Mysterious circles in the Namib Desert: review of hypotheses on their origin

M.W. van Rooyen[a],*, G.K. Theron[a], N. van Rooyen[a], W.J. Jankowitz[b], W.S. Matthews[c]

[a] *Department of Botany, University of Pretoria, Pretoria 0002, South Africa*
[b] *School of Natural Resources and Tourism, Polytechnic of Namibia, Windhoek, Namibia*
[c] *Tembe Elephant Park, Private Bag X356, KwaNgwanase 3973, South Africa*

Abstract

Circular, slightly concave depressions, devoid of vegetation and often surrounded by a fringe of tall grasses occur in a broken belt in the pro-Namib zone of the west coast of southern Africa. Several hypotheses have been proposed to explain the origin of these so-called fairy circles. The most important of these relate to areas of localized radioactivity; termite activity; or allelopathic compounds released by dead *Euphorbia damarana* plants. No evidence of increased radioactivity could be detected in soil samples collected from these sites. Although termites occur at these localities no evidence was found to link termite activity directly to the formation of barren patches. Bioassays conducted on soil collected from the centre of the barren patch clearly demonstrated an inhibition of plant growth, while soil collected from the edge of the barren patch had a stimulatory effect on plant growth. No indication of growth inhibition was found in soil collected beneath *E. damarana* plants. At this stage none of the proposed hypotheses can satisfactorily explain the origin of the fairy circles.
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1. Introduction

One of the most fascinating and at the same time enigmatic phenomena in the desert regions of southern Africa are the so-called 'fairy circles' or 'fairy rings' of

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*Corresponding author. Tel.: +27-12-420-2009; fax: +27-12-362-5099.
E-mail address: gvrooyen@nsnper1.up.ac.za (M.W. van Rooyen).

Namibia. Fairy circles occur in a broken belt in the pro-Namib zone of the west coast of southern Africa (Fig. 1), extending from southern Angola through Namibia to just south of the Orange River in South Africa (Moll, 1994; Jürgens et al., 1997, pp. 189–214; Becker and Getzin, 2000). These circular, slightly concave depressions are devoid of vegetation and often surrounded by a fringe of tall grasses (Fig. 2). Although seedlings are sometimes found in these barren patches after good rainfall, they usually do not survive, leaving the patches completely bare for most of the time.
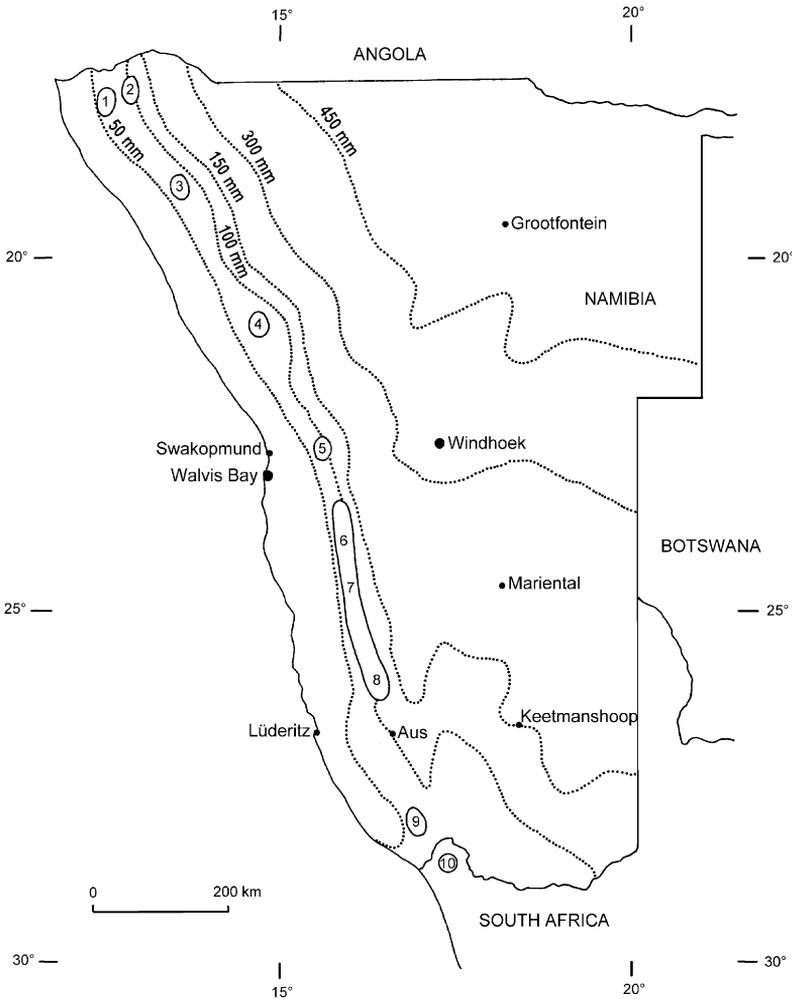
Fig. 1. Map of Namibia indicating the distribution of fairy circles and the approximate locations where soil samples were collected. (1) Hartmann's Valley∗, (2) Marienfluss∗, (3) Giribes Plain∗, (4) Brandberg, (5) Khan, (6) Escourt Experimental Farm∗, (7) Sesriem∗, (8) Namtib Guest Farm∗, (9) Rooiduin, (10) Kubus∗. Asterisk denotes sites where soil samples were taken, …. rainfall isohyets.

Fig. 2. Typical fairy circle in the Marienfluss clearly showing the fringe of tall *S. giessii* plants on the edge of the barren patch and *S. obtusa* growing in the matrix.

