



Research article

Plant water stress, not termite herbivory, causes Namibia's fairy circles

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ABSTRACT

The fairy circles of Namibia form a remarkable gap pattern in arid grassland along the Namib Desert. The origin of the fairy circles is subject to an ongoing debate. Solving the mystery of the fairy circles (FCs) requires the right timing in fieldwork after rainfall, as the newly appearing grasses complete their life cycle within only a few weeks. Here we followed the rains along the Namib between 2020 and 2022 and assessed the cause of the grass death within FCs at different time intervals after grass-triggering rainfall. To assess whether termite herbivory was the cause, we used grass excavations and observations on the roots and shoots. To test if edaphic differences may explain the grass death in FCs, we undertook infiltration measurements in 10 FC-hotspot regions. Finally, we used continuous soil-moisture measurements from the dry into the rainy seasons to examine how the newly emerging grasses affect the soil-water content in space and time. Generally, in study plots that received grass-triggering rainfall most recently, the roots of the dead grasses in FCs were in 100 % of the cases undamaged, root-shoot ratios were significantly greater, and the roots were as long or even longer as those of the surrounding matrix grasses outside of the FCs. This indicates that drought stress caused grasses in the FCs to invest resources into roots to reach the percolating water. The results also show that the cause of the grass death in fairy circles was not induced by termite herbivory. Also, we found no systematic differences in the rate of water infiltration between FCs and the matrix, hence the plant wilting cannot result from quicker percolation within FCs. However, the soil-moisture measurements indicate that the matrix grasses strongly depleted the upper soil water of the FCs after rainfall, which explains why most grasses cannot establish and quickly die in the FCs. The research shows that grass death in fairy circles occurs immediately after rainfall due to plant water stress but not due to termite activity. Our results conform with previous fieldwork, pattern analysis and theoretical modeling, suggesting that Namibia's fairy circles are a self-organized vegetation phenomenon induced by ecohydrological feedbacks.

1. Introduction

The eastern margins of the Namib Desert in southwestern Africa are home to the mysterious fairy circles, whose origin is disputed (Sahagian, 2017). Millions of these circular grassland gaps with diameters of a few meters occur about 80–140 km inland from the coast. There, the growth of the annual grasses is an erratic short-term response to rare precipitation events, as this desert is characterized by strong aridity and unpredictable rainfall. During the rainy season from January to April, larger cloud fronts only rarely cross over the mountain ridge of the Great Escarpment and reach these eastern margins of the Namib. As a consequence, rainfall in these ephemeral grasslands is very patchy at a spatial scale of a few kilometers and there is also a high temporal variability in

precipitation (Henschel et al., 2005). The predominant grass species like *Stipagrostis ciliata*, *S. obtusa* or *S. uniplumis* require as little as 10 mm rainfall to leave seed dormancy, to start germinating and to complete their life cycle within a short growing season (Jacobson, 1997; Henschel et al., 2007).

Viewed from the air, the fairy circles (FCs) appear as a highly regular pattern and many sites with FCs show a spatially periodic distribution with an extraordinary degree of spatial ordering (Getzin et al., 2015a,b, 2019, 2021a,b). It has been hypothesized that this highly regular pattern of the FCs and its relative permanence may indicate that it is critical to the optimal functioning of the ecosystem in terms of utilizing and recycling the limited resources (van Rooyen et al., 2004). In line with this, research has demonstrated that the FCs respond to the long-term

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dynamics of wet or drought cycles. After several years with above average rainfall, the FCs tend to shrink in diameter or FCs may even disappear, while after cumulative drought years, FCs may enlarge in size and new ones tend to form (Zelnik et al., 2015). Given that the core area of FC occurrence along the Namib is confined to a narrow, approximately 60 km wide belt between the 70–120 mm rainfall isohyets (Fig. 1), it has been argued that the FCs are an emergent self-organized vegetation pattern that is caused by intense plant competition for soil moisture (Cramer and Barger, 2013; Getzin et al., 2015a, 2015b; Cramer et al., 2017; Ravi et al., 2017).

Generally, it is well known that FCs store underground water and that the soil moisture can be several times higher inside the FCs than outside in the matrix, which we define as the vegetation in between the FCs. The higher soil moisture, however, occurs predominantly at a depth between 30 and 100 cm and is far less pronounced in the upper soil horizon where new grass seedlings would typically germinate (Albrecht et al., 2001; Picker et al., 2012; Ravi et al., 2017). Proponents of the vegetation self-organization theory argue that the gaps remain bare because the ecohydrological feedbacks between the grasses that surround the FCs are depleting the soil moisture to an extent that revegetation of the gap interior is hardly possible due to critical plant water stress. In the Namib, the pattern-forming feedback is caused by a high rate of water uptake by the plants and by fast lateral soil-water diffusion, relative to biomass expansion (Zelnik et al., 2015). Given that the permanently transpiring *Stipagrostis* grasses with their laterally confined

roots create “soil-moisture vacuums” around the root zone, the so-called “uptake-diffusion feedback” leads to antiphase spatial biomass–water distributions and thus vegetation gaps in the sandy soils of the Namib (Kinast et al., 2014; Getzin et al., 2016). The higher soil moisture within the FCs is not a permanent source of water that would enable an additional vegetation growth inside the FC, but it is merely sufficient to sustain the higher grass biomass surrounding the FCs (Getzin et al., 2015b). In line with this, Cramer et al. (2017) showed for NamibRand that the tall grasses around the periphery of the FCs had a 10-fold higher total biomass than the matrix grasses in between the FCs, and they ascribed these spatial trends to short-range facilitation and long-range competition between plants.

This type of resource concentration and local aggregation of biomass leads globally often to self-organized patchiness where pattern-forming biomass–water feedbacks result in periodically ordered vegetation in drylands (Rietkerk et al., 2004; Meron, 2012, 2016). In these cases of emergent vegetation patterns, short-range positive ecohydrological feedbacks lead to long-range water depletion, and the periodically ordered vegetation morphologies follow specific rules of pattern-formation theory (Couteron and Lejeune, 2001; Meron, 2012). Specifically, such self-organized vegetation gaps are known from shrublands in Africa (Barbier et al., 2008) or from ecosystem engineering of hummock grasses that form identical fairy-circle patterns in Western Australia (Getzin et al., 2016, 2021c). Ultimately, the periodic pattern of the fairy-circle gaps and of related vegetation stripes and spots

