameter, occur on areas of stony soils east of Gobabeb, in the Namib Desert, South West Africa/Namibia. These circles tend to be regular in spacing and often show a conspicuous lag gravel border. Some circles show evidence of recent occupancy by gerbils and they correspond closely in size to active or recently active gerbil colonies. Water infiltration rates are much higher within the circles than outside them. Soil disturbance by rodents is postulated to have increased the permeability of the soil to water, thus favouring growth of dense stands of annual grasses after periods of rain.

Introduction

Many observers have noted that the abundance of annual plants in deserts is related closely to the amount and intensity of rainfall. However, few studies have examined the relationship of the pattern of annual plant growth to small-scale differences in water infiltration and storage in the soil. Beatley (1974) commented that the scattered pattern of germination of annuals following autumn rains of 15–25 mm was probably the result of differences in infiltration rates. In the Namib Desert, Ollier & Seely (1977) and Watson (1980) described polygonal networks of *Stipagrostis gonatostachys* and other short-lived grasses. Watson (1980) found that these polygons result from subsurface fissures filled with sandy surface material, that either permit greater infiltration and storage of moisture, favouring plant growth, or create excessively drained microsites, preventing growth of plants.

Louw & Seely (1982, p. 143) also described circles and rings of grasses near Gobabeb and attributed these to the effects of animal burrowing. Although the digging activities of rodents and other animals are known to influence soil permeability (Knapp, 1971) and to create microsites for plant establishment (e.g. Grant & McBrayer, 1981; Laycock, 1958; Platt, 1975), the indirect impact of rodent activity on vegetation, by the modification of physical conditions of the substrate, has received little study.

The objective of this study was to test the hypothesis that the Gobabeb circles are the result of rodent disturbance of the soil, and to ascertain the specific factors favouring plant growth in these areas.

Study areas and methods

Observations were made at various locations along the Mirabib Road between the Desert Ecological Research Unit (DERU) at Gobabeb and Mirabib Kopje, 41 km east of DERU,

* Department of Biology, San Diego State University, San Diego, CA 92182–0057, U.S.A.

0140–1963/87/060237+07 $03.00/0

between 10 and 28 February 1984. Detailed measurements were obtained on a 1·55-ha study plot south of the road and 21·7 km east of DERU. The maximum and minimum diameters and the distance to the nearest neighbouring circle (centre to centre) were measured for all vegetation circles on this plot. The degree of development of a lag gravel ring at the outer edge of the circle, and the tendency for vegetation to be concentrated in a ring as opposed to covering the full area of the circle, were evaluated on a four-point scale (none, weak, strong, very strong). The presence of tunnels or surface heaps indicative of the former presence of gerbil colonies was noted, as was the presence of fragments of calcrete exposed at the surface. The numbers of dead clump bases of grasses, probably mostly *Stipagrostis ciliata* (M. K. Seely, personal communication), were counted in transects 30 cm wide along the major and minor axes of the circles. Data on plant density, heaps or tunnels of gerbils, and the presence of surface calcrete fragments were also taken in an equal-area circle adjacent to the vegetation circle at a point chosen randomly.

On this same plot, water infiltration rates were measured along transects from the centre of six circles to points one circle radius beyond their edge. Measurements were made at five locations on each transect: circle centre, half-radius, edge, half-radius beyond edge, full radius beyond edge. At each location a metal cylinder 7·3 cm in diameter (41·8 cm^2 area) was pushed 4–5 cm into the soil and 200 cm^3 of water poured into the cylinder. The time for complete infiltration was recorded.

Active or recently active nest colonies of gerbils (*Gerbillus* spp.) and ground squirrels (*Xerus inauris*) were examined at various localities along the Mirabib Road. Ten such gerbil sites were measured and mapped between DERU and the study plot 21·7 km to the east.

Results

A total of 50 distinct vegetation circles existed on the 1·55-ha study plot. These circles averaged 5·3 ± 1.5 m (SD) in diameter; the smallest was 2·3 m in diameter and the largest, 11·3–11·5 m (minimum–maximum) in diameter.