Most of the localities where fairy circles occur lie between the 50 and 100 mm isohyet, with some of them extending between the 100 and 150 mm isohyet (Fig. 1). Because fog is still frequent up to 80 km inland (Louw and Seely, 1982; Jürgens et al., 1997), fog may be an additional source of moisture at some sites. In general, the altitude ranges between 500 and 1000 m. The localities are found roughly between 60 and 120 km inland.

The vegetation on the sandy plains where these barren patches typically occur, is generally scant, except following rain when a grassland, composed mainly of *Stipagrostis* species, covers the plains (Viljoen, 1980; Louw and Seely, 1982). In the Kaokoveld (north-west Namibia) the most extensive fairy circle locations are in the Hartmann's Valley, Marienfluss and Giribes Plain. In these areas the vegetation between barren patches (matrix) is composed mainly of a short-lived grass species, *Stipagrostis uniplumis* (Licht.) De Winter, and the conspicuous fringe around the edge of the patch consists of either *S. giessii* Kers or *S. hochstetteriana* (Beck ex Hack.) De Winter, which are both perennial species. South of the Kuiseb River *S. obtusa* (Del.) Nees replaces *S. uniplumis* in the matrix, and *S. ciliata* (Desf.) De Winter forms the edge. In some cases *S. obtusa* forms both the matrix and the edge. In the Richtersveld and the far southern part of Namibia fairy circles also occur in a succulent shrubland with almost no grasses.

In general, fairy circles decrease in size from north to south and the edge of the circle is not as well developed (often even absent) in the southern part of the distribution range. In the Hartmann's Valley fairy circles are on average the largest with a mean diameter of 10 m; in the Marienfluss mean diameter is 7.5 m; in the Giribes Plain 6.2 m; at Escourt Experimental Farm near Tsondab Vlei 5 m; while in

the Sperrgebiet at Rooiduin and in the Richtersveld near Kubus circles have a mean diameter of only 2 m.

The earliest scientific reference to the formation of fairy circles is found in Tinley (1971, 1974) who proposed that they were fossil termitaria formed when the annual rainfall was considerably higher. Theron (1979) hypothesized that an allelopathic compound released by dead *Euphorbia damarana* plants could be responsible for the barren patches. Eicker et al. (1982) reported on a microbiological study of the barren patches in the Giribes Plain, but offered no explanation for their origin. Moll (1994) suggested that these bare circles were caused by termites consuming all the grass seeds in the immediate vicinity of their nests and implicated *Hodotermes mossambicus* as the most probable termite species. Becker and Getzin (2000) elaborated on Moll's hypothesis without providing conclusive evidence. In 2001 Albrecht et al. claimed that these barren patches are caused by a semi-volatile chemical substance associated with viable termite nests.

The aim of this paper is to report on observations and experiments done on fairy circles over a 22-year period and to re-evaluate the strengths and shortcomings of the hypotheses on their origin in the light of our current knowledge. Fairy circles are compared to other spatial vegetation patterns and the possible advantage of such patterning is discussed.

2. Methods

2.1. Long-term observations

In 1978, a site in the Giribes Plain in the Kaokoveld was selected where fairy circles are well-developed. To determine the longevity of these circles, five barren patches were marked permanently with steel droppers inserted to a depth of 1 m. This site was revisited in 2000 to relocate the droppers and note any visible changes. Unfortunately, the diameters of the barren patches were not measured in 1978 and no changes in size could be established on returning to the site in 2000.

To test the allelopathic hypothesis a site in the Giribes Plain where *E. damarana* grows in the matrix between barren patches was selected in 1979. The positions of all barren patches, all live and all dead *E. damarana* plants within a hectare were plotted on scale. In 2000, after 21 years, this site was revisited to determine whether the dead *E. damarana* patches had developed into barren patches as predicted by the allelopathy hypothesis.

2.2. Bioassay of soil

In April 2000, soil samples were collected from the three most prominent fairy circle localities in the Kaokoveld: Giribes Plain, Hartmann's Valley and Marienfluss. At all these sites fairy circles occur in deep sandy soil on plains. At the time of sampling both the Giribes Plain and Hartmann's Valley were extremely dry and the *S. uniplumis* matrix grassland was almost absent. However, barren patches were

clearly demarcated by the stubbles of *S. giessii* or *S. hochstetteriana* on the edge. In contrast, the Marienfluss had received good rain some weeks earlier and a well-developed *S. uniplumis* grassland covered the valley floor. At all three sites soil samples were collected from the top 200 mm soil in the (a) matrix; (b) edge of the barren patch; and (c) centre of the barren patch. In the Giribes Plain samples were also collected at the site where *E. damarana* grows (see section on long-term observations). At this site soil samples were collected from the (a) matrix; (b) edge of the barren patch; (c) centre of the barren patch; (d) beneath a live *E. damarana* plant; and (e) beneath a dead *E. damarana* plant. One soil sample was also collected at a depth of approximately 0.5 m in the centre of the barren patch. At this depth a layer of gravel and pebbles was encountered.

Bioassays were conducted on the collected soil at the University of Pretoria using *Lolium multiflorum* Lam. as bio-indicator. This species was chosen because it is a small-seeded species and cannot rely on seed reserves for a long time. It also germinates well and grows quickly. Although it would have been ideal to use an indigenous grass species from the area as bio-indicator, the seeds of indigenous grass species often have dormancy patterns making them less suitable for bioassays.