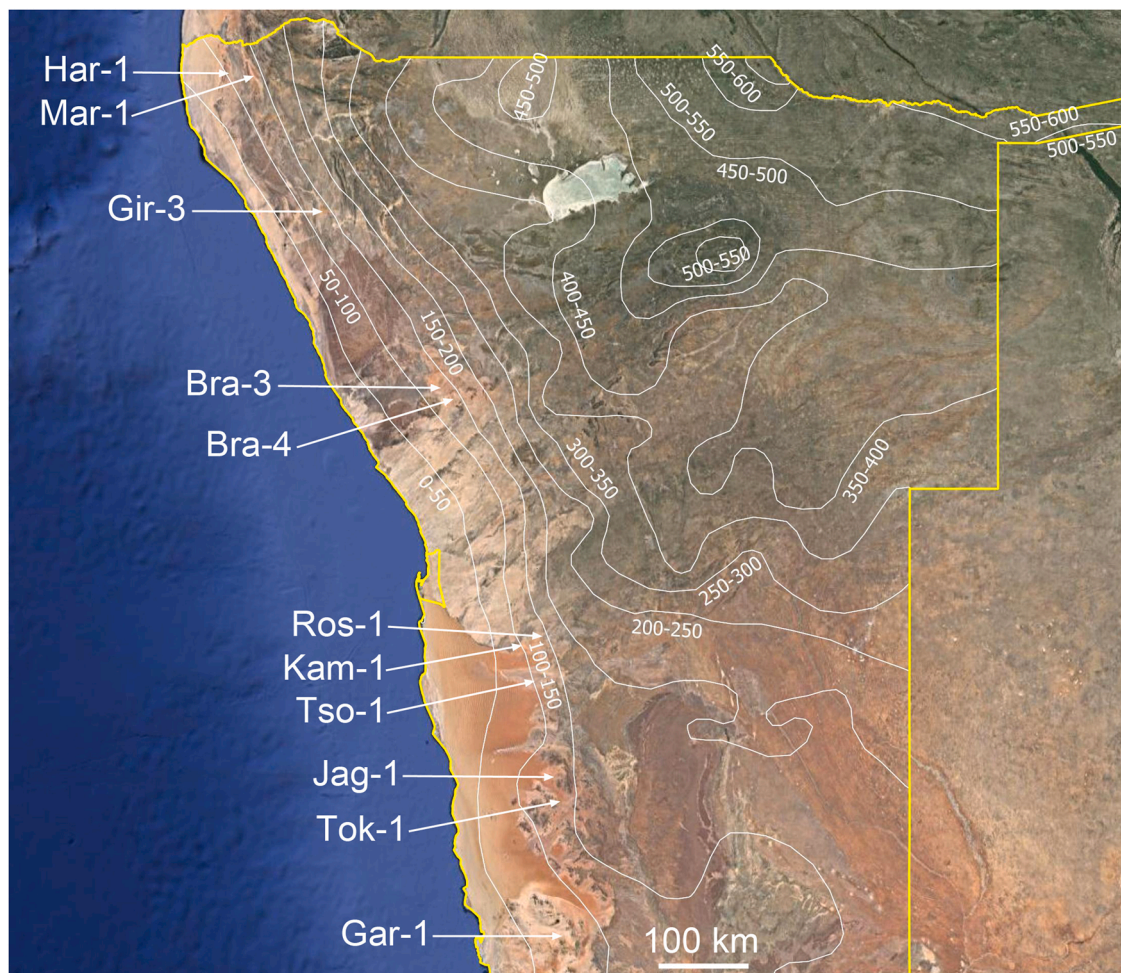


Fig. 1. Location of the study plots and rainfall isohyets of mean annual precipitation (mm, white lines) shown in Google satellite imagery. Grass excavations have been undertaken from Garub (Gar-1) in the south to Brandberg (Bra-3, Bra-4) further north. Infiltration measurements have been done in 10 regions across 1000 km from north to south, covering the hotspot areas with fairy circles in Namibia. Permanent soil-moisture measurements were done with data loggers at Mount Jagkop (Jag-1) in the NamibRand Nature Reserve.

in drylands reflects that there is not sufficient rainfall in the region to sustain a continuous layer of plants (Borgogno et al., 2009; Deblauwe et al., 2011).

The origin of the fairy circles is disputed because external factors such as faunal activities have also been hypothesized to be causal (Moll, 1994; Picker et al., 2012). In this respect, especially the sand termite hypothesis stands in stark contrast to the hypothesis of self-organization of plants (Sahagian, 2017). Primarily, it has been suggested that root herbivory by the sand termite, *Psammotermes allocerus* (Juergens, 2013; Vlieghe et al., 2015), would be causing the FCs. This sand termite hypothesis of Juergens (2013) claims that the foraging of *Psammotermes allocerus* “on the roots of freshly germinated grasses kills them and keeps the bare patch free of vegetation”. According to this theory, the insects would be actively destroying the grasses inside the FCs.

While the mechanistic simplicity of this termite theory enjoys popularity, it has been questioned over the years for several reasons. Most researchers have shown with extensive excavations of FCs that termites or their nests are largely absent and that termite correlation with some FCs does not imply causation (Theron, 1979; van Rooyen et al., 2004; Tschinkel, 2010, 2012, 2015; Picker et al., 2012; Cramer et al., 2017; Ravi et al., 2017; Meyer et al., 2020; Getzin et al., 2021a). For example, Sahagian (2017) summarized the study of Ravi et al. (2017): “Neither sand termites nor other secondary fairy circle inhabitants, e.g., *Anoplolepis steingroeveri* or any *Messor* spp., were present at any of the studied fairy circles, and evidence of root damage from past termites was also absent.” Sand termites have been also classified as litter feeders which prefer specifically the dead lignified parts of the Namib grasses and thus plant detritus (Crawford and Seely, 1994; Jacobson et al., 2015). Hence, even if root damage can be found at the grasses within FCs, it does not necessarily imply a termite causation but just a secondary effect of insect herbivory. Consequently, the right timing in fieldwork after rainfall is crucial in order to reveal the initial causes of grass death within FCs.

In the discussion on the origin of the fairy circles, primary and secondary causal effects need to be separated. For example, abiotic secondary processes may also be responsible for the death of the grasses within the FCs. As has been shown, wind action and subsequent sand erosion may lead to concave FC depressions, causing a de-rooting of established grasses at the edge of FCs (Getzin and Yizhaq, 2019). For FCs on gravel in the central Namib, Ravi et al. (2017) found coarser soil textures with lower moisture retention and more water infiltration in the FC centers, and eolian erosion processes during the winter months were suggested to cause the deposition of fine-textured sediments in the matrix areas. These authors proposed that such differences in water infiltration may contribute to the predominant lack of plant establishment within the FCs. Opposing trends of water infiltration were found for other regions of the Namib by Moll (1994) and Getzin et al. (2021b). However, so far a systematic comparison of infiltration rates in many FC regions along the Namib is still missing.

When it comes to investigating specific hypotheses on the cause and maintenance of the Namib FCs, it is critical to employ a high temporal resolution of research activities during the wet season. This is essential because some patches with FCs may only once experience a single rainfall event where the germination of annual *Stipagrostis* grasses is triggered shortly thereafter (Henschel et al., 2005, 2007). Given that the grasses transpire water permanently, the wilting process and death of the grasses may start soon if no further rainfall occurs. But even under more favorable conditions with repeated showers of rainfall during the wet season, the active growth period of the grasses is merely one or two months long before all the grasses lignify and die. Consequently, if the goal is to assess the precise circumstances of the death of grasses within FCs, a fundamental pre-requisite is to conduct research activities at short time intervals. Only an examination of grass death shortly after rainfall will reveal the cause of the fairy circles and will adequately account for secondary processes such as the potential succession of biota within the FCs.

