

The fairy circles of Kaokoland (North-West Namibia) – origin, distribution, and characteristics

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Abstract

Embedded in species-poor grasslands, fairy circles are circular or sub-circular patches devoid of any vegetation. Characteristically, the circumference of each circle shows a band of more densely packed taller tussocks within a shorter, more sparse grassland matrix. The average diameter of the circles is between 5–8 m. Restricted to sites showing deep sandy deposits, in Namibia, fairy circles occur in a broken belt in the pro-Namib from southern Angola to the Orange River (Republic of South Africa). The distribution of fairy circles is significantly limited to areas with an average of 50–100 mm of annual precipitation. Based on remote sensing methods and expeditions, a map of the distribution area of fairy circles in Kaokoland (NW Namibia) was drawn up. The map indicates that fairy circles are more widely spread over the western parts of Kaokoland than previously reported. The two different active biological hypotheses of the fairy circles' origin comprise 1. the allelopathic interaction between *Euphorbia damarana* and the contemporary herbaceous vegetation (Theron 1979) and 2. the involvement of harvester termites (Moll 1994). Both hypotheses are discussed and a model about the origin and dynamic of fairy circles is presented. This model includes the foraging behaviour of the harvester termite *Hodotermes mossambicus* which is the prime causal factor in forming the fairy circles of Kaokoland.

Eingebettet in artenarme Grasländer, bilden Feenkreise runde bzw. kreisförmige vegetationslose Flächen. Als typisches Merkmal besitzen diese Flächen einen Rand, der aus dicht stehenden großen Grashorsten gebildet wird und sich deutlich von der spärlichen Grasland-Matrix abhebt. Der Durchmesser der Feenkreise liegt häufig zwischen 5 und 8 m. Beschränkt auf Gebiete mit tiefgründigen, sandigen Substraten, treten Feenkreise in einem unterbrochenen Streifen in der Vor-namib vom südlichen Angola bis zum Orange (Republik Südafrika) auf. Das Areal der Feenkreise ist hier auf Gebiete mit einer durchschnittlichen Jahresniederschlagsmenge von 50–100 mm beschränkt. Auf der Grundlage fernerkundlicher Verfahren und Geländeuntersuchungen wurde eine Karte des Verbreitungsgebietes von Feenkreisen im Kaokoland (NW Namibia) erstellt. Die Karte zeigt, dass Feenkreise im Kaokoland eine größere Verbreitung haben, als es zuvor bekannt war. Die beiden aktuellen Hypothesen zur Entstehung der Feenkreise umfassen 1. die allelopathische Interaktion zwischen *Euphorbia damarana* und der rezenten krautigen Vegetation (Theron 1979) und 2. die Beteiligung einer auf Gras als Nahrung spezialisierten Termitenart (Moll 1994). Beide Hypothesen werden diskutiert und ein Modell der Entstehung und Dynamik von Feenkreisen

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wird vorgestellt. Dieses Modell bezieht das spezielle Fraßverhalten der Termitenart *Hodotermes mossambicus* mit ein. *Hodotermes mossambicus* ist der primäre Faktor für die Entstehung von Feenkreisen im Kaokoland.

Key words: pro-Namib – species-poor ephemeral grassland – sandy deposits – harvester termites

Introduction

Fairy circles represent one of the most conspicuous botanical features of the pro-Namib which is the transition zone between the Namib Desert and the Great Escarpment in Namibia. Embedded in species-poor ephemeral grasslands fairy circles are often devoid of any vegetation. Occurring in a broken belt extending from southern Angola to the Orange River, characteristically, the circumference of each circle shows a band of more densely packed taller tussocks within a shorter, more sparse grassland matrix (Fig. 1 and Fig. 2).



Fig. 1. Fairy circles in the Marienfluss area.

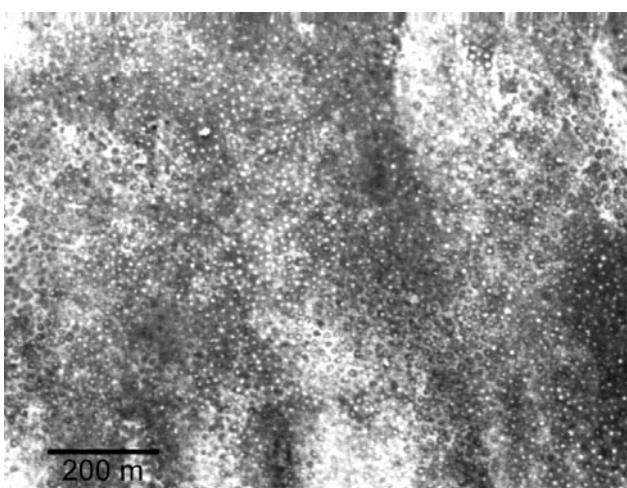


Fig. 2. Aerial photograph of fairy circles in Marienfluss (photograph taken in September 1996).