One dm^3 pots were filled with soil samples and seeded with 50 seeds of *L. multiflorum*. Plants were watered daily with distilled water. Leaching of the soil was prevented by standing each pot in a collecting tray and circulating any drained water. Seedlings were thinned to 20 per pot within 14 days. Four replicates of each treatment were used.

After 3 months, all 20 plants per pot were harvested and the lengths of the shoots of each individual plant measured. Above- and below-ground dry masses per pot were determined after drying the plant material at 70°C until a constant dry mass was reached. Data were analysed statistically by means of an analysis of variance (ANOVA) at a 5% level of significance using the STATISTICA 5 computer package (STATISTICA for Windows, StatSoft Inc. 2300 East 14th Street, Tulsa, OK 74104).

2.3. Soil analyses

Two field trips were undertaken to collect soil samples for the present study. The first field trip was in April 2000 and covered the Kaokoveld sites. The second field trip to the southern sites was during June/July 2001. Standard soil analyses, including pH, resistance, nitrogen, phosphorus, calcium, potassium, magnesium and sodium content, were performed by the Department of Soil Science, University of Pretoria, on the soil collected for the bioassay during 2000.

Soil samples of the top 200 mm, in the matrix, edge and centre of the barren patch from all the collection sites in both 2000 and 2001 were used for the radiation tests. At Escourt Experimental Farm additional samples were also taken at 0.5 m intervals to a depth of 2 m from the centre of the barren patch and in the matrix. Samples were tested for the presence of radiation by a calibrated Eberline ESP-2 contamination monitor with an alpha-beta-gamma-probe HP-260 by the Radiation Metrology Laboratory at the South African Bureau of Standards.

2.4. Termite activity

With the exception of Kubus, one to two well-developed fairy circles were selected at each of the sampling sites visited in 2000 and 2001. Trenches were dug from the centre of the barren patch to 0.5 m into the matrix and the soil profile in these trenches was inspected carefully for termite activity. Any sign of above-ground termite activity was also noted. The depth of the trenches varied from 0.5 to 2.2 m, depending on the depth at which a compact layer was encountered. Only at Escourt Experimental Farm was the trench dug through this layer to a depth of 2.2 m. From 1978 to 1983 several trenches through fairy circles in the Kaokoveld had been investigated in a similar way in different seasons.

3. Results and discussion

3.1. Long-term observations

All five marked barren patches in the Giribes Plain were relocated, and after 22 years were still clearly discernible as barren patches with no visible signs that the patch was recovering.

At the *E. damarana* site in the Giribes Plain all the plotted barren patches within the 1 ha site could be relocated and none of the patches had disappeared. All the dead *E. damarana* plants could also be relocated. Decomposition in this arid area is so slow, that the remains of dead *E. damarana* plants were still present and no signs could be found of new barren patches being formed at dead *E. damarana* positions. The only change that was noted, was that some of the live *E. damarana* plants had died in the intervening 21 years, without any recruitment of new plants occurring.

3.2. Bioassay of soil

At the time of harvest all plants were still alive, but the plants in the barren patch soil showed signs of severe chlorosis. If the growth in the matrix soil is taken as the norm an analysis of the shoot biomass, root biomass and shoot length of *L. multiflorum* plants grown in soil from the Giribes Plain (Fig. 3a and b, Tables 1 and 2) revealed the following trends:

> Shoot and root growth were severely inhibited in the topsoil from the centre of the barren patch;
> Shoot and root growth were significantly stimulated in the topsoil from the edge of the barren patch;
> No inhibition of shoot or root growth was evident in the topsoil beneath either live or dead *E. damarana* plants;
> Soil beneath dead *E. damarana* plants had a stimulatory effect on shoot and root growth; and
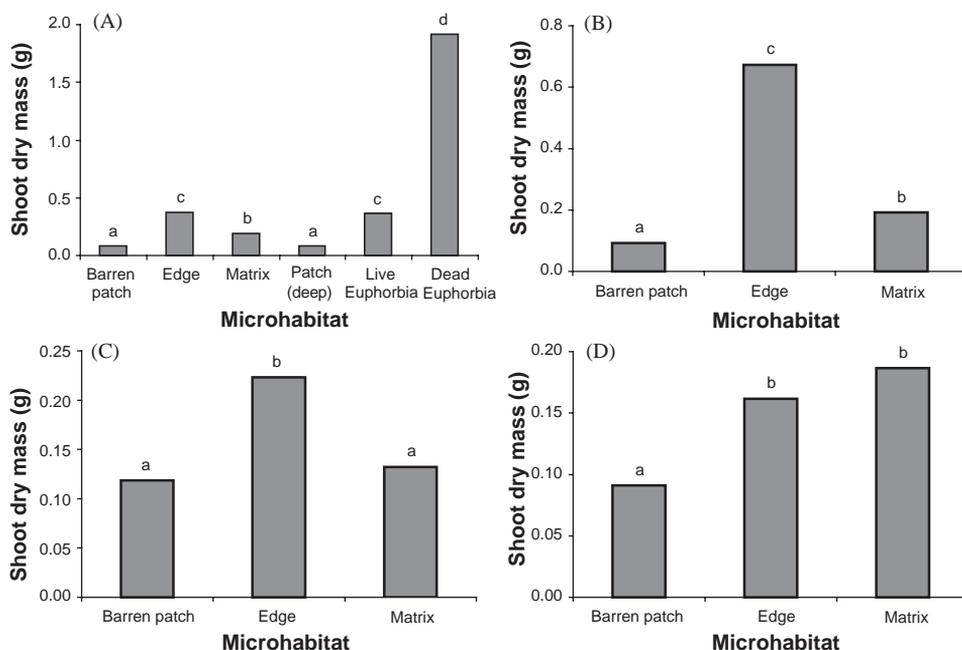
Fig. 3. Bioassays of soils collected at different locations. (A) Giribes Plain site with *E. damarana*; (B) Giribes Plain site without *E. damarana*; (C) Marienfluss; and (D) Hartmann's Valley.