For these reasons, we have followed the rains along the Namib Desert in the wet seasons 2020–2022 and investigated the FCs in regions at several time intervals after the first grass-triggering rainfall events. Working in the Namib Desert and thus in a stochastically dominated ecosystem with patchy rainfall across 1000 km is highly challenging. Hence, our research is mainly a descriptive study, that for the first time employs a high-resolution temporal analysis of the FC and matrix grasses after rainfall. In the following we list three main hypotheses that we investigated with this systematic survey.

- 1) *Grass death in fairy circles after rainfall happens independently of potential root herbivory by termites.* Hence the roots of the dying grasses are initially undamaged. We investigated this hypothesis for five study plots in four regions of Namibia, using grass excavations in FCs and outside in the matrix.
- 2) *Water infiltration rates inside fairy circles, as compared to outside in the matrix, are not generally faster, and thus cannot explain the cause of initial grass desiccation in FCs.* This hypothesis is based on recent findings for the regions Brandberg, Giribes and Garub (Getzin et al., 2021b) but is now investigated for 10 regions across 1000 km, covering the hotspot areas with fairy circles along the Namib Desert.
- 3) *Grasses of the matrix actively deplete the upper soil moisture of the fairy circles after rainfall because ecohydrological feedbacks are the drivers of the vegetation pattern.* This hypothesis is based on the so-called “up-take-diffusion feedback” where the permanently transpiring grasses draw water along moisture gradients by diffusion (Kinast et al., 2014; Getzin et al., 2015b, 2016). It is also based on previous fieldwork, demonstrating that water may move horizontally between the FCs up to more than seven meters within a short time (Cramer et al., 2017). While we did not directly measure the horizontal flow of water, we investigated this hypothesis indirectly by using continuous recordings of soil-moisture sensors that have been placed at short distances along a transect connecting two exemplary FCs in the NamibRand Nature Reserve. Additionally, we measured the soil moisture directly at the desiccating grasses within FCs and compared it to the moisture around the vital grasses in the matrix vegetation.

With these hypotheses we have focused on the temporal aspects of the FC dynamics because if investigations after rainfall are undertaken too late, essential processes may be missed.

2. Materials and methods

2.1. Study plots and data collection

The death of grasses in FCs was investigated within five plots about 25 ha in size, across four Namibian regions from Garub in the south to Brandberg further north. In addition, infiltration measurements were done but extended to 10 regions along the Namib Desert. In one of the plots located in the NamibRand Nature Reserve, we also installed data loggers and recorded soil-moisture continuously over time. For all these plots we show in Fig. 1 their location on the map, and we provide in Table 1 the coordinates and the type of data collection. The investigated study plots and the field sampling will be described in chronological order.

2.2. Grass excavations after triggering rainfall

In February and March 2020, we drove along the Namib Desert in search for recent rain events that were sufficient to trigger the growth of freshly germinated grasses. On 12th March we spotted a circa 2 km × 2 km large green patch east of the Kuiseb River and about 8 km south-west of the Kamberg (Figs. 1, 2a, b). This study plot called “Kam-1” was located in the Namib-Naukluft National Park (Table 1). According to observations of local residents, there was only a single but strong rain event on 4th March 2020 that triggered the germination of

Table 1
Overview of the study plots and type of data collection during fieldwork.

Plot name	Coordinates	Type of data collection
Kam-1	23°38'45"S; 15°37'57"E	Grass excavations in 2020, initial observations already 8–9 days after rainfall, main excavations 19–20 days after rainfall; 10 dead grasses in each of 5 FCs sampled and 3 transects, each 5 m long established: from 0 m (periphery) to 5 m every 1 m one grass was sampled; in total 50 FC + 90 matrix grasses Kam-1 was revisited in 2022 and the dead grasses within the same 5 FCs were visually assessed for termite damage Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Jag-1	24°57'0.30"S; 15°58'6.83"E	Grass excavations in 2021, 53 days after rainfall; 10 dead grasses in each of 5 FCs sampled and 2 transects, each 5 m long established: from 0 m (periphery) to 5 m every 1 m one grass was sampled; in total 50 FC + 60 matrix grasses Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions Continuous soil-moisture measurements from Feb 2020 to Apr 2022, using moisture sensors at 20 cm depth
Gar-1	26°36'16"S; 16°1'2"E	Grass excavations in 2021, 59 days after rainfall; same design as for Jag-1; in total 50 FC + 60 matrix grasses Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Bra-3	20°58'46"S; 14°40'24"E	Grass excavations in 2021, 47 days after rainfall; same design as for Jag-1; in total 50 FC + 60 matrix grasses Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Bra-4	21°2'5.37"S; 14°51'33.30"E	Grass excavations in 2021, 35 days after rainfall; 10 dead grasses in 1 FC sampled and 10 dead grasses randomly sampled in matrix; in total 10 FC + 10 matrix grasses
Gir-3	19°1'55"S; 13°20'33"E	Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Mar-1	17°35'41.62"S; 12°35'54.43"E	Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Har-1	17°31'10.72"S; 12°16'11.80"E	Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Ros-1	23°32'49.70"S; 15°49'31.13"E	Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Tso-1	24°3'5.17"S; 15°46'23.68"E	Infiltration measurements, 3 each in 3 FCs and 3 each in 3 matrix positions
Tok-1	25°15'57.46"S; 16°1'59.85"E	Infiltration measurements, 3 each in FCs and 3 each in 3 matrix positions

grasses, albeit the amount of rainfall was unknown (Jan Sturm pers. comm.).

The Kam-1 plot was visited on 12th/13th March and again on 23rd/24th March. During the first visit, eight and nine days after rainfall, we noticed that young *Stipagrostis ciliata* grasses with a height of only a few centimetres had established on the totally bare soil. This happened predominantly outside the FCs in the matrix and most of the FC interior remained bare (Fig. 2a–c). These grasses in the matrix in between the FCs were soft and green. By contrast, the few grasses that grew inside the FCs started already to wilt and the leaves became stiff (Video A.1; <https://data.mendeley.com/datasets/4m3c54btmk/1>). Upon this first visit, we decided to collect data about 10 days later in order to find potentially more pronounced differences between the grasses within FCs and those of the matrix. On 23rd/24th March, we noticed that all grasses within the FCs were completely desiccated, yellow and hard (Fig. 2d,h) while grasses in the matrix were still green and soft. We selected five FCs with dead grasses for plant and soil-moisture measurements. Notably, many other FCs in the surrounding area had no germinated grasses at all.

