

Origin of the enigmatic, circular, barren patches ('Fairy Rings') of the pro-Namib

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We have studied the enigmatic, circular, barren patches on the edge of the pro-Namib Desert in Namibia. An aerial photograph of the Wolwedans area (25°4.5'S, 15°59.5'E) showed that the patches had an average diameter of 6.1 m and an ordered distribution with an *R*-value of 1.68, suggesting a termite-associated origin. We postulate that there is an active evolutionary process of circular patch formation, involving genesis, growth, maturation and extinction. *Stipagrostis uniplumis* seedlings growing in the moist inner soil of barren patches, after rains, appeared to lack root side-hairs when compared to similar plants growing outside the patch and these seedlings invariably died when the rains subsided. Growth experiments with *Cynodon dactylon* in inner and outer soil samples showed that these grass seedlings could survive cycles of dehydration and hydration only when growing in outer soil. Seedlings in the inner soil collapsed and died under similar conditions. This suggested that there is a biological factor in the inner soil, which inhibits resistance to dehydration, possibly through inhibition of side-root growth and/or maintenance. We postulate that termites are linked to this biological factor in some unknown manner and that the barren patches have an evolutionary advantage for the termites by acting as water traps. Direct experiments showed five-fold more water in soil samples from the barren patches than between them. Preliminary attempts to indicate or isolate the putative abiosis factor with HPLC were not successful and more sophisticated analytical techniques are called for.

Background

An intriguing and as yet unexplained feature of the pro-Namib is the presence of hundreds of almost circular, barren patches, which have been referred to as 'Fairy Rings'.¹ Patch diameters of 2.2–12.2 m have been recorded.¹ No plants are found growing inside the mature patches and their periphery is punctuated with mature tufts of *Stipagrostis giessii*, while *Stipagrostis uniplumis* is found between patches.² Many of the patches are concave, probably due to wind erosion.

A number of hypotheses have been advanced to explain this enigmatic phenomenon. Initially, Tinley proposed that the rings were fossil termitaria formed when the average annual rainfall (100–150 mm) was considerably higher.³ More trivial explanations have been proffered, for instance, impact points of broken-up meteorites, rolling spots for zebras, indications of locations of Ovahimba huts, localized radioactivity and even landing locations of 'Flying Saucers'!

More seriously, Theron reported in 1979 on circular barren patches found in the Hartmann valley and Giribes plain in Kaokoland, Namibia.² This area is west of the escarpment mountains at the transition with the pro-Namib. He found that the

patches ranged in average diameter from 6.2–9.3 m and that after rains moisture could be found inside the rings up to a depth of one metre while between rings, where grass was growing, only to a depth of 0.3 m. He also noticed that during rains grass seedlings did initiate growth in the rings but invariably died when the rains were over. He postulated that the barren, circular patches were caused by the release of a so-called allelopathic chemical from extinct plants, especially *Euphorbia damarana*, which grows in the area of study and has an average diameter close to that of the rings, that is, 6.4–6.8 m. He proposed that the allelopathic chemical remained in the upper layers of the soil for a long time owing to the low rainfall. A single result was presented showing that *Eragrostis teff* grew considerably more slowly in soil from within a circular patch than in soil from between patches. He suggested that the factor was an inorganic cation but no evidence was presented. In a subsequent microbiological study, Theron and colleagues reported that the highest density of fungal populations was found on the edge of the rings and lowest within the rings, whereas a higher density of anaerobic bacterial colonies were grown from soil sampled from inside circular patches compared to the edges and between the patches. No specific organism(s) was correlated with the inside or edge of the circular patches.⁴

In 1989, Moll conducted extensive research on what he called 'Fairy Rings' in Namibia.¹ He came to the conclusion that termites were the main agents in Fairy Ring formation and that the lack of vegetation in the rings was compatible with surface foraging by the termites. In support of this theory he found termite casts and a few individual termites after digging a trench 0.75 m deep and 0.30 m wide through a number of Fairy Rings. The termites were identified as *Baicaliatermes hainsei* (Fuller) and *Psammotermes allocerus* (Silvestri). He also reported that, according to an aerial photograph, it was clear that there are rings in different stages of colonization by plants. From this he concluded that the Fairy Rings were 'dynamic'. Moll's hypothesis has been summarized by Lovegrove⁵ as follows:

Moll suggested that the elusive 'fairies' may be one of three possible termite species: *Hodotermes mossambicus*, *Psammotermes allocerus* or *Baicaliatermes hainsei*. Physical and chemical clues in the circle soils certainly support Professor Moll's idea that the bare patches are caused by the termites having eaten all the grass seeds in the immediate vicinity of their nests. He also suggests that colonies may die out after several successive years of poor rainfall — every 17 years or so — which would explain the vanishing act of the fairy rings. After good rains the area may be colonized again by winged alates blown north by the prevailing winds from well-established colonies.