The fairy circles are a well known phenomenon to the Namibian public and descriptions of them can be found in guidebooks as well as in southern African textbooks about environmental issues (e.g. Lovegrove 1993, Owen-Smith 1996). During the last 30 years several attempts have been made to explain the origin of the fairy circles in Namibia. Tinley (1974) considered that the circles are fossils of termitaria from a period of time when rainfall was much higher than today. Another suggestion to explain the fairy circles is the allelopathic interaction between *Euphorbia damarana* and the contemporary herbaceous vegetation (Theron 1979). According to Moll's hypothesis (1994), termites are the most likely agents in the formation of fairy circles. When he matched the distribution maps of Namibian termites with the occurrence of fairy circles, he found that the closest match was with *Psammotermes allocerus* and the harvester termite *Hodotermes mossambicus*. On the basis of the specific behaviour of *H. mossambicus* Moll (1994) concluded that this termite species is probably responsible for the formation of the circles.

Apart from scientific approaches there are many popular scientific or traditional explanations for the occurrence of fairy circles. These explanations range from electromagnetic waves, land mines, radiation, UFOs, meteorites, dancing fairies or the poisoning of the trees which once allegedly dominated the landscape to the traditional explanation of the Himba people who inhabit Kaokoland. They say that the fairy circles "were made by god and have always been there".

We would like to add some pieces to the jigsaw on the origin, the distribution and the characteristics of fairy circles in Kaokoland.

Study area

Kaokoland is situated in the north-western part of Namibia. While its southern border is formed by the Hoanib River, the Kunene River marks the border between Angola and Kaokoland in the north. Kaokoland does not include the Skeleton Coast Park, which is the northern part of the Namib Desert. The Ovamboland and the fence of the Etosha Game Reserve mark the boundary in the east. The study area is situ-

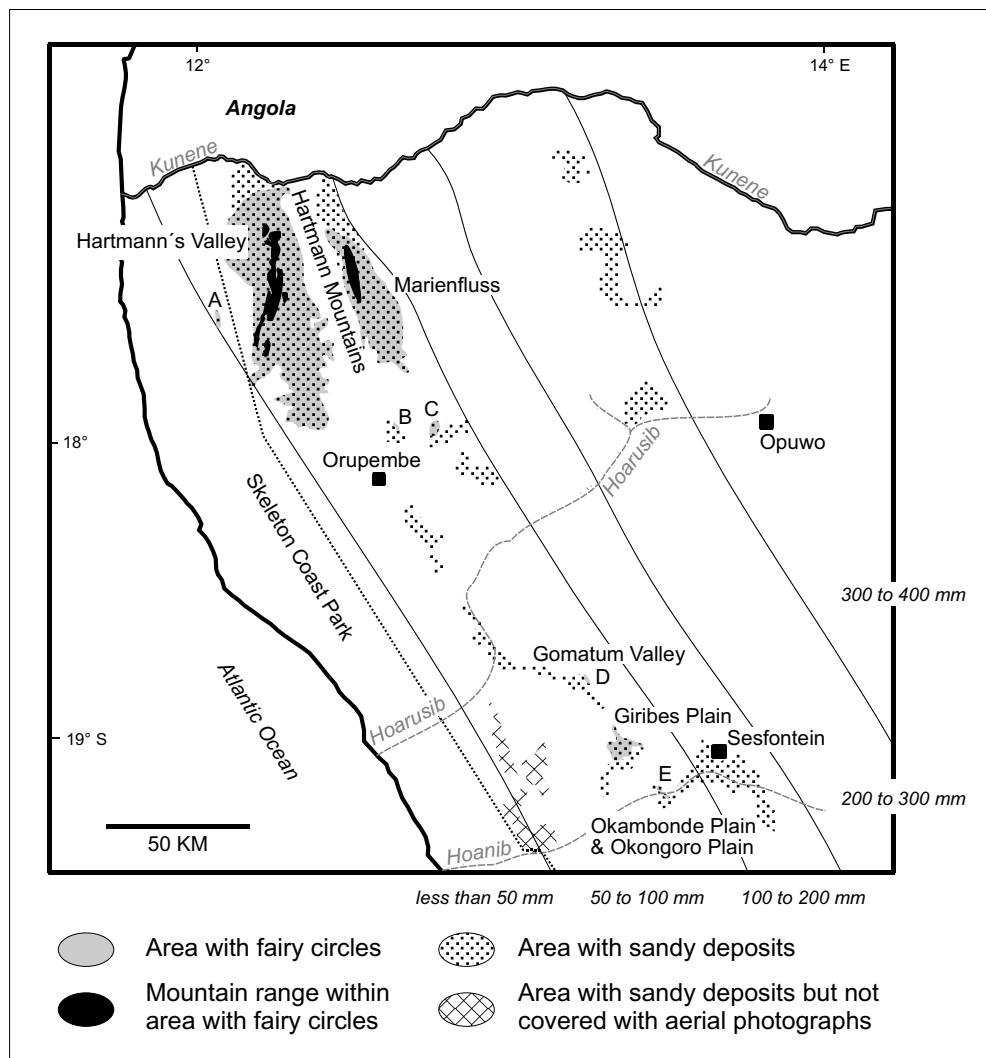


Fig. 3. Distribution area of fairy circles in Kaokoland (A–E: small areas showing fairy circles; precipitation in mm/year from van der Merwe 1983).

ated in the central and western part of Kaokoland (Fig. 3).