In each of the five FCs we selected 10 dead grass individuals for measurements. At first, we measured the volumetric soil-water content (SWC in %) at about 5 cm away from each grass by vertically inserting 20 cm long rods of a TDR (Time Domain Reflectometer, HydroSense II, Campbell Scientific). After each TDR measurement we gently pulled out the grass with its entire root using a small shovel (Video A.1; <https://data.mendeley.com/datasets/4m3c54btmk/1>). The grass color was then classified as either green, green-yellow or yellow and it was also assessed as either being soft or hard. Additionally, we inspected the grass roots for any damage by termites or insects (cf. Fig. S9 in Juergens, 2013) and we also recorded if there was any sign of termite individuals, a termite hole or *Psammotermes* burrows with a black tapetum near each grass individual. Finally, we measured the length of the root and shoot using a ruler. The shoot length was based on the average length of all leaves of a grass plant. For the root measurement the root was gently pulled along the ruler so that it did not bend. The diameter and GPS position of each FC were also recorded.

The same measurements were then repeated along three 5 m long transects that were placed around each FC using a measuring tape.

Along each transect, we did six measurements. The first was done at distance 0 m, which is just outside on the periphery of a FC. Then, every 1 m another measurement was taken up to the maximal distance of 5 m away from the FC periphery. Consequently, we recorded 6×3 transects \times 5 FCs = 90 individual measurements for the matrix grasses and 10×5 FCs = 50 measurements for the grasses inside the FCs (Tables 1, 2). This study plot was revisited on 7th March 2022 during an exceptionally wet rainy season. Without repeating the same quantitative analysis as in 2020, the dead grasses within the identical FCs were again examined for termite herbivory and associated root damage, and compared to the roots of the matrix grasses (Fig. A.1).

During the much wetter rainy season from February to April 2021, this design based on 5 m long transects was principally copied for the next three study plots described below. However, in order to optimize the labor effort, we reduced the recordings in the matrix to two transects. Hence, 50 FC grasses were compared to 60 matrix grasses.

Our second plot, called “Jag-1”, was located about 5 km north-east of Mount Jagkop in the NamibRand Nature Reserve (Table 1, Figs. 1, 3a). In that plot, we installed in February 2020 soil-moisture sensors (see below), hence we knew that this plot received its first grass-triggering rainfall on 3rd January 2021 and a second much stronger rainfall occurred on 24th January (Fig. A.2). Our grass sampling was undertaken on 25th February, hence with 53 days and about 7.5 weeks, relatively late after the first grass-triggering rain.

The third plot “Gar-1” near Garub in the south was located in an interdune valley and has been described in detail in Getzin et al. (2021b). According to information by locals, this area received its first major rainfall on 4th January 2021. Grass sampling was done 59 days later on 4th March, hence comparatively late after rainfall (Fig. 3c).

Our fourth plot “Bra-3” north-east of Brandberg has been described in detail in Getzin et al. (2021b). According to the managers of the nearby Brandberg White Lady Lodge, this area received its first major rainfall (circa 12 mm) on 23rd January 2021, and another 12 mm fell on 9th/10th February. Grass excavations were undertaken on 11th March, hence 47 days after the first triggering rain (Fig. 3e).

A fifth study plot, called “Bra-4” and located in the same region as Bra-3, was added on 5th April because we found that one interesting FC

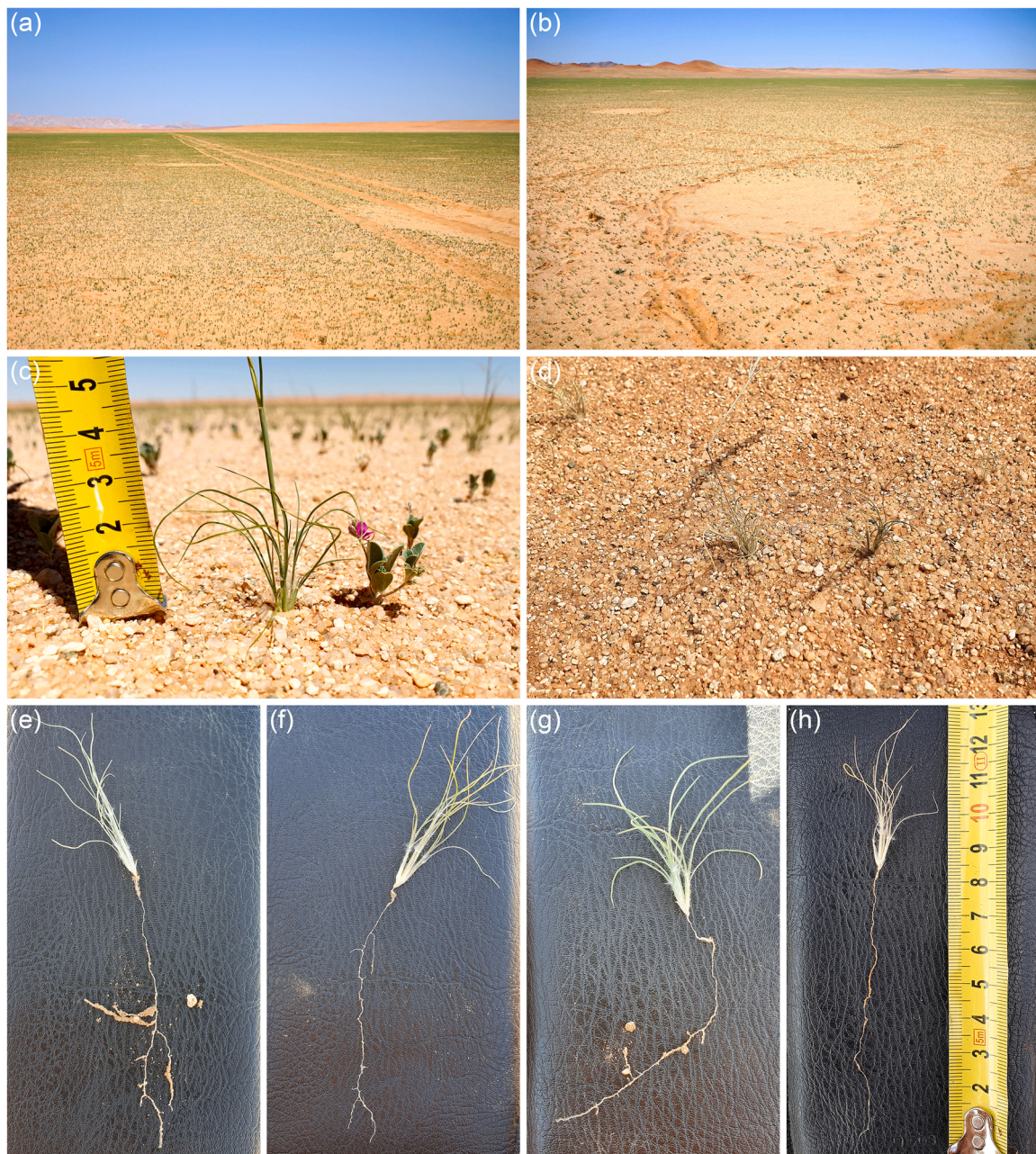


Fig. 2. The study plot Kam-1 in the central Namib in March 2020. Ground images taken on 12th March where a single rainfall event on 4th March triggered the growth of new grasses (a,b). Nearly no new plants established within the FCs but only the surrounding matrix became green. A small *Stipagrostis ciliata* grass in the matrix, growing left of a small *Indigostrum argyraeum* on 13th March (c). Two dead *S. ciliata* grasses inside a fairy circle, 20 days after rainfall on 24th March (d). Examples of excavated grasses from FCs nine days (e–g) and 19 days (h) after rainfall. Desiccation of grasses started already nine days after rainfall and leaves became hard (e–g). Another 10 days later, grasses within FCs turned completely yellow and became stiff (h).