In this article we present the hypothesis that the circular, barren patches are caused by a semi-volatile chemical factor associated with viable termite nests, which induces an inhibition of dehydration-stress resistance in *Stipagrostis* sp. plants, thus forming 'water traps' which are of survival value to the termites.

Methods and results

Location

We began our studies in 1993 and focused on circular barren patches located on the farm Wolwedans, which is part of the

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NamibRand Nature Reserve. The site was visited again in 1996 and 1997. The exact location where the patches were studied is on the west side of the Losberg mountain adjacent to the dunes of the Namib Desert at 25°4.5'S, 15°59.5'E. This position was pinpointed using aerial photograph No. 5236/777 from the Chief Director of Surveys and Land Affairs, Mowbray, Cape Town, with permission of the Surveyor General of Namibia.

Analyses of aerial photograph

An area showing hundreds of circles in the aerial photograph (5236/777) taken on 31 May 1977 was enlarged 10-fold (Fig. 1) and used to study the distribution, density and average size of the rings.

The pattern of distribution, or spatial relationship, of the circles was analysed according to the 'distance to nearest neighbour' method of Clark and Evans.⁶ According to this method, an 'R-value' is calculated, which is zero when all objects are aggregated in one lump and 1.0 if the objects are randomly distributed. Objects distributed in a perfect hexagonal pattern give a value of 2.149. Nearest-neighbour distances were measured for 292 circles and the R-value was calculated to be 1.68 (± 0.05). The average nearest-neighbour distance was 14.4 m and the density of circles was 3484 per km² (about 7.3% of the total surface area studied).

These measurements are of interest because they can be compared to similar measurements recorded for the so-called Mima-like mounds ('Heuweltjies') of the southern and western Cape of South Africa, south of the Orange River. Mima-like mounds are different from the Namibian circular barren patches in a number of aspects. Basically, they are well vegetated and are usually covered by plants such as grass or members of the genus *Euphorbia*. Mima-like mounds have been extensively researched by Lovegrove and Siegfried.^{7,8} They found R-values of spatial distribution of 1.7 and a density of 335.37 (± 19.29) per km² and a nearest-neighbour distance of 47.14 m. They postulate that termites and molerats are the principal agents involved in the construction of the mounds. Numerous studies have shown that regularity in the spacing patterns can be attributed to intra-specific competition for space among animals such as antlions, limpets, crabs, birds (nests) and corals.⁸ The R-values for the barren circles (1.68, reported here) and the 'Heuweltjies' (1.7) are remarkably close and suggest that termites are involved in both phenomena.

Size of circular, barren patches

Five representative areas of Fig. 1 were scanned (Genius Color Page HR5 scanner) using Adobe Photoshop software and applying the 'inversion' and 'brightness/contrast' modes. In this way barren patches appeared as black objects on a white background and diameters could be readily measured. At the final magnification, 1 mm was equivalent to 1 m, and the following distribution of sizes was found: 3 m (3%), 4 m (4%), 5 m (20%), 6 m (24%), 7 m (32%), 8 m (11%), 9 m (6%). No circles were found larger than 9 m or smaller than 3 m (probably the resolution limit of the aerial photograph). The average diameter was 6.17 m. This suggested that the barren circles studied had a size at maturity of between 6 and 7 m and that 27% of the circles with smaller diameters may be less mature and in the process of growing larger. Moll also reported a range of diameters from 1.2–6.7 m for barren circles in the Rooilepel area, about 300 km south of Wolwedans.¹

Moisture content of soil

Twelve soil samples were collected from the middle of a mature barren circle, one after another, in a vertical direction to a