Based on the climate classification evolved by Köppen (1936), Kaokoland has a BWhw-climate, that is a hot desert with rainfall during summer (van der Merwe 1983). With its position between 17° and 19°30'S latitude Kaokoland is highly dependent on rainfall originating from the Southern Innertropical Convergence (SITC). This convergence follows the summer sun's zenith up to 23° S latitude and enters Kaokoland mainly from a north-easterly direction (Hutchinson 1995). Main rainfall events occur from February to April (Sander & Becker 2000). Depending on the development of the SITC rainfall amounts can vary drastically from year to year. One important characteristic of the study area is the strong decrease in the amount of rainfall from the eastern part, with 300 mm to 400 mm annual precipitation, to the western part, with only 50 mm to 100 mm (Fig. 3). Paral-

lel to this factor the variability of annual amount of rainfall increases significantly while the length of the rainy season decreases from 2 to 4 months in the east down to a period shorter than 1 month in the west (van der Merwe 1983). These climate features result in an increasingly patchy distribution of rainfall events from east to west.

Kaokoland, which covers an area of approximately 49.000 km², is a low-mountain region with a comparatively strong geological heterogeneity (mainly limestone, metasedimentary rocks, schist, and basalt). Topographically, Kaokoland can be divided into three major regions: (a) the interior highlands or escarpment zone, which reaches a maximum altitude of just over 2000 m; (b) the pro-Namib coastal plains; and (c) the plains of the Northern Namib Desert (Hilton-Taylor 1994). Due to a high diversification of edaphic conditions, vegetation patterns can change within small distances.

With respect to the phytogeographical context, the eastern part of the study area is an integral part of the Sudano-Zambezian Region. The western part of Kaokoland where fairy circles can actually be found, belongs to the Nama Karoo Region which from east to west comprises the Damaraland-Kaokoland Domain and the Namib District representing a sub-division of the Namaland Domain (Jürgens 1991). With a total number of about 1000 species, Kaokoland is a centre of plant diversity with a high number of endemic species (Hilton-Taylor 1994, Maggs et al. 1994, Barnard 1998, Maggs et al. 1998). Broadly speaking, the vegetation of the study area mainly consists of different types of savanna and ephemeral grassland (Viljoen 1980, Becker & Jürgens 2000a). Due to the mainly mountainous character of Kaokoland, transitions between the different vegetation units are less clearly defined than in the central and southern parts of Namibia (Hilton-Taylor 1994). Pastoral utilisation of the area has taken place over a period of about 2000 years (Smith & Jacobson 1995, Vogelsang 2000).

The main focus of field work centred on the Giribes Plain, the Hartmann's Valley, and Marienfluss since the fairy circles were known to occur in these areas from previous expeditions in Kaokoland and reported by Theron (1979), Viljoen (1980), Eicker et al. (1982), and Moll (1994). The vegetation of these areas can be described as a *Stipagrostis uniplumis*-*S. giessii* Valley Grassland community (Viljoen 1980) or ephemeral a *Stipagrostis uniplumis* Grassland (Becker & Jürgens 2000a), respectively. The substrata dominating these areas which are situated 500 to 700 m above sea-level consists of deep sandy aeolian deposits.

Material and methods

In order to describe the distribution of fairy circles in Kaokoland a set of aerial photographs (scale 1:78000, taken in September 1996) was used to detect fairy circles in the remote and barely accessible areas of Kaokoland. Since it was reported that fairy circles do typically occur on sandy soils (Moll 1994) three Landsat TM images covering the area west of 14° E were used to detect regions dominated by sandy deposits (Landsat TM images 182-72, 181-72, 181-73; taken in 1984 and 1986, respectively). During our field work which took place in March/April 2000, we visited the Giribes Plain, the Hartmann's Valley, and the Marienfluss area. Several specimens of ant and termite species were collected. Due to the fact that extensive biological, physical, and chemical soil analyses have already been conducted by Theron (1979), Eicker et al. (1982), and Moll (1994) no supplementary soil samples were taken.

Results and Discussion

Distribution of fairy circles in Kaokoland

As indicated in Fig. 3, the occurrence of fairy circles is significantly restricted to areas which receive an average annual precipitation between 50 to 100 mm and are dominated by sandy deposits. The main distribution of the circles is to be found in the Hartmann's Valley and Marienfluss including the adjacent southern areas. Another important but much smaller area showing fairy circles, is the Giribes Plain. Apart from these regions, fairy circles can only be found in very restricted areas in the Skeleton Coast Park (site A), the Otjihaa Plain (sites B and C), the valley of the Gomatum River (site D), the Okongoro Plain (site E), and in the Okambonde Plain (site E). This indicates that fairy circles are more widely spread over the western parts of Kaokoland than it was reported by Theron (1979), Viljoen (1980), and Moll (1994). While the sandy substrata of the Hartmann's Valley, Marienfluss, the Giribes Plain, and area A (west of the Hartmann's Valley) are of aeolian origin, the areas B to E represent alluvial lands formed by the Otjihaa River (B, C), the Gomatum River (D) and the Hoanib River (E), respectively.