showed a continuous layer of dead grasses inside the FC while the matrix was dominated by green and vital grasses (Fig. 3g). We drone mapped this 25-ha plot already on 10th March 2021 and again on 5th April 2021. We do not have rainfall data from 2021 for this plot as there is no rain gauge nearby. However, according to drone imagery the investigated FC had a thin layer of new grasses already on 10th March and by 5th April all the grasses inside the FC were dead (Video A.2). It can be estimated that this first green layer of grasses appearing on 10th March resulted from a first grass-triggering rainfall around 1st March 2021. Hence grass sampling on 5th April was done circa 35 days after the first rain. In this plot we only measured 10 grasses within the FC and another 10 grasses about 2–3 m away from the FC in the matrix. Accordingly, we also measured soil moisture with a TDR. This reduced sampling was done

because this single FC with a continuous dead grass layer shall function as an example for strong grass death after relatively recent rainfall.

2.3. Infiltration measurements

In order to test the hypothesis that edaphic differences in rain-water infiltration could explain the observed differences in plant vitality, we undertook infiltration measurements in the four study plots Kam-1, Jag-1, Gar-1, and Bra-3, each representing the regions Kamberg, Jagkop, Garub, and Brandberg, respectively. To cover also most other parts of the fairy-circle range in Namibia, we measured infiltration in six more regions, namely in the Giribes Plains (plot “Gir-3”), Marienfluss Valley (“Mar-1”), Hartmann’s Valley (“Har-1”), Rostock (“Ros-1”), Tsondab

Table 2

Structural properties of excavated grasses inside fairy circles (FCs) and outside in the matrix vegetation. Median values are given since the data were not normally distributed. The asterisks refer to two-sided, non-parametric Wilcoxon rank-sum tests with * indicating significant differences between the medians of the samples at $p < 0.05$, ** at $p < 0.01$, and *** at $p < 0.001$.

Plot properties	Kam-1 FC	Kam-1 Matrix	Jag-1 FC	Jag-1 Matrix	Gar-1 FC	Gar-1 Matrix	Bra-3 FC	Bra-3 Matrix	Bra-4 FC	Bra-4 Matrix
Number of days after triggering rain	19–20	19–20	53	53	59	59	47	47	35	35
Number of excavated grasses	50	90	50	60	50	60	50	60	10	10
Median shoot length (cm)	3.0	3.5***	8.0	9.8**	3.3	4.5***	4.0	5.0***	4.5	6.5***
Median root length (cm)	9.0	9.0	8.5	15.0***	8.5	14.0***	8.0	11.3***	12.5	9.8***
Median root-shoot ratio	3.2	2.7**	1.1	1.6***	2.6	3.3**	2.3	2.4	3.1	1.6*
Percent grass roots without damage (%)	100	100	74	100	82	100	68	100	100	100
Median soil-water content at grasses (%)	1.9	2.0	3.1	2.5***	4.0	5.0***	3.0	1.9***	3.8	4.4***

Valley (“Tso-1”), and at Tok Tokkie Trail in the southern NamibRand Nature Reserve (“Tok-1”). These data were collected between 18th February and 3rd April 2021 and the locations are shown in Fig. 1 and Table 1.

We randomly selected three FCs in each of the 10 study plots and undertook three infiltration measurements inside each FC and three measurements outside, about 2–3 m away from the FC peripheries (Fig. A.3). For each plot, this resulted in nine measurements inside FCs and nine outside in the matrix. The time of 60 ml water infiltration was assessed with a mini-disc infiltrometer (www.metergroup.com). For comparative reasons, we used the same suction rate, and we focused on the rate of water percolation to make our results directly comparable to previous research (Moll, 1994; Meyer et al., 2020; Getzin et al., 2016, 2021b). For each of the 10 study regions we plotted the recorded infiltration time in seconds for all measurements, in terms of the means and medians (Fig. 4). Finally, two-sided *t*-tests were used to evaluate if there were significant differences with $p < 0.05$ in the means of the infiltration rates between FCs and the matrix.

2.4. Continuous soil-water measurements from dry to rainy season

In order to investigate the effects of active grass growth on the soil-water distribution in the wet season, we installed 12 soil-moisture sensors along a transect, connecting two FCs at the plot Jag-1 in NamibRand. The installation was done on 18th February 2020 during an extended drought period in which there was no grass growth during that rainy season, but the soil remained bare until the next rainy season in 2021. The two chosen FCs were part of a spatially periodic, hexagonal arrangement and thus represent the typical FC patterns found at Jagkop (Fig. A.2). The diameters of the two FCs were 7.0 m and 7.7 m, respectively, and the shortest distance from periphery to periphery was 11.2 m. We used ECH₂O EC-5 moisture sensors (www.metergroup.com) to measure the volumetric soil-water content (SWC) in percent at 20 cm depth. We have chosen that depth as a compromise to account for the deep roots of the perennial grasses around the FC periphery (cf. Cramer and Barger, 2013), as well as for the maximum observed depth of 20 cm root length which can be attained by new emerging annuals in the matrix. In a mirroring design, the sensors were placed in the centers of the two FCs (position “FC”), then inside the FC but 1.5 m away from the center (“Half-FC”), at the periphery (“P”), and at certain distances away from the periphery where sensors “M1”, “M2”, and “M3” were 1.6 m, 3.6 m, and 4.8 m away from P, respectively (Fig. 5a). The 2 × 6 sensors thus represent three distinct positions in the fairy-circle landscape: FC & Half-FC are the fairy circles, P & M1 represent the area around the periphery of the FCs, and M2 & M3 are the typical matrix positions, being furthest away from the FCs. Given that a pair of two FCs was analyzed with such a connecting transect, this design generates four replicates for each of the three types of positions (i.e. FC, periphery and matrix). Each of the six sensors per FC was connected to a fully autonomous, solar-powered ZL6 data logger (www.metergroup.com) and the

soil-water content was recorded every 30 min. The data for the first season with strong rainfall in 2021 are shown until the 11th of April 2021, thereby covering all rainfall events that happened from early January till the end of that rainy season (Table 3, Fig. A.2). The two data loggers continued the recording into the rainy season 2022. However, for one logger two moisture sensors stopped working for unknown reasons. Consequently, we provide the recordings of only one data logger (November 2021–April 2022, see Table 3 and Fig. 5).