Measurements of distance to nearest neighbour were analysed to determine the dispersion pattern shown by the circles. Since these circles have a substantial diameter, they violate the assumption of Clark & Evans' (1954) nearest-neighbour analysis that the objects in question are points, and create the potential for a bias toward a uniform dispersion index due to inability to recognise very close neighbours as distinct (Ebert & McMaster, 1981). Thus, I employed a modified nearest-neighbour technique for circles that may overlap (Cox, 1987). The observed mean distance to nearest neighbour ($\bar{r}_A$) for vegetation circles in the study plot was 11·2 ± 3·4 m (SD). The minimum separation distance d (between centres) for recognition of these circles as distinct, was considered to be half their mean diameter, or 2·6 m. Using this value, the expected mean nearest-neighbour distance $\bar{r}_E$ for a random pattern, and its standard error $\sigma_{\bar{r}_E}$, were obtained by the equations:

$$\bar{r}_E = d + \frac{e^{\rho\pi d^2}}{\sqrt{\rho}} \int_{\sqrt{2\rho\pi}\cdot d}^{\infty} \frac{1}{\sqrt{2\pi}} e^{-t^2/2} dt \qquad (1)$$

and

$$\sigma_{\bar{r}_E} = \sqrt{d^2 + \frac{1}{\rho\pi} - \bar{r}^2} \Big/ \sqrt{N} \qquad (2)$$

where ρ is circle density (50 circles per 15,500 m^2), the integral in equation (1) is the area under the normal curve from $z = \sqrt{2\rho\pi}\cdot d$ to ∞ (obtained from a table of normal curve areas), and N is the number of measurements (50). The dispersion index R for this pattern was:

$$R = \bar{r}_A/\bar{r}_E = 1{\cdot}20 \quad (3)$$

which indicates a pattern tending toward uniformity. The deviation of $\bar{r}_A$ from $\bar{r}_E$ was tested by a z-test:

$$z = (\bar{r}_A - \bar{r}_E)/\sigma_{\bar{r}_E} = 3{\cdot}01 \quad (4)$$

which indicates a strongly significant ($p < 0{\cdot}01$) tendency toward uniform spacing. However, no significant relationship was detected between distance to nearest neighbour and size of nearest neighbour.

Development of an outer ring of lag gravel varied considerably among the circles on the study plot but only six were judged to lack such a ring. The development of this ring was directly, although rather weakly, correlated with the diameter of the circle ($r = 0{\cdot}350$, $t = 2{\cdot}589$, $p < 0{\cdot}025$). Fragments of calcrete were present at the surface in 11 of the 50 circles but no relationship was noted between their presence and other variables. The mean density of dead clump bases of grasses was $23{\cdot}5 \pm 10{\cdot}1$ m^{-2} (SD) within the vegetation circles and $3{\cdot}7 \pm 4{\cdot}1$ m^{-2} (SD) in the areas outside the circles ($N = 50$). Density was higher within the circle than outside in all instances. In 13 of 50 cases, the vegetation was judged to be concentrated in a ring, rather than uniform in density throughout the area within the circle. For these circles, grass density (entire circle area) was negatively correlated with circle area ($r = -0{\cdot}670$, $p < 0{\cdot}025$), while for the remaining 37 circles no relation existed between grass density and circle area ($r = 0{\cdot}083$, $p \gg 0{\cdot}05$).

Tunnel openings and remnant surface heaps of gerbil burrow systems were noted in three and 25 of the 50 circles, respectively. However, none of these burrow systems appeared to be occupied. No tunnel openings or heaps were noted in the equal-area circles outside the vegetation circles.

The ten active or recently active gerbil colonies examined ranged from 2·9 to 9·6 m in mean diameter, averaging $5{\cdot}9 \pm 1{\cdot}9$ m (SD). The mean diameter of these colonies was not significantly different from that of the circles on the 1·55-ha study plot ($t = 1{\cdot}20$, d.f. $= 58$, $p > 0{\cdot}05$). Soil heaps at the mouths of tunnel openings at the periphery of these colony sites, showed a strong tendency to be located on the outer side of the tunnel opening. The soil of these heaps contained pebbles up to several centimetres in diameter and wind erosion of the heaps had exposed many of these. The central zone of some of the recently abandoned sites had collapsed, forming a depression 10–15 cm deep. Several colonies possessed small numbers of dead grass clumps but none showed a concentration equal to that of the vegetation circles. One recently active ground squirrel nest complex east of Mirabib was 18–20 m in diameter. Mean water infiltration rates (Fig. 1) ranged from 1·97 cm/minute at the edge of the vegetation circles to 2·82 cm/minute at their centres. Outside the circles, infiltration rates were 0·25–0.32 cm/minute. The lowest infiltration rates were for the three smallest circles, and the highest rates for the three largest. Infiltration rates were highly variable for sites outside the vegetation circles.