Table 1
Root biomass (g) of *L. multiflorum* plants grown in soil from different locations and microhabitats

	Root biomass (g)			
	Giribes Plain[a]	Giribes Plain[b]	Marienfluss	Hartmann's valley
Barren patch (topsoil)	0.333 ± 0.048	0.348 ± 0.510	0.443 ± 0.050	0.384 ± 0.089
Edge of patch	1.235 ± 0.067	2.343 ± 0.177	0.921 ± 0.112	0.770 ± 0.051
Matrix	0.776 ± 0.093	0.692 ± 0.089	0.593 ± 0.089	0.825 ± 0.136
Barren patch (deep soil)	0.287 ± 0.007		0.509 ± 0.083	
Under live *Euphorbia* plants	0.718 ± 0.216			
Under dead *Euphorbia* plants	1.139 ± 0.244			
P-value	3.22E–07	1.44E–08	9.72E–05	7.12E–04

[a] Site with *E. damarana* plants.
[b] Site without *E. damarana* plants.

Soil collected at a depth of 0.5 m in the centre of the barren patch still inhibited shoot as well as root growth.

Therefore, the bioassay clearly indicated that growth was influenced by the microhabitat of the soil sample. However, Theron (1979), Moll (1994) and Albrecht

Table 2
Shoot length (mm) of *L. multiflorum* plants grown in soil from different locations and microhabitats

	Shoot length (mm)			
	Giribes Plain[a]	Giribes Plain[b]	Marienfluss	Hartmann's valley
Barren patch (topsoil)	61.03 + 5.68	63.00 + 5.83	68.78 + 3.88	66.40 + 4.63
Edge of patch	127.38 + 13.86	159.23 + 10.36	100.93 + 1.20	83.83 + 2.38
Matrix	91.68 + 4.07	92.75 + 2.49	74.13 + 6.81	87.48 + 4.40
Barren patch (deep soil)	63.75 + 3.89		100.70 + 3.22	
Under live *Euphorbia* plants	137.88 + 13.18			
Under dead *Euphorbia* plants	252.53 + 111.40			
P-value	1.15E–10	1.21E–07	2.43E–08	2.24E–04

[a] Site with *E. damarana* plants.
[b] Site without *E. damarana* plants.

et al. (2001) all concluded that germination was not significantly reduced in barren patch soil.

Results obtained with soil from Marienfluss indicated a stimulation of shoot and root growth in the edge soil (Fig. 3c; Table 1 and 2) but no significant growth inhibition in barren patch soil. Although earlier bioassays of soil collected at the Marienfluss exhibited the typical inhibitory action of barren patch soil (Theron, pers. com.), samples collected in 2000 did not show a significant reduction of growth in the barren patch soil. It is possible that the inhibitory substance(s) was(were) leached to a depth below 200 mm (sampling depth) by the good rainfall prior to soil collection. Under field conditions seedlings do become established after a good rain, but most of them die off. Seedling death could be caused by the inhibitory substance being translocated to the surface layers again as the soil dries out, or because roots come into contact with the inhibitory substance when deeper layers are penetrated.

During the field visit to the Marienfluss in 2000 several different types of fairy circles were noticed. A small number of fairy circles were observed where *S. uniplumis* had established within the patch. In some cases the plants in the centre of the patch had died after growing only a few centimetres tall, but the dead plants were still present in the patch, whereas in other cases the plants had grown to maturity but could be distinguished from the surrounding vegetation by their light yellow–green foliage. Another interesting phenomenon noticed in the Marienfluss was the formation of concentric zones within the barren patch (Fig. 4). The centre of these patches was bare and surrounded by a circle of relatively healthy *S. uniplumis* plants. On the outside of this circle a zone of small dying plants was encountered before reaching the permanent edge composed of *S. giessii*.

Results obtained with soil from Hartmann's Valley (Fig. 3d; Tables 1 and 2) indicated that growth was inhibited in topsoil from the barren patch, however the stimulatory effect of the edge soil could not be demonstrated in potting trials. At the time of sampling the circular arrangement of *S. giessii* plants was conspicuous in the field, however, the plants were widely spaced and the soil sample was collected between plants. Because it is impossible to detect the exact boundaries of the edge
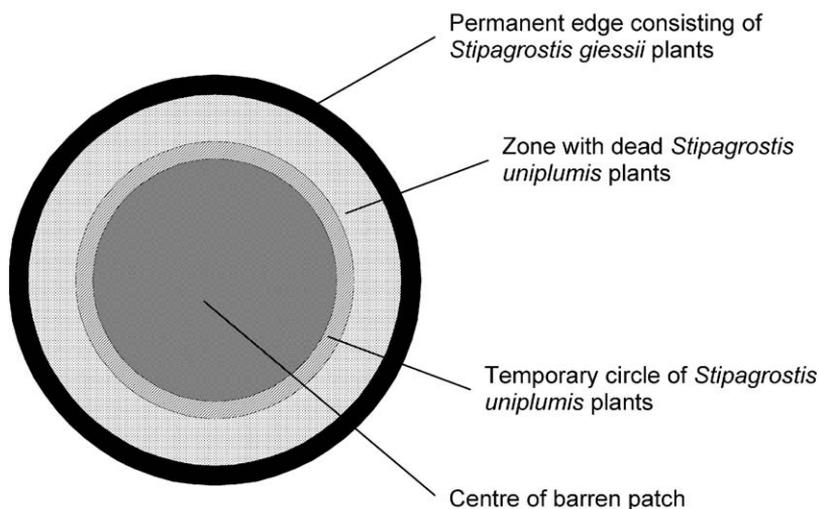
Fig. 4. Diagram indicating the presence of concentric zones in fairy circles in the Marienfluss.