3. Results

3.1. Grass excavations after triggering rainfall

The systematic observations on grass death in fairy circles revealed four main findings:

First, as the Kam-1 plot demonstrates, already eight to nine days after grass-triggering rainfall, FCs largely remained unvegetated and the few germinated grasses within FCs started wilting (Fig. 2). Already 19–20 days after rainfall, the germinated grasses within FCs were completely desiccated and dead (Fig. 2d,h), while the grasses in the matrix were still green and soft.

Second, root excavations at plots that experienced grass-triggering rainfall most recently with regard to the date of fieldwork revealed that the median root length inside FCs was equal or even greater compared to that of grasses growing outside of FCs. While these root lengths were equal at Kam-1, the roots in the FC of the Bra-4 plot were with 12.5 cm significantly longer than the 9.8 cm long roots in the matrix (Table 2, Fig. 3g,h). In both of these plots, the root-shoot ratios were significantly larger inside FCs than outside. Only in the plots where rainfall occurred with 47–59 days relatively long ago and thus matrix grasses could continue their growth for a long time, the roots were significantly shorter within FCs.

Third, corresponding to the measured root lengths in the two plots Kam-1 and Bra-4, all sampled grasses (100 %) within these FCs showed no signs of damage induced by termite herbivory (Table 2, Figs. 2, 3, Videos A.1, A.2). Moreover, dead grasses within FCs of the Kam-1 plot had also undamaged roots, when we revisited the identical FCs two years later when grass growth was much more vigorous due to more rainfall in 2022 (Fig. A.1). Only in the plots Jag-1, Gar-1, and Bra-3 where rainfall occurred with 1.5–2 months longer ago, a minority of grasses (18–32 %) showed signs of damage which could be attributed to termites feeding on the already desiccated grass roots (Table 2). But the majority of roots of dead grasses also in these three study plots did not show signs of damage within FCs (Figs. 3, A.4). A black termite-induced tapetum around excavated roots was only found at three out of 210 grass individuals and this was within two FCs of the Jag-1 plot. Generally, the death of grasses within FCs happened despite the fact that many grasses had a rhizosheath around the roots (Fig. 3b,d,f).

Fourth, in the Bra-4 and Gar-1 plots, the soil-water content (SWC) as measured with the TDR rods across the upper 20 cm was significantly

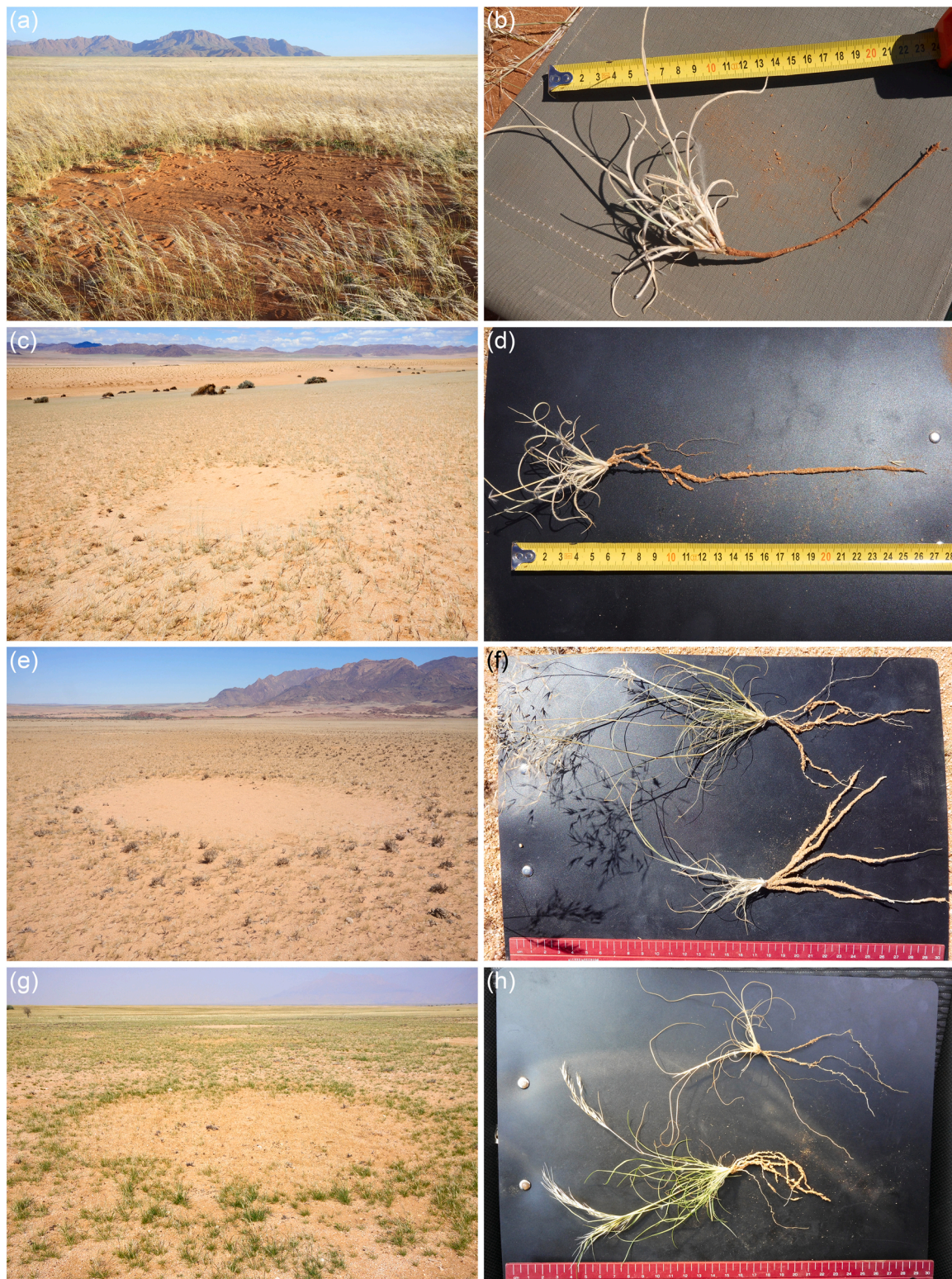


Fig. 3. Examples of grass excavations undertaken in 2021 at Jagkop (a,b), Garub (c,d), and Brandberg (e–h). The dead grasses within FCs showed no signs of root herbivory. Often a rhizosheath was present, such as at the study plots Jag-1 (b), Gar-1 (d) or Bra-3 (f). Image (f) illustrates on top a vital green grass from the matrix and below a dead grass from the FC. Image (g) shows a continuous cover of dead grasses within the FC at Bra-4 plot and (h) shows one of these grasses on top and a vital matrix grass below. More images of undamaged grass roots can be found in Figs. A.1 and A.4 [<https://data.mendeley.com/datasets/4m3c54btmk/1>].