Discussion

The vegetation circles of the gravel plains east of Gobabeb are probably located on sites of old rodent colonies. The diameters of these circles are not significantly different from those of recently active gerbil colonies in nearby areas. The circles also show a significant tendency toward uniform spacing, as expected by the territorial behaviour of such animals. In addition, the uniformity of spacing implies that most of the circles were active rodent colonies at the same time. The lack of correlation of the size and nearest-neighbour distance of circles is inconsistent with the hypothesis that they represent former tree or shrub sites, since desert plants of this sort tend to show size-related spacing patterns (Yeaton, Travis *et al.*, 1977). Many of the vegetation circles also showed tunnel openings

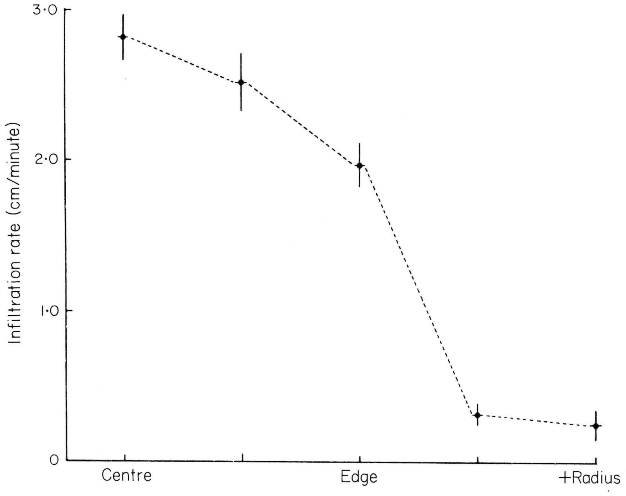

Figure 1. Water infiltration rates at equally spaced points from the centre of vegetation circles to a distance of one radius beyond their edge, central Namib Desert, South West Africa/Namibia. Vertical bars indicate standard error of infiltration rate means.

and soil heaps similar to those of recently active gerbil colonies, while such features were absent from areas between circles.

The rodents responsible for the colonies which gave rise to the vegetation circles were probably *Gerbillus setzeri* (now considered to be synonymous with *G. vallinus*; M. Griffin *fide* M. K. Seely). *G. setzeri* (including *vallinus*), a species with a body ranging from *c.* 34 (female) to 40 (male) grams, occurs both on the gravel plains north of the Kuiseb River (Schlitter, 1973) and on the dunes to the south (Coetzee, 1969). In years of high rainfall and lush growth of annual plants (e.g. 1963), *G. setzeri* is abundant on the plains near and east of Gobabeb (Schlitter, 1973). At these same times, other species of gerbils, including *Gerbillurus paeba*, *Desmodrillus auricularis* and *Tatera leucogaster*, as well as the ground squirrel, *Xeris inauris*, may also be present. These rodents build burrow systems similar to those of *G. setzeri*

The formation of these circles bears a close relationship to the characteristics of the soils. The soils of the gravel plains are calcareous gypsum soils (Scholtz, 1972) with an underlying calcrete horizon (Goudie, 1972). The soil profile on the study plot, 21·7 km east of Gobabeb, was similar to that illustrated by Watson (1980, Fig. 2*A*): a thin, sandy surface layer bearing a weak desert pavement of quartz pebbles underlain by a partially consolidated silty clay horizon resting on the calcrete basement (Fig. 2). The dense nature of the silty clay horizon impedes infiltration of water (Fig. 1) and thus its storage in the deeper soil layers. The development of vegetation circles (Fig. 2) probably begins with the excavation of a system of tunnels and nest chambers by gerbils. The mined soil is deposited in surface heaps that tend to be oriented outward from the colony centre, although openings and heaps occur in the central zone of the colony as well as in a peripheral circle. The mined soil, which is very porous, and the tunnels themselves favour the infiltration of water during rainy periods. Eventual collapse of the tunnels and nest chambers also creates a depression, evident in some of the recently abandoned gerbil nests, that favours water accumulation. Collapse of the tunnels and chambers may also be caused by large ungulates, such as the mountain zebra, *Equus zebra hartmannae*, and gemsbok, *Oryx gazella*, attracted to colony sites by an abundance of annual grasses. Wind erosion eventually removes fine soil materials from the surface heaps, leaving a lag gravel deposit, and fills the central depression with sandy material which is still very porous. Thus, the