As an extension of their well known distribution area in the Hartmann's Valley, fairy circles also occur on the sandy deposits of the tributaries of the Ondondjengo River and the Munutum River up to 17°47'S which is 25 km north-west of Orupembe. Stretching across about 80 km from north to south and 25 km from east to west this region represents the largest cohesive area showing fairy circles in the whole of Namibia. Embedded in a *Stipagrostis hirtigluma* grassland matrix, even on more coarse substrata, fairy circles can be found on the pro-Namib plain up to the border of the Skeleton Coast Park. The westernmost site showing fairy circles is located some kilometres west of the park's border (site A). This location is separated from the sites of the Hartmann's Valley by an extensive field of sand dunes where no fairy circles occur.

Probably due to the decreasing precipitation, on the pro-Namib plain the density of fairy circles decreases from east to west. Characteristically, the circles here only occur near small water courses or are even crossed by them (Fig. 4).

Due to the limited range of sandy deposits south of Marienfluss, in this region, fairy circles only occur up to 17°46'S which is 32.5 km north of Orupembe. Adding up all the areas north of Orupembe showing fairy circles, the total area is about 3500 km², only interrupted by sand dune fields and the mountain ranges of the Hartmann Mountains.



Fig. 4. Fairy circle on the pro-Namib plain west of the Hartmann's Valley, traversed by two small water courses.



Fig. 5. Fairy circles along a track in Marienfluss.

Apart from these areas there are five smaller locations where fairy circles occur (Fig. 3). While the sites A, B, C, and E were detected by using aerial photographs, area D (Gomatum Valley) was found during a previous expedition. Because of the restricted resolution of the aerial photographs no statement can be made about the matrix vegetation at sites B, C, and E. The fairy circles found in the valley of the Gomatum River (site D) are embedded in an ephemeral *Stipagrostis uniplumis* Grassland matrix (Becker & Jürgens 2000a).

Characteristics of fairy circles

Theron (1979), Viljoen (1980), Eicker et al. (1982), and Moll (1994) are in agreement that one typical characteristic of fairy circles occurring in the Giribes Plain, Marienfluss, and the Hartmann's Valley is a surrounding ring with densely packed tussocks of *Stipagrostis giessii*. Therefore, the vegetation of these areas was classified as a *Stipagrostis uniplumis*-*S. giessii* Valley Grassland community by these authors. In March/April 2000, we could find hardly any fairy circles showing this allegedly typical feature. The only site, where we found fairy circles with *Stipagrostis giessii* tussocks on their circumference fringe was a fairly restricted area in the southern part of Marienfluss. According to Viljoen (1980), in Kaokoland the occurrence of *S. giessii* is limited to areas showing a comparatively good water-supply, e.g. water courses (see also Gibbs Russel et al. 1991). Within the complex of the Hartmann's Valley and Marienfluss, the southern part of Marienfluss receives the highest amount of rainfall and thus shows the best water-supply. It is only in this area that *S. giessii* is quite abundant and dominates the circles' fringe. Where these circles were found, the matrix vegetation consisted either of *Stipagrostis uniplumis* or *Schmidtia kalahariensis*.

In some cases *S. giesii* itself formed the matrix vegetation. In general, we found that the densely packed tussocks around the circles were of the same grass species that formed the matrix vegetation. In all areas where we conducted our field studies, *Stipagrostis uniplumis* was found to be the most important grass forming the matrix vegetation of the fairy circles. Therefore, it is the most important species for forming the fringes of fairy circles in Kaokoland. Due to the characteristic abundance of *Stipagrostis uniplumis* Becker & Jürgens (2000a) classified the vegetation of the Hartmann's Valley, Marienfluss, and the Giribes Plain as an ephemeral *Stipagrostis uniplumis* Grassland.

We propose that three reasons are responsible for the better vitality of the grass tussocks forming the circumference fringe of a fairy circle: **A.** Because the circle is typically devoid of any other plants, there is less competition for water and nutrients for the specimens building the circumference fringe than for any other specimen in the matrix vegetation. In other words, the grasses forming the ring take advantage of a better supply of water and nutrients and thus grow higher and more densely than the grasses forming the matrix vegetation. This hypothesis is supported by Fig. 5, which shows that grass inhabiting the verge of tracks, where the conditions are similar to the fringe of a fairy circle, takes advantage of the same favourable conditions and thus grows more vitally than the neighbouring tussocks. **B.** Very often fairy circles display a concave form (depression). This can easily be explained by the wind eroding the sand from the bare circle whereas the sand body within the matrix vegetation is protected from erosion by the tussocks (see also Theron 1979). In comparison to the adjacent ground level, the depth of a circle can be up to 40 cm. Fairy circles that have this depression collect more