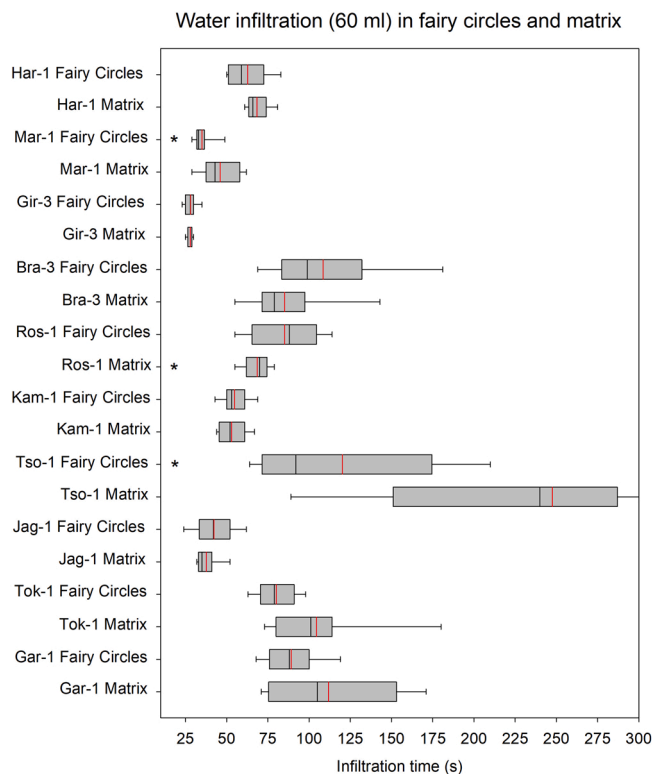


Fig. 4. The time of water infiltration in seconds in fairy circles and the matrix, shown for 10 regions from north to south along the Namib. In the box and whisker plot, the mean and median are indicated by the red and black vertical segments, respectively. The whisker lines outside the box reach from the lower quartile to the minimum and from the upper quartile to the maximum. An asterisk indicates significantly faster infiltration times either in fairy circles (Mar-1, Tso-1) or the matrix (Ros-1). The Tso-1 matrix had with 316 s and 582 s exceptionally long infiltration times for two individual measurements. For better readability of all other plots, the x-axis was reduced to a maximum of 300 s.

lower at the dead grasses inside the FCs than at the vital grasses of the matrix. For the Kam-1 plot, the SWC within the FCs was also lower but the difference with the matrix was not significant. Only at the two plots Jag-1 and Bra-3, the SWC was significantly higher within the FC than in the matrix (Table 2).

3.2. Infiltration measurements

The rate of water infiltration did not show consistent differences between FCs and the matrix (Fig. 4). In five regions, 60 ml water percolated quicker within FCs than in the matrix. For these plots, the mean infiltration time for FCs vs matrix was: 89 vs 112 s in Gar-1, 35 vs 46 s in Mar-1, 63 vs 68 s in Har-1, 120 vs 248 s in Tso-1, and 80 vs 105 s in Tok-1. However, the differences were only significant for the Mar-1 and Tso-1 plots (Fig. 4). The Tso-1 plot in the Tsondab Valley had the least sandy substrate, which explains the slow infiltration and large spread in the data (Fig. A.3c).

In four regions the mean infiltration time was slower in FCs than in the matrix: 55 vs 53 s in Kam-1, 42 vs 38 s in Jag-1, 109 vs 85 s in Bra-3, and 85 vs 69 s in Ros-1. However, the difference was only significant in Ros-1. Finally, in the Gir-3 plot the time for infiltration was with 28 s equal in FCs and in the matrix. Generally, the fastest infiltration rates occurred in the regions Jagkop, Marienfluss, and Giribes which are characterized by homogeneous deep sands and spatially periodic FC patterns.

3.3. Continuous soil-water measurements from dry to rainy season

There were two main rainfall events in 2021 at the Jag-1 plot – a smaller grass triggering event occurred on 3rd January and a major rainfall event occurred on 24th January, which doubled the volumetric soil-water content, as measured with the ECH₂O EC-5 moisture sensors at 20 cm depth (Fig. A.2). We have selected specific days that represent the key spatio-temporal dynamics of SWC before, during, and after these rainfall events (Table 3). On 1st November 2020 in the dry season with totally bare soil, SWC was very low with only 3.2 % inside the FCs and 2.6 % in the typical matrix positions M2 & M3, about 4–5 m away from the FCs. On 10th January, hence one week after the first rainfall, the SWC at all positions increased strongly with values ranging between 8.3 % and 9.1 %. Two weeks after this rainfall, the SWC inside the FCs remained stable but in the M2 & M3 positions in the matrix, it dropped slightly from 8.8 % to 8.2 % (Table 3). A major rain event occurred on 24th January. One week after this second rainfall, on 31st January, the SWC had high values within the FCs and in the matrix. Two weeks later, on 7th February, the SWC dropped sharply in the matrix M2 & M3 from 10.6 % to 6.1 % (by – 4.5 %), indicating that the new matrix grasses strongly used up that water. But also within the FCs the SWC dropped from 12.0 % to 9.8 % (by – 2.2 %), despite the fact that the FCs were not covered by transpiring grasses.

During the time of grass sampling, on 25th February 2021 and thus 7.5 weeks after the first grass-triggering rainfall, all the *Stipagrostis ciliata* grasses were at full bloom, ranging in height between 40 and 70 cm (Fig. A.5). However, despite their vital status and rich biomass in the matrix, the SWC at M2 & M3 dropped only by – 1.1 % from 6.1 % to 5.0 %. But in stark contrast, the SWC in the unvegetated fairy circles, FC & Half-FC, dropped by – 3.3 % from 9.8 % to 6.5 % (Table 3). Towards the end of the rainy season on 11th April, the SWC in the matrix dropped from 5.0 % to 3.8 % and thus at a similar magnitude as before (– 1.2 %). The SWC inside the FCs dropped by – 1.7 %.

These general trends were also observed during the rainy season in 2022, which was wetter than in 2021, as indicated by higher values of soil moisture after rainfall (Table 3). On 28th January and thus one week after the first grass-triggering rains, the SWC was with 12.5 % equally high in the FC and in the matrix M1 & M2. Until another week later on 4th February, the SWC dropped by only – 1.4 % and – 1.2 % in the FC and matrix, respectively, because transpiring grasses were not yet well established.

On 21st February, one week after the second rainfall event, the SWC has risen again to almost equally high levels as on the 28th January: it was 12.8 % and 12.7 % in the FC and matrix, respectively. But this time with fully established and intensively transpiring grasses in the matrix, the SWC dropped strongly during the next week until 28th February. Remarkably, the SWC did not only drop by – 6.0 % in the matrix, but also by – 3.9 % in the unvegetated FC (Table 3). This strong drop by – 3.9 % in the FC is 2.8 times higher than the small loss in SWC after the first rainfall event, when in the absence of established grasses, the value dropped only by 1.4 % from a similarly high value of 12.5 % (Fig. 5b). This indicates that the matrix grasses did have an active effect on the loss in SWC within the FC.