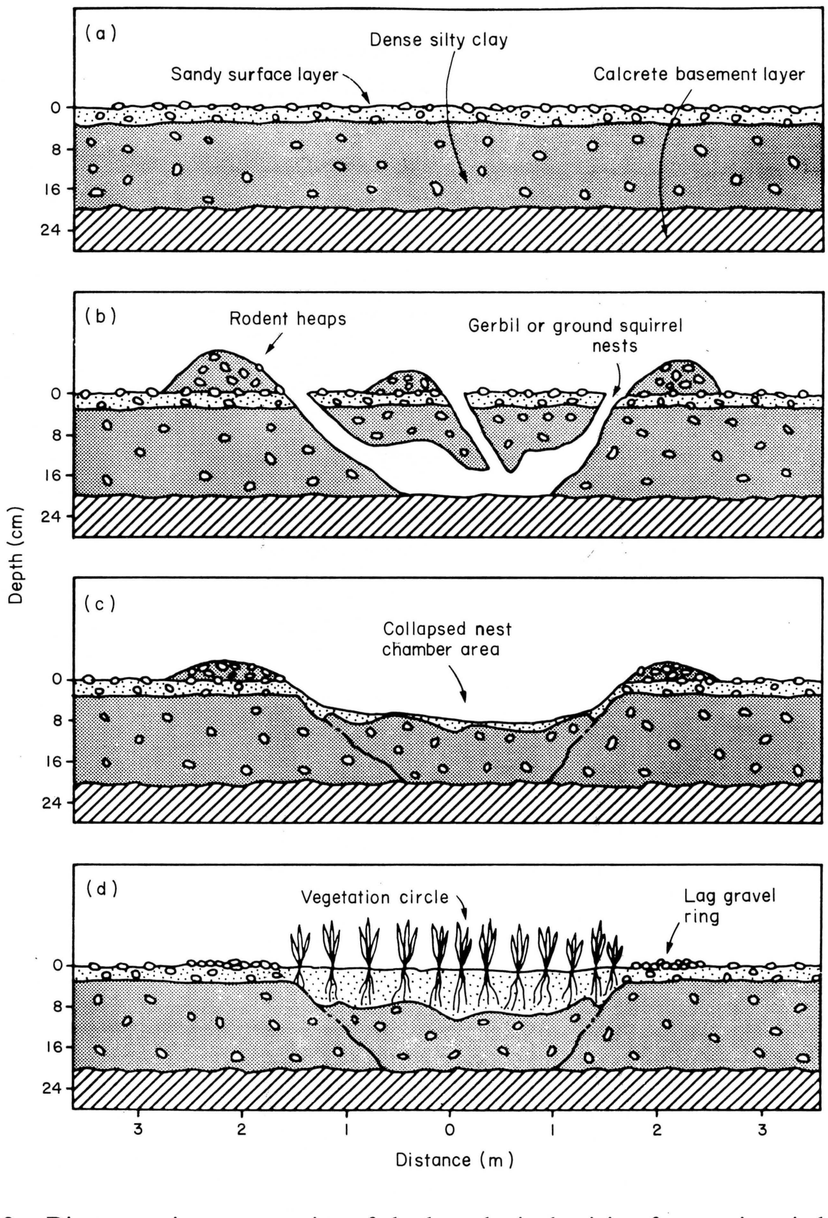

Figure 2. Diagrammatic representation of the hypothesised origin of vegetation circles from abandoned gerbil burrow systems on stony soils of the central Namib Desert, South West Africa/ Namibia.

soil system is restructured in a fashion favouring the infiltration and storage of water for many years — a period well beyond that at which surface evidence of the former gerbil colony has been obliterated.

This process may operate in many other desert and grassland areas of Africa and Asia where gerbils are common. Senzota (1984) examined colonies of the gerbil, *Tatera robusta*, in Serengeti National Park, Tanzania. He noted the same tendency for heaps of excavated soil to be oriented outward from the colony centre, and mapped three burrow systems that averaged *c*. 5·6 m in diameter, a value intermediate between those for recently occupied gerbil colonies and the vegetation circles in the present study.

The presence of calcrete fragments at the surface in some of the circles may reflect, in part, their mining and transport to the surface by gerbils. Some of the larger fragments also may have been brought to the surface by large predators digging for rodents. Near Mirabib Kopje, however, the root systems of scattered *Moringa ovifolia* trees have penetrated into the calcrete zone, causing fragments of calcrete to be thrust to the surface. Thus, some of the circles with surface calcrete fragments may be centred on former tree sites. Trees may have been more abundant over this area about 400 AD, when higher rainfall and better grazing allowed pastoralist peoples to base their activities at Mirabib (Sandelowsky, 1977; Ward, Seely *et al.*, 1983).