zone, it could have been missed by the sampling. Furthermore, if the edge effect is associated with the perennial plants and does not form a continuous band, the stimulatory effect would also have been missed by sampling between plants.

These patterns observed for plant biomass are paralleled by patterns of microbial population densities and diversity (Eicker et al., 1982). The lowest microbial activity occurred in the barren patch, the highest on the edge and the matrix intermediate. The diversity of fungi reflected the same pattern, however, in the case of anaerobic bacteria the order was reversed with the highest activity recorded in the barren patch and the lowest at the edge.

3.3. Soil analysis

The only attribute correlating with the growth of plants in soil from different microhabitats was soil resistance—being highest in the barren patch soil and lowest in the edge soil (Table 3). The difference in resistance between the different microhabitats was however not statistically significant ($p = 0.09$). The pH, phosphorus, sodium, magnesium, potassium and nitrogen contents did not show any significant trends between microhabitats ($p > 0.05$) although the differences between sites for pH, phosphorus, calcium and potassium were statistically significant. On the whole, the soil analysis indicated that differences between the soils of the various microhabitats at one site were slight and not sufficient to result in such a marked response in plant growth.

Almost no difference in organic matter content was observed in soil collected from different microhabitats in the Giribes Plain in a dry season (Verleur, 1977). The organic matter constituted 0.76% of the soil dry mass for the barren patch soil, as

Table 3
Chemical analysis of soil at different sites and microhabitats

Position	Locality	pH H$_2$O	Resistance (Ω)	(P Bray) (mg kg^{-1})	Ammoniumacetate extractable cations				
					Ca (mg kg^{-1})	K (mg kg^{-1})	Mg (mg kg^{-1})	Na (mg kg^{-1})	Total N (mg kg^{-1})
Barren patch	Giribes Plain[a]	9.4	10000	13.9	1245	43	43	22	14
	Giribes Plain[b]	9.4	7500	16.9	1205	119	49	12	84
	Marienfluss	6.7	6000	16.3	300	76	258	22	294
	Hartmann's Valley	7.9	10000	11.9	260	51	100	23	168
Edge	Giribes Plain[a]	8.9	2500	19.6	811	69	49	41	84
	Giribes Plain[b]	9.1	1500	17.7	930	144	87	49	154
	Marienfluss	7.0	5500	19.9	336	100	159	12	140
	Hartmann's Valley	8.9	8500	12.4	295	54	85	21	154
Matrix	Giribes Plain[a]	9.4	7500	19.3	834	66	43	26	98
	Giribes Plain[b]	9.3	5000	15.8	2350	152	93	46	70
	Marienfluss	7.8	9000	20.4	222	73	174	24	112
	Hartmann's Valley	8.7	7500	12.2	526	56	493	227	98
Beneath *Euphorbia*	Live plants	8.7	1000	24.9	1550	173	168	76	546
	Dead plants	7.6	450	122.3	2115	449	452	252	0[c]

[a] Site with *E. damarana* plants.
[b] Site without *E. damarana* plants.
[c] Unable to determine.

against 0.80% for the edge soil and 0.78% for the matrix soil (Verleur, 1977). However, the organic matter content of the soil will vary between seasons and is highly dependent on the seasonal rainfall.

Moll (1994) compared the compaction, infiltration rate and soil texture in a barren patch with the matrix. He found that fairy circle soils were slightly more compact than those in the matrix and that water percolates slower inside than out (no statistical analyses were quoted). He attributed these differences to the higher clay content in the soils of the fairy circles (4% in the circle as opposed to 3% in the matrix) and concluded that these differences were due to the activities of termites. A spectrophotometric analysis also revealed a larger fraction of suspended particles in the soil from the barren patch compared with matrix soil (Verleur, 1977).

In none of the samples examined was a significant increase in background reading detected in the radiation test.

3.4. Termite activity

According to Coaton and Sheasby (1975) a maze of galleries about 12 mm in diameter is found where *H. mossambicus* is active. These galleries link the hive with the surface soil dumps, foraging ports and storage chambers and are concentrated mainly in the upper 300 mm of soil surface (Coaton and Sheasby, 1975). However, none of the trenches revealed any termite tunnels. Although termites were observed above-ground during the field investigations, their activities were not noticeably associated with fairy circles but rather seemed restricted to isolated grass tufts in the matrix without any indication of the initiation of a new fairy circle.

4. Evaluation of hypotheses

4.1. Vegetative growth patterns

Danin and Orshan (1995) studied the circular arrangement of *S. ciliata* clumps in the Negev Desert in Israel as well as near Gokaeb in Namibia. They suggested that the formation of circles was caused by a specific type of vegetative multiplication. The authors mention that *S. giessii* has the same growth pattern and imply that the edge of fairy circles are derived in this way. The inhibition of growth in the centre of the circle is, however, not explained by this mechanism.