Fig. 6. Margin of a fairy circle in Kaokoland showing the accumulation of dead biomass (Marienfluss).

water than a point outside a fairy circle. Similar to Theron's (1979) measurements a heavy rain resulted in soil moisture to a depth of 80 cm at the deepest point of a circle (not necessarily its centre). In comparison, outside the circle the water had percolated the soil only down to a depth of 30 cm. C. Due to the hyperarid conditions in the western part of Kaokoland decomposition of organic substances occurs very slowly. Thus, wind plays a major role in shifting dead biomass. Generally, litter is uniformly collected by tussocks of the grassland matrix. Consequently, tussocks surrounding patches devoid of vegetation can collect a larger amount of organic substances than tussocks forming the matrix vegetation. Because sandy soils contain a comparatively low amount of nutrients, decomposition of organic substances is an important source of nutrients for plants. Compared with the tussocks forming the matrix vegetation, tussocks surrounding bare patches can collect more organic material and are therefore favourably supplied by nutrients (Fig. 6). This idea is supported by germination experiments conducted by Theron (1979) and a study on the microbial population of fairy circles (Eicker et al. 1982).

Wind is probably responsible for some fairy circles not showing a circular but a concave, oval shape. Due to wind erosion the roots of marginal tussocks become exposed, the plants dry out and are easily blown away by the wind. Gradually, the original circle forms an oval, concave shape orientated to the prevailing wind direction.

The origin of fairy circles

Two main theories have been evolved on the origin of fairy circles in Namibia. According to Theron (1979) fairy circles are the result of an allelopathic interac-

tion between *Euphorbia damarana* and the contemporary herbaceous vegetation. Germination experiments revealed that *Eragrostis tef* shows weak growth on soil taken from the inside of the circles. The same grass species showed best growth on soil taken from the circumference fringe of the fairy circles. An intermediate result was achieved with *E. tef* grown in soil taken from outside the fairy circles (Theron 1979). *E. tef* originates from the north-eastern part of Africa and was introduced to many other tropical parts of the world, including southern Africa. In Namibia, the species' range is restricted to the central part of the country (Gibbs Russel et al. 1991, van Oudtshoorn 1999). According to Theron's conclusion it is most probably the different content of a cation which causes the differences in the vitality of *E. tef*. Theron suggested that this inhibiting cation is a product of the decomposition of *Euphorbia damarana* plants.

Indeed, the photograph presented by Theron (1979) shows a large fairy circle close to a stand of *E. damarana*. According to Eicker et al. (1982) *E. damarana* and *Parkinsonia africana* are the most abundant shrub species of the Giribes Plain. Referring to Moll (1994) the density of fairy rings on the Giribes Plain varies from 36 to 47/ha and Theron reports that in Marienfluss there are only 11 circles/ha (see Fig. 2). Due to weak grass cover as a result of poor rain, in 1998, 1999, and 2000 we could only find a few fairy circles in the Giribes Plain. In contrast to *Parkinsonia africana* which formed more or less patchily distributed dense stands we could not find any *Euphorbia damarana* specimens within the part of the Giribes Plain which was accessible to us. Because we did not find any *E. damarana* specimens either in Marienfluss, the Hartmann's Valley or on site D (see Fig. 3) we think that the reported common occurrence of *E. damarana* and fairy circles is probably of coincidental nature (see also Günster 1993). Apart from these observations, in Kaokoland and in the central part of the Namib desert, *E. damarana* seems to be a characteristic species of areas consisting of either very coarse material (e.g. Etendeka basalt) or having a very shallow layer of top soil. This species almost never occurs on deep sandy soil which is a characteristic feature of areas showing fairy circles (Hachfeld 1996, Becker & Jürgens 2000b). In conclusion, the hypothesis of *Euphorbia damarana* causing the fairy circles can not be supported.

As mentioned before, from the range and behaviour of *Hodotermes mossambicus* Moll (1994) concluded that this harvester termite could be responsible for the formation of fairy circles in Kaokoland. *H. mossambicus* is assigned to the primitive family HODOTERMITIDAE (*Isoptera*). All species grouped together in the sub-family HODOTERMITINAE are true harvester termites which do not attack wood but



Fig. 7. *Hodotermes mossambicus* feeding on *Stipagrostis uniplumis* (Marienfluss).