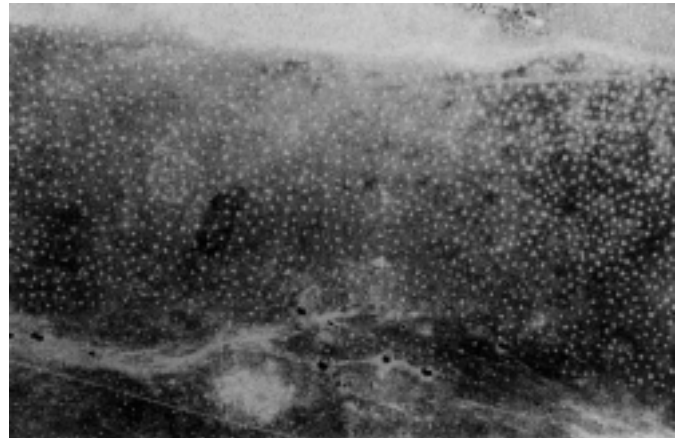


Fig. 1. Aerial photograph of circular, barren patches lying between the edge of the Namib desert (top) and a dry river bed (bottom). Note different patch diameters (average of 6.17 m) and semi-regular spacing.

depth of one metre. This was done at the beginning of April 1997, after extensive rains 12 days before sampling. (According to records of the NamibRand Nature Reserve, where the studies were done, 36 mm of rain was recorded on 18 March and 30 mm on 11 February 1997. This was exceptional because the average annual rainfall for the pro-Namib is between 90 and 120 mm⁹). Representative samples were stored in 10-ml glass test tubes with tight-fitting rubber stoppers and stored upside-down to keep the moisture trapped. A similar set was collected from a spot between two barren circles. Subsequently, the soil samples were weighed and exposed to ambient conditions (temperature maximum = 32°C), for a few days, until constant weight. Weight loss (expressed as a percentage) for samples from the middle of the barren patch was as follows: sample 1 (top) to sample 12 (bottom): 0, 0.13, 0.15, 1.08, 0.57, 1.1, 2.2, 0.83, 3.02, 0.93, 1.73 and 1.77%. For soil samples taken from outside the barren patch, the following results were obtained; sample 1 (top) to sample 12 (bottom): 0, 0, 0, 0.07, 0.13, 0.14, 0.39, 0.38, 0.32, 0.39, 0.28 and 0.35%. The percentage weight loss per sample was interpreted to represent loss of water. The average weight loss for soil taken from the middle of the barren patch was 1.13%, while that for soil taken outside the circle was 0.20%. These results suggest that, for this particular set of samples, on average, the inner soil contained five times more water than the outer soil and that this difference was mainly in the soil found between about 32 cm (sample 4) and 100 cm (sample 12) below the surface. Water retention in the soil from inside the barren patch is probably due to a total absence of plants and transpiration as well as the concave shape of the barren patches that helps to create a 'water trap' that collects run-on water after rains. Indeed, locals have mentioned to us that, after extensive rains, the barren patches appear as 'small swimming pools'.

Natural evolution of barren patches

Our observations of many dozens of barren patches have suggested that these circles go through a natural evolutionary process of genesis, development and eventual extinction. Searching revealed a small number (less than 5%) of open patches containing mature tufts of *Stipagrostis giessii* that appeared dead. These patches had markedly diminished grass cover, were not clearly circular and were less than 6 m in diameter (Fig. 2). We consider these patches to represent the genesis of circular barren patches.

An equally small number of more circular patches were found, also studded internally with dead, mature tufts of *S. giessii* and

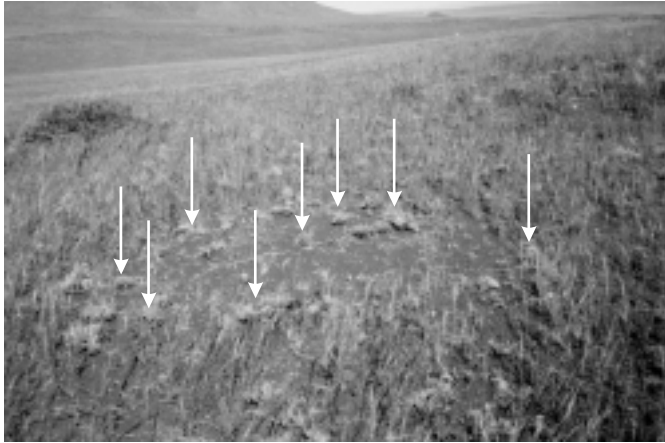


Fig. 2. Genesis of a new patch is characterized by dead tufts of *Stipagrostis giessii* (arrows), diminished grass cover and irregular outline.