Louw and Seely (1982) also described circles and rings of grasses near Gobabeb in the Namib. The vegetation circles or patches described by them show exactly the opposite pattern to fairy circles, by having a much higher grass cover within the circle (Louw and Seely, 1982). However, many of these vegetation patches are bare in the centre with only the circle of grasses remaining on the edge, giving them the appearance of a fairy circle. The vegetation circles studied by Danin and Orshan (1995) are the same as those described by Louw and Seely (1982) and should not be confused with fairy circles. In contrast to fairy circles which occur in sandy soil, these vegetation circles occur in stony soil. Vegetation circles produced by *S. ciliata* in

these stony soils are also considerably smaller (only slightly more than 2 m in diameter) than fairy circles, which can become up to 14 m in diameter. Excavations done by the present authors at these sites indicated that the calcrete basement was considerably deeper in the vegetated patch than outside. This differs from fairy circles where soil depth in the circle and the matrix is always the same. Cox (1987) investigated these vegetation circles in more detail and postulated that rodents increased the permeability of the soil to water and as a result dense stands of annuals could develop after periods of rain. Rodent activity is, however, probably not the cause of the patches but a consequence of the deeper soil.

4.2. Radioactivity hypothesis

According to the radioactivity hypothesis the sand in the plains were derived from granites of the Damara geosincline, which often contain radioactive elements such as Uranium and Potassium 40 (Karaerua, 2000). Field studies investigating the effect of radiation on vegetation have reported the establishment of different zones (Fraley, 1987). After 9 years of chronic radiation Fraley (1987) identified a 'lethal zone', where all vegetation had died, an 'effects zone', where some species decreased and others increased and a 'no effects zone', where no changes were detected. The vegetation zones described by Fraley (1987) are similar to those observed for fairy circles. However, soil samples analysed by the South African Bureau of Standards showed no increased radiation and this hypothesis cannot be supported.

4.3. Allelopathy hypothesis

This hypothesis was primarily based on the fact that the mean diameter of barren patches and those of *E. damarana* plants in the Giribes Plain are very similar (Theron, 1979) The spatial distribution pattern of barren patches also resembles the arrangement of live *E. damarana* plants. It was proposed that *E. damarana* plants produced an allelopathic compound or accumulated large amounts of minerals, which were released into the soil after the plants had died. These minerals could exert a toxic or allelopathic effect on growth of other plant species.

The main shortcoming of this hypothesis is that *E. damarana* prefers a stony habitat and that it seldom occurs in the sandy habitats where most of the fairy circles are found—the site selected in the Giribes Plain being an exception to the rule. It was therefore suggested that *E. damarana* was once plentiful in the plains and that plants had died after the sand was deposited making their habitat unfavourable. Because allelopathic compounds usually degrade with time, the longevity of the circles argues against an allelopathic origin. Even if the decomposition is slow in such an arid environment, it is unlikely that an allelopathic effect of *E. damarana* could still be active if no signs of any *Euphorbia* plants can be found on most of the plains. A modification of the allelopathy hypothesis has also been suggested, i.e. that when *E. damarana* is burnt, it releases a stable compound that is toxic to plant growth. Although fire is not common in a desert environment, in years of good rainfall the grassy plains, such as those found at Giribes and Marienfluss, support enough plant cover to carry a fire.

According to the allelopathy hypothesis the soil collected beneath dead *E. damarana* plants should inhibit plant growth. However, no sign of growth inhibition was found in the bioassay of this soil, rather a stimulation of plant growth was obtained and as a result the allelopathy hypothesis has to be rejected.

4.4. Termite related hypotheses

Fairy circles in Namibia are often linked to the mima mounds ('heuweltjies') found in the Succulent and Nama Karoo Biomes in South Africa and are regarded as the northern counterpart of these mounds (Lovegrove, 1993). In the Richtersveld, the southernmost distribution of fairy circles and the northernmost distribution of heuweltjies (earth mounds) overlap. Heuweltjies in the Richterveld are also sometimes mistaken for fairy circles, because heuweltjies in this region are often also devoid of vegetation and do not always have the typical mound shape. Examination of eroded and intact heuweltjies in the Clanwilliam district, South Africa, could conclusively show that they were well-established active termitaria of the harvester termite, *Microhodotermes viator*, while the unoccupied lower portions of the mounds contained fossil evidence of earlier inhabitation by the same species (Moore and Picker, 1991).

Although Moll (1994) was the first author to suggest *H. mossambicus* as the agent of fairy circle formation he was unable to collect this species during field observations. He found a few individuals of *Baucaliotermes hainsei* as well as *Psammotermes allocerus* but stated that these species are unlikely to be responsible for fairy ring formation. Becker and Getzin (2000) collected *H. mossambicus* and developed a hypothesis linking this species directly to fairy circle formation. According to their hypothesis in years with average precipitation *H. mossambicus* only harvests in the vicinity of the breeding nest, which is placed in the centre of the nest system, but not beneath a fairy circle. Foraging results in circular or sub-circular denuded patches. If the grass cover becomes scarce in the vicinity of the nest, workers extend their subterranean galleries and build new foraging ports. As a result new denuded patches are formed further from the nest while the abandoned old patches begin to recover. This process can be reversed once conditions become favourable again in the vicinity of the nest.

Albrecht et al. (2001) calculated the dispersion index (Clark and Evans, 1954) for barren patches in the Wolwedans area in Namibia and compared their value to that calculated by Lovegrove and Siegfried (1986, 1989) for heuweltjies. The R-values were remarkably close (1.68 for fairy circles and 1.7 for heuweltjies) and as a result they suggested that termites were involved in both phenomena.