Fig. 8. Foraging hole of *Hodotermes mossambicus* surrounded by pieces of *Stipagrostis uniplumis* (Marienfluss).

feed on grass, leaves, bark and the less woody twigs of shrubs. As reported by Coaton (1958) foraging is carried out on the soil surface in an entirely unconcealed manner. Apart from *Hodotermes mossambicus*, the genus *Hodotermes* Hagen contains only one other species. While *H. erithreensis* is recorded only in Eritrea and Somalia, *H. mossambicus* ranges from Ethiopia to the southern karroid sectors of the Cape Province, South Africa (Coaton & Sheasby 1975). Assigned to the genus *Microhodotermes* there is only one other harvester termite species occurring in southern Africa. The range of *Microhodotermes viator* is more or less limited to the winter rainfall region of southern Africa, whereas *Hodotermes mossambicus* is widely distributed in all parts of southern Africa where the average annual rainfall does not exceed 750 mm. Primarily, *H. mossambicus* is an inhabitant of the drier grassland and bush regions, where the

grass flora is unstable and liable to speedy removal by heavy grazing, fire etc. (Coaton 1958). The species was recorded in the dune valleys in the vicinity of the Kuiseb River at Gobabeb where the average annual rainfall is less than 50 mm as well as in Kaokoland (Coaton & Sheasby 1972, Coaton & Sheasby 1975, Werger 1978, van der Merwe 1983). Apart from Moll's deduction about the involvement of *Hodotermes mossambicus*, the activity of *H. mossambicus* causing the fairy circles in Kaokoland has never been presented. When we did our field studies we had the chance to observe *H. mossambicus*, whose activities above ground are very time limited (Fig. 7 and Fig. 8).

From the detailed studies on the biology of *H. mossambicus* by Coaton (1958) and additionally by Coaton & Sheasby (1972) and Coaton & Sheasby (1975) Tab. 1 summarises the most important features of the biology of *H. mossambicus*.

Table 1. Important features of the biology of *H. mossambicus* (from Coaton 1958, Coaton & Sheasby 1972, 1975)

Life cycle	Nesting and feeding habits	Foraging
<ul style="list-style-type: none"> swarming flights take place after showers of rain have fallen during the spring and summer months, usually during the hours 6 to 8 p.m. the peak month of swarming is December each swarming period lasts for approximately one or two hours each mated de-alated pair will breed and found a new colony given adequate food supplies and freedom from disease the colony is potentially immortal only during the brief spells of swarming in spring and summer the alate caste can be observed above the soil surface 	<ul style="list-style-type: none"> prominent surface mounds of hard, cemented soil are never constructed the waste soil is dispersed on the surface at numerous, separated, irregularly spaced dumping points hives can be located up to 7.5 m below the soil surface the nest system has a maze-like structure (see Fig. 9) when food supplies on the surface become depleted, workers drive their subterranean galleries progressively further afield in search of food material if new grass becomes available near the hub of the colony, the furthestmost foraging holes become redundant and fall into disuse 	<ul style="list-style-type: none"> when not in use, the foraging holes are sealed off to exclude air, water and predatory insects unused forage holes are almost completely camouflaged the frequency of foraging depends on the grass supply (the better the grass supply, the longer the period between foraging) the duration of foraging may be cut short artificially by predatory insects before the food stocks in the hives can be replenished adequately in areas where the surface temperature becomes extremely high foraging takes place in the late evening and early morning in dense and even stands of grass foraging results in sub-circular denuded patches

Possibly due to the destructive behaviour *H. mossambicus* shows in areas under cultivation (e.g. pastoral areas) much effort has been made to describe the biology of this termite species (Coaton 1953, Skaife 1955, Coaton 1958). It has to be mentioned that detailed studies about the biology of *H. mossambicus* have been mainly conducted in regions of South Africa (Heilbron district and in the vicinity of Johannesburg). According to the climate classification of Köppen, this region shows a temperate climate. With an average annual rainfall between 400 to 600 mm (Klimm et al. 1980) precipitation is considerably higher than in the distribution area of fairy circles in Kaokoland (see Fig. 3). The vegetation can be classified as a *Cymbopogon-Themedia* Grassland, showing a much higher species diversity than the species-poor grassland regions where fairy circles range in Kaokoland (Acocks 1953, Viljoen 1980, Becker & Jürgens 2000a, 2000b). It is quite within the bounds of probability, that *H. mossambicus* may exhibit a multitude of behavioural adaptations as a response to different habitats.

Fig. 9 represents our model on the origin of fairy circles deduced from the background information of

the biology of *Hodotermes mossambicus* and our field observations. Part A represents the structure of the excavated nest system of a colony of *H. mossambicus* on a grassy slope near Johannesburg (Coaton 1958). This semi-diagrammatic sketch consists of a breeding hive and different subterranean galleries. These galleries stretch over more than 250 m. B. In years with average precipitation, *H. mossambicus* only harvests in the vicinity of the breeding hive which is placed in the centre of the nest system. The galleries lead to foraging holes from where foraging starts. Due to the homogeneous species-poor grassland, harvesting results in circular or sub-circular denuded patches only leaving a little stubble within the patch. Differences in the intensity of foraging may cause different diameters of the circular forms. Due to the extraordinary efficiency of harvesting, it can be estimated that the area of an averaged sized fairy circle (according to Eicker et al. 1982, the circles' average diameter is 5 m to 8 m) can be denuded within 5–7 days (see also Coaton 1953, 1958). C. Should the grass cover become more sparse, e.g. due to poor rainfall or grazing, the workers extend the galleries in order to harvest sufficient edible biomass for the colony. This results in the oc-