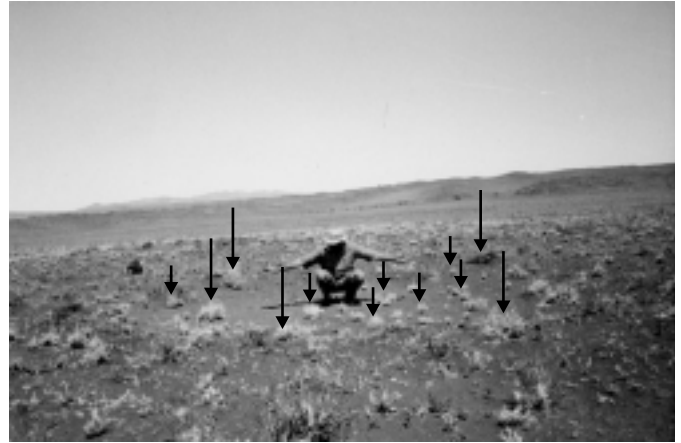


Fig. 5. An extinct barren patch is characterized by a concave shape and living tufts of *Stipagrostis giessii* (long arrows) and *S. uniplumis* (short arrows) growing inside and outside the patch.



Fig. 3. A developing patch is characterized by tufts of dead *Stipagrostis giessii*, more extensive loss of grass cover, a more circular shape and a diameter of up to 6 m.

had diameters of about 6 m (Fig. 3). We consider these patches to be in the process of developing into more mature forms. The majority of patches were 6–7 m in diameter, with no plant cover and demarcated with a prominent ring of *S. giessii* which were alive and growing (Fig. 4). Having achieved maximum diameter, these circular patches were considered to be mature. A few circles were also found that we considered to be extinct (Fig. 5). They were overgrown with mature, living *S. giessii* and



Fig. 4. A mature barren patch has a diameter greater than 6 m, a total lack of grass cover and mature, living tufts of *Stipagrostis giessii* growing on the near perfect, circular periphery.

new, growing seedlings of *S. uniplumis* and had the characteristic concave shape, which is thought to be caused by prolonged exposure to the wind.¹

The demarcation between the bare soil inside the circle and the grass growing on the edge is quite sharp, and is well characterized especially after a good rainy season (as was the case in April 1997) and is demonstrated in Fig. 6. Figures 2–5 were recorded in April 1993 after a drought period had been broken by rains falling about 14 days previously.

Root morphology of Stipagrostis uniplumis

During a visit to Wolwedans in April 1997, after extensive rains, grass seedlings (*S. uniplumis*) had begun to grow inside and outside barren circles. Many of the plants inside the circles were growing close to the edge and some of them were clearly desiccated and dead, whereas others outside the circles were alive. Similar observations have also been reported by Moll.¹

Thirteen plants were collected from inside and outside circles. Roots were carefully dislodged from the loose sand. Whereas plants from outside the circles had roots that were tenaciously coated with sand, roots from plants inside the circles had little sand attached (Fig. 7). Most (92%) of the root lengths of plants growing outside the circles were covered with sand compared with only 32% for plants growing inside the circles. Observation of the roots under a dissecting microscope at $\times 100$ magnification showed that the sand particles were tenaciously attached by



Fig. 6. A typical, mature, barren patch surrounded by *Stipagrostis giessii* tufts after copious rains. Notice the sharp demarcation between the inside and outside of the patch.

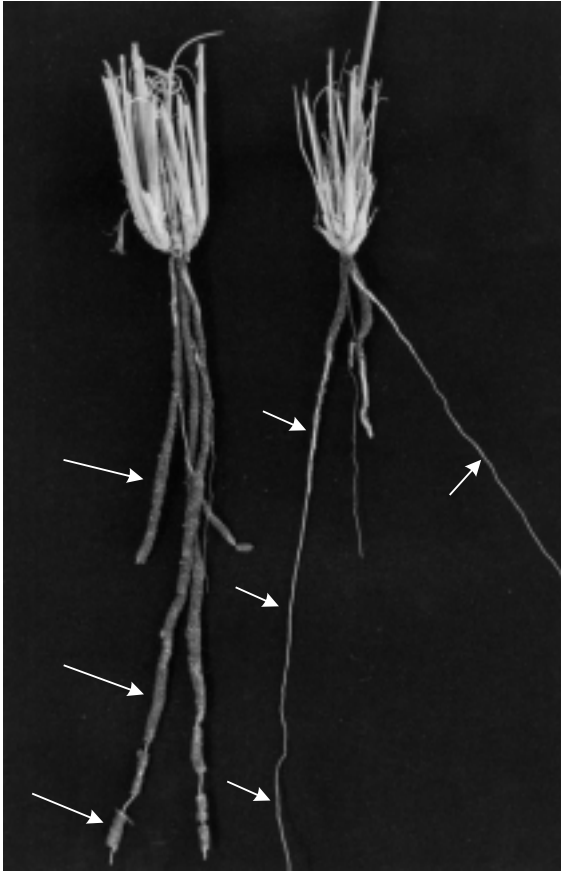


Fig. 7. Examples of a *Stipagrostis uniplumis* plant from outside (left) and inside (right) a mature, barren patch. Note the extensive coating of the roots with tenaciously attached sand (left, long arrows) compared to the uncoated roots of the plant growing inside the patch (right, short arrows).

side-root hairs. Very few side-root hairs were present on roots of plants growing inside the circles.