While the magnitude of the phenomenon favours the termite origin for fairy circles, the mechanism, as presently proposed by Moll (1994), Becker and Getzin (2000) or Albrecht et al. (2001), cannot satisfactorily account for many important findings. The shortcomings of the termite hypotheses are:

- The fact that all marked patches were still clearly discernible after 22 years refutes the statement that the location of patches is dynamic (Moll, 1994; Becker and

Getzin, 2000) and that they disappear (Lovegrove, 1993) after a number of consecutive years of poor rainfall. Between 1979 and 2000 dry periods were experienced and fairy circles should therefore have disappeared.

- Moll (1994) suggested that the lack of vegetation in fairy circles was merely the result of termites having eaten all the grass seeds in the immediate vicinity of their nests. However, after good rainfall many small seedlings are noticed in the barren patches indicating that a lack of seeds is not the prime cause of barren patches. Patches remain bare because seedlings do not survive.
- Grube (2002) pointed out that the model by Becker and Getzin (2000) did not adequately take the behaviour of *H. mossambicus* into account. Observations in the Kaokoveld on actively foraging termites did not reveal that they harvested in circular patches and in areas with a dense grass cover foraging activity left hardly visible irregular bare areas (Grube, 2002). Furthermore, termites do not eat a plant totally, i.e. the leaves, the tuft itself as well as the roots. In general, no remnants of grass or any other plant are to be found in barren patches. In most cases where plant material was found in the patches, the entire dried remains, mostly of immature plants, were still visible. If the termite foraging hypothesis is valid many newly denuded patches with only grass stubbles left, should have been noticed after the good rains of the 2000 and 2001 seasons, when sampling by the present authors was done.
- The foraging hypothesis is also unable to explain the inhibition of growth observed in plants grown in soil collected from barren patches.
- Because termites can shift their surface activity from the hot daytime to the cooler night-time to protect workers from unfavourable temperatures, Becker and Getzin's (2000) explanation of how high temperature limits the size of barren patches is questioned by Grube (2002).
- Albrecht et al.'s (2001) hypothesis assumes that barren patches act as water traps to enhance the survival of termites. They sampled one barren patch 12 days after extensive rains and found that the soil within the patch contained more water than outside the patch. In our investigations of many patches in the Giribes Plain and Marienfluss this pattern was not consistent. Moll (1994) also indicated that water infiltrated slower into barren patch soil than matrix soil.
- The desiccation susceptibility hypothesis proposed by Albrecht et al. (2001) relies 'in some unknown way' on the presence of an active termite nest beneath the barren patch, which produces a semi-volatile substance 'inhibiting resistance to dehydration'. However, in potting trials (Fig. 3) growth inhibition was not linked to dehydration but occurred even in well-watered plants grown in barren patch soil. Rather than being the cause of the barren patch itself, the desiccation susceptibility might be a consequence of the inhibitory effects of the barren patch soil. The semi-volatile substance, supposedly present in barren patch soil, could not yet be demonstrated by Albrecht et al. (2001).
- The lack of the sheath around the roots of *Stipagrostis* plants growing in barren patches reported by Albrecht et al. (2001) could not be confirmed by the present authors.
- Damage by *H. mossambicus* usually takes the form of denuded patches fringed by grasses with horizontally cut-off stalks, leaving stubs with finely serrated edges

(Coaton and Sheasby, 1975). Plants on the edge of fairy circles, however, grew vigorously and did not show characteristic cut-off stalks.

- The proponents of the termite hypotheses differ regarding the location of the termite nest. According to Moll (1994) and Albrecht et al. (2001) the nest is located beneath the fairy circle, whereas Becker and Getzin (2000) suggest that the nest lies between circles. The presence of termite nests beneath the circle has yet to be demonstrated. Being deep under ground, between 1.5 and 6 m deep, the nests of *H. mossambicus* are apparently difficult to find and few people other than determined entomologists succeed in unearthing them (Skaife, 1979; Scholtz and Holm, 1985). However, even if the nests could not be found, termite tunnels should have been noticed in the trenches if termites were active (Coaton and Sheasby, 1975). The fact that the barren patch soil contains a larger fraction of suspended soil particles (Verleur, 1977; Moll, 1994) may indicate past termite activity.
- The distribution range of *H. mossambicus* covers most of southern Africa where rainfall is less than 750 mm per annum (Coaton and Sheasby, 1975). Fairy circles are limited to a small portion of this range with no similar phenomenon found in the rest of the termite's range. Furthermore, according to Coaton and Sheasby (1975) the habitat of this species does not extend into the dunes. However, in the central to southern part of the distribution range of fairy circles, barren patches do occur on dune slopes.
- According to the termite hypothesis the edge effect is not directly related to termite activity. Becker and Getzin (2000) suggest that plants on the edge have more water and nutrients available to them. Potting trials, however, indicated that the stimulatory effect that the soil on the edge of the barren patch has on plant growth is not merely due to an increased water supply. Growth of plants receiving exactly the same amount of water, was still promoted in soil from the edge of the barren patch (Fig. 3). It is possible that a dense circle of grasses can accumulate more litter than the matrix. Once such a dense stand has been established and litter is continuously accumulated, growing conditions will become more favourable at the edge, and the edge-effect should become self-sustaining. In some areas, grass tufts on the edge are not so densely packed that the edge can act as a litter trap. The absence of growth stimulation in the edge soil from the Hartmann's Valley, where grass tufts were widely spaced, is in keeping with this notion.