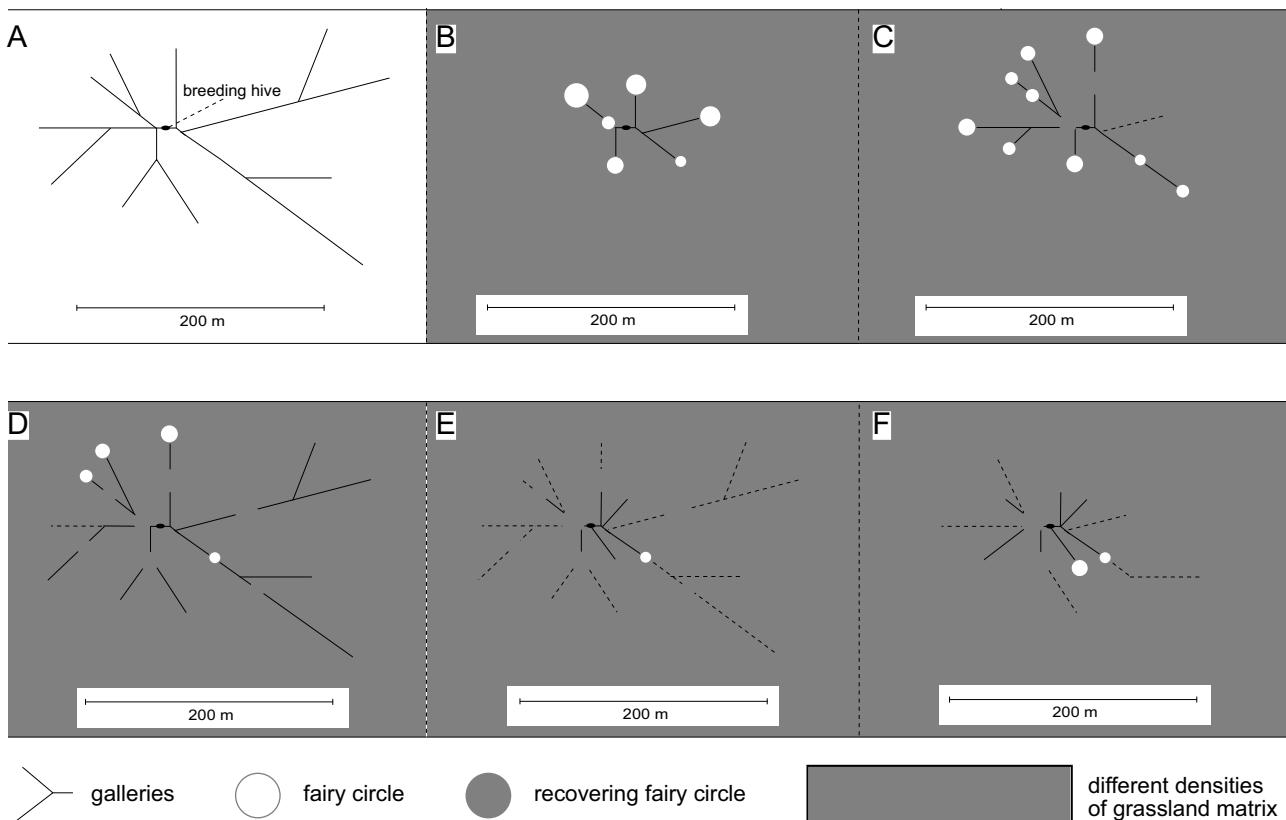


Fig. 9. Model of the expansion and reduction of the nest system of a colony of *Hodotermes mossambicus* (part A is taken from Coaton 1958).

currence of new denuded circular patches while abandoned patches begin to recover. Due to the loss of organic substances within the denuded patch and the inability of the bare soil to collect shifting organic substances the soil of the fairy circle becomes infertile. Thus, the regeneration process progresses relatively slowly. **D.** Should the condition of the grass cover

worsen, the workers proceed in extending the subterranean galleries and in building new foraging holes. As a consequence, at a larger distance from the hub new fairy circles start to emerge. Concurrently, some circles fall into disuse and start to recover (Fig. 10). **E.** With an improvement of foraging conditions near the hub of the colony, e.g. due to good rainfall or a decreased number of grazers, the furthermost foraging holes and supplementary hives become redundant and thus fall into disuse. The surrounding denuded patches can start to recover. **F.** Should the good foraging conditions in the vicinity of the hub stabilise, the disused circles can completely recover and thus become a part of the matrix vegetation again (Fig. 11).

An undisturbed pattern of fairy circles as shown in Fig. 9 can most probably develop on previously uninhabited sites after the swarming flights of the alates have taken place. Each mated de-alated pair will breed and found a new colony (Coaton 1958). This results in the forming of numerous new fairy circles. In contrast, where the grassland is infested very densely and evenly, the overlapping of foraging areas results in a denuded patch with an uneven margin (Fig. 12).