Germination experiments with *Cynodon dactylon*

Moll reported that none of his germination experiments with commercially available alfalfa and grass seeds showed any significant difference between emergence rates in inner and outer soil samples.¹ We tested this observation by first collecting seven soil samples as follows from a mature circular patch: (1) 3 m from the edge outside the circle, (2) on the edge, (3) halfway between the edge and centre, (4) the centre, (5) halfway between the centre and the opposite edge, (6) the opposite edge and (7) 3 m from the opposite edge outside the circle. Thirty grams of

each of these seven soil samples was placed in a plastic 'ice-cube' tray, made moist with distilled water and seeded with about 100 seeds of *Cynodon dactylon* (GRO-PAK Cape Royal Lawn Grass Seed, Batch N9541, Straathof's Seeds, Honeydew). Seeds were grown at ambient temperature, indoors (daily maximum 32°C during the summer of 1999 in Cape Town). The seedling tray was meticulously watered twice a day with distilled water. Fifteen days after germination began, the different soil samples contained the following numbers of growing seedlings: sample 1 = 74, sample 2 = 74, sample 3 = 63, sample 4 = 50, sample 5 = 64, sample 6 = 59 and sample 7 = 49. There did not appear to be a statistically significant difference between the number of seedlings in the different wells correlating with inner and outer soil samples, as was reported by Moll for other seeds. After 22 days of growth and continuous addition of water, the tray with the seven samples was placed in direct sunlight and allowed to dry out for 24 h in order to simulate conditions of intermittent rains in the pro-Namib. After this dry-out period, there were no macroscopic differences among the seedlings, and the plants were subjected to dehydration every second day followed by rehydration. After 5 days of hydration and dehydration episodes, some of the seedling shoots started to collapse. The number of upright shoots in the different soil samples were counted, after 5 days of hydration and dehydration, and gave the following results: sample 1, 43; sample 2, 55; sample 3, 20; sample 4, 7; sample 5, 21; sample 6, 22 and sample 7, 19. Thirty-five days after the start of the experiment and 12 days after daily episodes of dehydration and re-hydration, the numbers of upright shoots in the different soil samples were; sample 1, 31; sample 2, 43; sample 3, 3; sample 4, 0; sample 5, 0; sample 6, 24 and sample 7, 12 as shown in Fig. 8. These results clearly show that the seedlings of *C. dactylon* could survive cycles of dehydration and re-hydration only when grown in soil samples from outside (samples 1 and 7) and on the edge (samples 2 and 6) of the circular barren patch, but not from inside the patch (samples 3, 4 and 5).

This result strongly suggests the presence of a factor in the inner soil of the barren patch that inhibits resistance to dehydration in plants.

Conclusions

We conclude that the enigmatic, circular barren patches found in the pro-Namib of Namibia, are caused by a biologically active factor related in some unknown way to the presence of active termite nests.

We postulate that the main biological effect of the factor is a subtle one, namely to inhibit the resistance to dehydration-stress of plants such as *Stipagrostis giessii*, *Stipagrostis uniplumis* and