The vegetation circles exist in a region of very irregular rainfall. The mean annual rainfall at Gobabeb is *c.* 26 mm but varies between 0 and over 100 mm (Robinson & Seely, 1980). Annual vegetation appears only when more than 20 mm of water falls in a short time (Holm & Scholz, 1980), an event that occurs about once in 14 years at Gobabeb but almost annually along the escarpment at the eastern edge of the desert (Seely, 1978). Two or more wet years sometimes fall together, however. In 1974, 130 mm fell at Mirabib (Gamble, 1980) and in 1976 and 1978, over 100 mm were recorded at both Mirabib and Gobabeb (Robinson & Seely, 1980; M. K. Seely, personal communication). During such wet periods, populations of gerbils and ground squirrels spread westward from locations close to the escarpment where they exist permanently. The youngest vegetation circles probably date from 1974–8, this most recent wet period.

I thank the Division of Nature Conservation of the Administration of South West Africa for permission to work in the Namib Desert Park, and for use of facilities of the Namib Research Institute. The support and assistance of the South African Council for Scientific and Industrial Research and the Transvaal Museum are also acknowledged. I express my appreciation to Mary K. Seely and Paul H. Zedler for comments and suggestions on the manuscript.

References

Beatley, J. (1974). Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology*, **55**: 856–863.

Clark, P. J. & Evans, F. C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, **35**: 445–453.

Coetzee, C. G. (1969). The distribution of mammals in the Namib Desert and adjoining inland escarpment. *Scientific Papers of the Namib Desert Research Station*, **40**: 23–36.

Cox, G. W. (1987). Nearest neighbour relationships of overlapping circles and the dispersion pattern of desert shrubs. *Journal of Ecology*, **75**: 193–199.

Ebert, T. A. & McMaster, G. S. (1981). Regular pattern of desert shrubs: a sampling artifact? *Journal of Ecology*, **69**: 559–564.

Gamble, F. M. (1980). Rainfall in the Namib Desert Park. *Madoqua*, **12**: 175–180.

Goudie, A. (1972). Climate, weathering, crust formation, dunes, and fluvial features of the central Namib Desert, near Gobabeb, South West Africa. *Madoqua*, **1**: 15–31.

Grant, W. E. & McBrayer, J. F. (1981). Effects of mound formation by pocket gophers (*Geomys bursarius*) on old field ecosystems. *Pedobiologia*, **69**: 559–564.

Holm, E. & Scholtz, C. H. (1980). Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. *Madoqua*, **12**: 6–39.

Knapp, R. (1971). Influence of indigenous animals on the dynamics of vegetation in conservation areas. *Symposium of the British Ecological Society*, **11**: 387–390.

Laycock, W. K. (1958). The initial pattern of revegetation of pocket gopher mounds. *Ecology*, **39**: 346–351.

Louw, G. N. & Seely, M. K. (1982). *Ecology of Desert Organisms*. London: Longman. 194 pp.

Ollier, C. D. & Seely, M. K. (1977). Patterned ground near Gobabeb, central Namib Desert. *Madoqua*, **11**: 213–214.

Platt, W. J. (1975). The colonization and formation of equilibrium plant species associations on badger disturbances in a tall grass prairie. *Ecological Monographs*, **45**: 285–305.

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

Sandelowsky, B.H. (1977). Mirabib — an archeological study in the Namib. *Madoqua*, **10**: 21–283.

Schlitter, D. A. (1973). A new species of gerbil from South West Africa with remarks on *Gerbillus tytonis* Bauer and Niethammer, 1959 (Rodentia: Gerbillinae). *Bulletin of the Southern California Academy of Sciences*, **72**: 13–18.

Scholtz, H. (1972). The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua*, **1**: 33–51.

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

Senzota, R. B. M. (1984). The habitat, abundance and burrowing habits of the gerbil, *Tatera robusta*, in the Serengeti National Park, Tanzania. *Mammalia*, **48**: 185–195.

Ward, J. D., Seely, M. K. & Lancaster, N. (1983). On the antiquity of the Namib. *South African Journal of Science*, **79**: 175–183.

Watson, A. (1980). Vegetation polygons in the central Namib Desert near Gobabeb. *Madoqua*, **11**: 315–325.

Yeaton, R. I., Travis, J. & Gilinsky, E. (1977). Competition and spacing in plant communities: the Arizona upland association. *Journal of Ecology*, **65**: 587–595.