An obvious feature of fairy circles is the variation of their diameters. The size of fairy circles is limited by various factors. One main factor is the sensitivity of *Hodotermes mossambicus* to the temperature of the soil surface. According to Coaton (1958), in hot areas *H. mossambicus* forages in the cooler hours, the late evening and early morning. On the other hand, during the night low temperatures limit the termite's surface activities. In areas, where the grass cover is sparse, e.g. due to livestock grazing, poor precipitation, fires or the harvesting of *H. mossambicus*, the workers are forced to forage all day and every day in order to guarantee the daily requirements of the colony or to replenish its food stock (Coaton 1958). With soil surface temperatures of 40 °C the insects show signs of distress and their movements become erratic. Temperatures of 41 °C cause the death of the termite due to overheating and loss of moisture (Skaife 1955). These surface temperatures can be easily reached in the western part of Kaokoland, where the daily maximum air temperature regularly exceeds 30 °C (Sander & Becker 2000). Since the termites can only move relatively slowly, they can not cover large distances without protection from the heat. With the denuded patch around the foraging hole becoming larger with the proceeding harvest and the barren desert soil not supplying sufficient protection from the heat, *H. mossambicus* can easily fall into a state of distress. From this moment, *H. mossambicus* is an easy prey for the thermophilic and insectivorous ants of the genus *Ocymyrmex*. These ants have adopted a unique temporal niche, specialising in foraging during the heat of



Fig. 10. Recovering fairy circle (Hartmann's Valley).



Fig. 11. Almost completely recovered fairy circle (Hartmann's Valley).



Fig. 12. Grassland densely infested by *Hodotermes mossambicus* in Marienfluss (note the partly sub-circular shape of the almost denuded patch).

the day (Marsh 1990). While *H. mossambicus* gets in the state of distress at 40 °C, *Ocymyrmex robustior*, for example, has its maximal foraging activity at 52 °C and only ceases activity as temperature approaches 70 °C (Marsh 1990). Ants of the genus *Ocymyrmex* are common in the Namib Desert and it is probably *Ocymyrmex velox* which can be found in numerous fairy circles. This individual foraging, insectivorous species preys principally on *Hodotermes mossambicus* and scavenges on dead arthropods when termites are not active (Marsh 1986, Wehner 1987). In Marienfluss as well as in the Hartmann's valley we observed *Ocymyrmex sp.* feeding on tenebrionid beetles and on *H. mossambicus*. Should one of the workers of *Hodotermes mossambicus* be attacked by an ant or a spider it warns its congeners by pouring out special pheromones. According to Wilson & Clark (1977) the workers of *H. mossambicus* immediately stop their foraging activities and rush underground (see also Coaton 1958). Apart from *Ocymyrmex sp.* a large variety of vertebrate and invertebrate predators prey on *H. mossambicus*, e.g. the bat-eared fox (*Otocyon megalotis*), the ant-bear (*Orycteropus afer*), numerous birds and reptiles (Coaton & Sheasby 1972, Bauer et al. 1989). Juvenile colonies of *H. mossambicus* are especially vulnerable to predators because the production rate of first generation workers is low. If these workers are destroyed regularly, the young queens will eventually die of starvation (Coaton & Sheasby 1972). Of course, the patches formerly used by the termites fall into disuse and therefore can start to recover.

Summary

In Kaokoland, the distribution area of fairy circles is restricted to regions dominated by sandy deposits with 50 mm to 100 mm of annual precipitation. The interpretation of aerial photographs indicates that fairy circles are more widely spread over the western part of Kaokoland than previously reported. The total distribution area adds up to about 3500 km² with the westernmost site showing fairy circles situated some kilometres west of the border of the Skeleton Coast Park. Embedded in species-poor grasslands, one typical feature of fairy circles is the surrounding fringe formed by densely packed tall tussocks. In general, these tussocks are of the same grass species that forms the shorter sparse matrix vegetation. The specimens forming the conspicuous fringe take advantage of a better supply of water and nutrients and thus grow higher and more densely than the matrix vegetation. For various reasons, Theron's hypothesis (1979) which suggests that fairy circles originate from an al-

lelopathic interaction between *Euphorbia damarana* and the contemporary herbaceous vegetation has to be rejected. The typical sites of *Euphorbia damarana* stands consist of either very coarse material or have a very shallow top soil layer. This species almost never occurs on deep sandy soil which is a characteristic feature of areas showing fairy circles. Within the examined areas no *Euphorbia damarana* specimens could be found.

Field observations in Kaokoland and studies on the biology of the harvester termite *Hodotermes mossambicus* indicate that this termite species is the prime causal factor for the forming of fairy circles. In species-poor homogenous grasslands the foraging activities of *H. mossambicus* can result in circular or sub-circular denuded patches. The size of the circles is limited by the colony's consumption, the heat sensitivity of *H. mossambicus*, and the activities of insectivorous animals preying on *H. mossambicus*. In Kaokoland, the most important predators seem to be thermophilic ant species assigned to the genus *Ocymyrmex*.

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