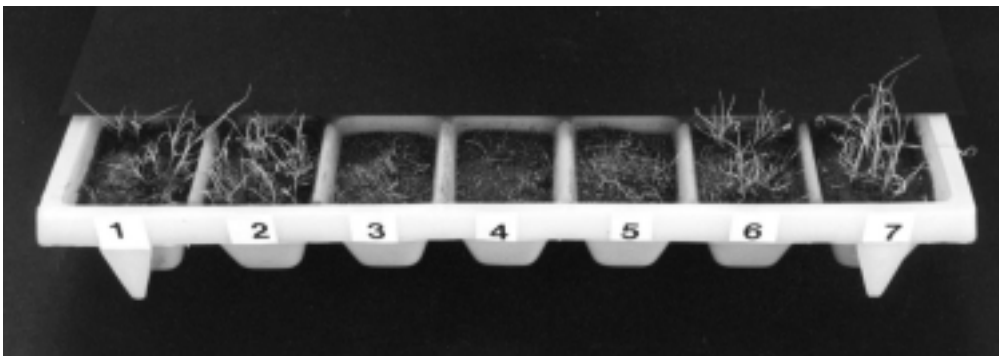


Fig. 8. Condition of shoots of *Cynodon dactylon* after 12 episodes of hydration and dehydration. The shoots remained upright in soil samples 1 and 7 from outside a barren patch and samples 2 and 6 from opposite edges of the patch, while the shoots collapsed in samples 3 and 5 from halfway between the centre and the opposite edges and also in sample 4 from the centre of the patch.

possibly also the test plant *Cynodon dactylon*. One obvious mechanism of such inhibition is inhibiting the growth or maintenance of side-root hairs as shown in Fig. 7. These side-roots increase the surface area of the roots of the plant in contact with the soil. This contact is vitally important in terms of the absorption of water and nutrients from the soil. We speculate that plants can germinate and grow in the barren patches when there is sufficient moisture from recent rains. Under these conditions, roots without root hairs could absorb sufficient water. Once the rains dissipate and the ground dries out, however, plants without adequate side-root hairs are doomed to die of dehydration.

It is also our belief that the circular barren patches have important survival value for termites by acting as 'water traps'. It has been proposed (Eric Holm, pers. comm.) that because termites are not covered by an extensive exoskeleton and are prone to rapid dehydration, they build their nests up to many metres under the ground and only come out at night. Consequently, if in some unknown way an abiosis factor could be produced by termites (or by organisms associated with them such as bacteria or fungi), and this factor could diffuse towards the surface, in a cone shape, this would lead to the formation of a circular barren patch. The barren patch could then act as a water trap after rains because the concave shape traps run-off water and transpiration is absent because of the absence of plants except on the edge. Our data support such a scenario as we found a fivefold higher concentration of water in the inner soil of a barren patch, compared to the outer soil.

At the heart of the hypothesis is the postulate of a biologically active abiosis factor. Preliminary experiments using methanol extracts of soil samples and analyses with an HPLC coupled to UV-diode-array-detection system¹⁰ revealed 19 distinct peaks in extracts from the inner and outer soil. Of these peaks, 18 were similar in retention time and UV spectrum and only one peak was present in the outer soil and absent in the inner (data not presented). Although these results do not support the hypothesis of a biological factor which is present only in the inner soil, it is clear that further chemical analyses with more sensitive apparatus such as GC-MS are required. The factor may be present at very low concentrations and may also be semi-volatile. This seems to be necessary to explain the circular shape of the patches. If the chemical had a high affinity for silica, it is difficult to imagine how it could diffuse to form such a large, almost perfectly circular, surface area. On the other hand, if the factor could diffuse readily to form a circular patch in which inhibition of plant growth occurs, there would need to be an active process whereby the agent is constantly replenished. We postulate that a viable termite nest below the circular patch is an essential feature of the active process but not necessarily the direct source of the factor. Isolation of the latter also depends on a suitable bioassay and, in this regard, *Cynodon dactylon* as reported here could be used with dehydration resistance (or lack of it) as an endpoint.

This hypothesis has much in common with that of Moll¹ except that our data, especially the result shown Fig. 8, point to a special factor in the inner soil causing intolerance to dehydration and do not rely on termites foraging seeds on the surface.

Understanding the factors that cause circular barren patches is principally driven by curiosity but may have relevance for a holistic understanding of the evolution of deserts. It is possible that a termite-induced peripheral zone of barren patches on the edge of the Namib, the oldest desert in the world, may help to extend the desert with time. The eventual isolation and biological evaluation of the putative abiosis factor may have implications for the control of plant growth and possibly even strategies aimed at preventing desertification.

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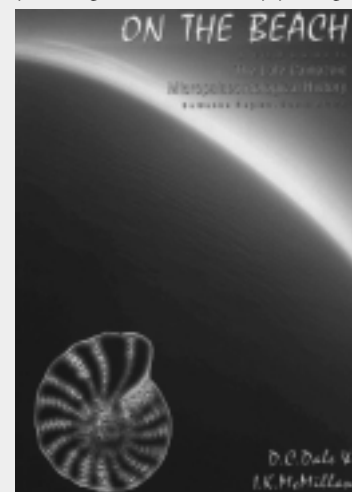
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