4.5. Vegetation pattern formation

In many arid and semi-arid environments throughout the world striking vegetation patterns, such as regular bands, spotted vegetation, labyrinths and bare patches have developed (Macfadyen, 1950; D'Herbes et al., 2001; Couteron and Lejeune, 2001; HilleRisLambers et al., 2001; Rietkerk et al., 2002). Different terms have been used to describe these vegetation patterns. The best known are probably the banded vegetation types, such as 'brousse tigrée' or tiger bush in West and East Africa (Seghieri et al., 1997; Couteron et al., 2000), 'mogote' in the Chihuahuan

Desert in northern Mexico (Mauchamp et al., 1994) and 'mulga' in Australia (Mabbutt and Fanning, 1987; Ludwig and Tongway, 1995; Ludwig et al., 1999). These landscapes are also often called two-phase mosaics because they form patches of bare soil alternating with patches of vegetation (Ludwig et al., 1999; Rietkerk et al., 2002). Although spotted vegetation and bare patches have been described for other parts of the world, the fairy circles of Namibia have never been mentioned in this context. Although the following discussion on vegetation pattern formation cannot offer an explanation for the origin of fairy circles the resemblance between the actual spatial patterns observed for fairy circles and the spatial patterns generated by two-phase mosaic models is striking (Couteron and Lejeune, 2001; Rietkerk et al., 2002).

No unifying mechanism has yet been suggested to explain the range of spatial patterns. One of the important considerations when dealing with two-phase mosaics is to determine whether the patterns are the result of pre-existing environmental heterogeneity or the result of self-organization, or both (Rietkerk et al., 2002). Most of the earlier explanations attribute the origin of banded systems to water re-allocation from bare areas to vegetated areas through run-off as overland sheet-flow (Tongway and Ludwig, 2001). These explanations require some form of environmental anisotropy, such as a gentle slope, to generate patterns. More recent models offer alternative explanations on how stable periodic patterns may arise.

The propagation-inhibition (PI) model (Lefever and Lejeune, 1997; Lejeune et al., 1999; Couteron and Lejeune, 2001) is based on the general premise that competitive interactions exert their influence over larger spatial scales than facilitative ones. This PI model could demonstrate that a slope-induced anisotropy was not essential to generate a spotted pattern of bare patches (Couteron and Lejeune, 2001). Factors such as herbivory, plant dispersal, rainfall and drought tolerance apparently determine under what conditions pattern formation is likely to occur but are not the primary factors generating patterns.

Vegetation patterns in arid ecosystems have also been ascribed to spatial self-organization caused by a mechanism whereby water infiltrates faster into vegetated soil than into bare soil, leading to a net displacement of surface water to vegetated patches (HilleRisLambers et al., 2001; Rietkerk et al., 2002). This model is fully mechanistic and also demonstrates that slope and underlying heterogeneity are not essential conditions. However, some initial differentiation into vegetated and non-vegetated areas is necessary to induce a redistribution of water. The spatial pattern that is generated by the model, i.e. whether bands or spots are produced, depends on the amount of rainfall. Such a mechanism could possibly offer an explanation of how the same *Stipagrostis* species form barren patches when the rainfall is less than 100 mm annually, but thrive in homogeneous fashion in the surrounding grasslands further inland where rainfall exceeds 100 mm annually.

Both the above-mentioned models seem to provide a mechanism whereby spatial vegetation patterns can be maintained on level ground without invoking environmental heterogeneity. Applying these principles it can be conceived how the edge of a fairy circle can be maintained once it has become established.

The occurrence of vegetation patterning seems to be coupled to conditions under which plants are severely stressed. Tongway and Ludwig (2001) developed a trigger-transfer-reserve-pulse framework to formalize how semi-arid landscapes function to regulate, conserve, utilize and cycle limited resources. Rainwater is redistributed spatially and captured in vegetation structures in the landscape which store the water along with the sediments and litter it carries. If a pulse of plant growth results, this pulse will normally feed materials back to the system. Under the extreme arid conditions in which fairy circles are found the fairy circle pattern and its relative permanence might be critical for the optimal functioning of the ecosystem to capture, store and recycle limited resources.

5. Conclusions

The belief that barren patches are dynamic, disappearing after a number of consecutive years of poor rainfall and establishing at new sites after good rainfall is shown to be a misconception. Barren patches are more stable and long-lived than previously suspected.

Bioassays of soil collected from the centre of the barren patch demonstrated an inhibitory or toxic effect exerted on plant growth. In contrast, the soil collected at the edge of the barren patch had a stimulatory action on plant growth. The present hypotheses fail to account for these observations. Ongoing research is aimed at identifying the nature of the substances causing inhibition and stimulation.

Although it is tempting to interpret barren patches as termite induced, it is important to note that to date no signs have been documented that could link termite activity directly to the formation of fairy circles. Furthermore, all hypotheses that have thus far been developed, have assumed that the factors causing the circles and those maintaining them are the same. These factors need not necessarily be identical, for example, termites could be part of the mechanism initiating fairy circles although they may not be responsible for maintaining them. To date, most of the hypotheses have also concentrated on a biological origin for barren patches while the physical/mechanical aspects have not been sufficiently investigated.

The occurrence of spatial vegetation patterns is apparently coupled to conditions under which plants are severely stressed. Under the extreme arid conditions in which fairy circles are found the relative permanence of this patterning might indicate that this pattern is critical to the optimal functioning of the system to capture, store and recycle limited resources.

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