Similar to the rainy season 2021, the absolute change in SWC was until 7.5 weeks after initial rainfall again higher within the FC than in the matrix. Towards the end of the rainy season on 1st April 2022 (Fig. 5c), the loss of soil water was also higher within the FC than in the matrix.

4. Discussion

Precipitation events in the Namib are spatially variable and a patch in the landscape may receive rainfall only once every few years (Henschel et al., 2005). Consequently, the right timing in fieldwork is critical to examine the fairy circles and the short life cycle of the appearing grasses, which is usually completed within a few weeks. With this study,

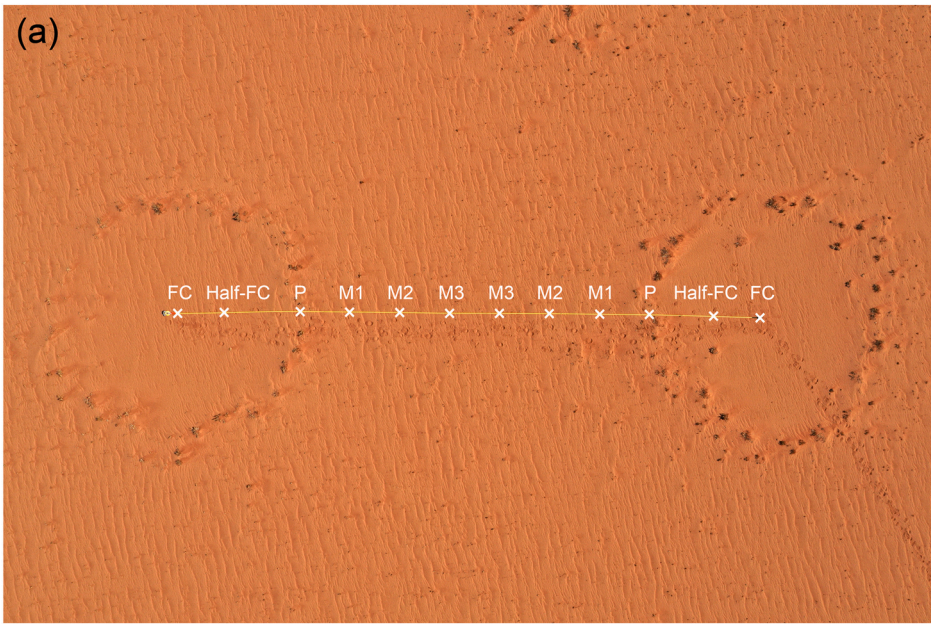


Fig. 5. Continuous soil-moisture measurements from dry to rainy seasons at Jagkop. Drone image of the two FCs without grass cover, taken on 18th February 2020 (a). The right “FC-1” is 7.0 m in diameter and the left “FC-2” measures 7.7 m. Soil-moisture sensors were placed at 20 cm depth and regular distances along the measuring tape. The distance between the two FC centers is 19 m. Results for soil-moisture recordings around “FC-2” (b). Two main rain events occurred in 2022: one on 21st January and one on 14th February. Two minor rain events occurred in between. Data were recorded until the 1st of April 2022. Without matrix grasses after initial rainfall, the drop in soil-water was very slow at all sensor positions (left blue line). But with a dense cover of transpiring grasses in the matrix a month later, the water loss in the unvegetated FC and in the matrix was very fast (right blue line). The data logger with “FC-2” is shown together with the dry matrix grasses on 1st April 2022 (c).

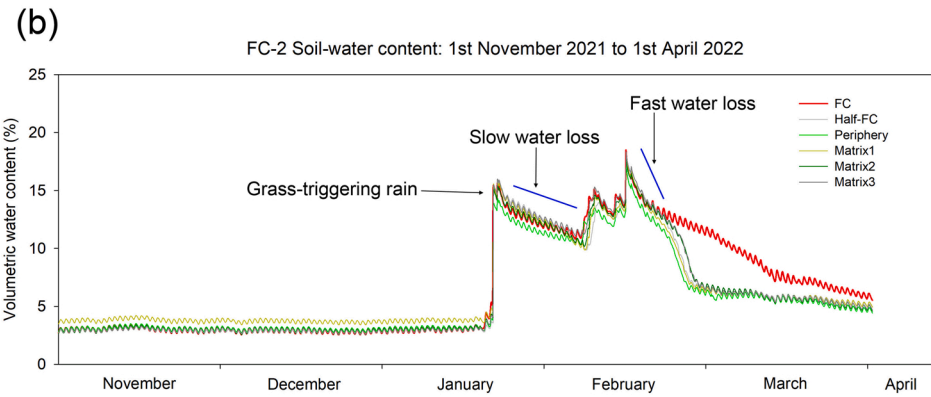


Table 3

Volumetric soil-water content (SWC in %) at the Jag-1 plot, recorded at 30 min intervals from 2020 to 2022. Shown are the measurements at 12 o'clock noon for selected days before, during, and at the end of the rainy seasons 2021 and 2022. The results show the mean values taken from the sensors at 20 cm depth that represent three distinct positions in the fairy-circle landscape. The absolute change in SWC refers to the gain or loss in water with reference to the previous date above. For comparative reasons, the time intervals after rainfall events are the same in 2022 as in 2021, except for the last one in 2022 because final download of logger data occurred 10 weeks after the 1st rainfall. Numbers in bold show that with the existence of established grasses in the matrix, the drop in SWC is much higher in the unvegetated FCs than without grasses early after the first grass-triggering rainfall.

Time relative to rainfall events	Date	Mean SWC (%) for positions			Absolute change in SWC (%) for positions		
		FC & Half-FC	P & M1	M2 & M3	FC & Half-FC	P & M1	M2 & M3
End of dry season	01 Nov 2020	3.2	3.0	2.6			
1 week after 1st rainfall	10 Jan 2021	9.1	8.3	8.8	5.9	5.3	6.2
2 weeks after 1st rainfall	17 Jan 2021	9.1	8.4	8.2	0.0	0.1	-0.6
1 week after 2nd rainfall	31 Jan 2021	12.0	9.4	10.6	2.9	1.0	2.4
2 weeks after 2nd rainfall	07 Feb 2021	9.8	6.3	6.1	-2.2	-3.1	-4.5
7.5 weeks after 1st rainfall	25 Feb 2021	6.5	5.4	5.0	-3.3	-0.9	-1.1
14 weeks after 1st rainfall	11 Apr 2021	4.8	4.2	3.8	-1.7	-1.2	-1.2
End of dry season	01 Nov 2021	2.7	3.2	2.7			
1 week after 1st rainfall	28 Jan 2022	12.5	12.0	12.5	9.8	8.8	9.8
2 weeks after 1st rainfall	04 Feb 2022	11.1	10.7	11.3	-1.4	-1.3	-1.2
1 week after 2nd rainfall	21 Feb 2022	12.8	11.8	12.7	1.7	1.1	1.4
2 weeks after 2nd rainfall	28 Feb 2022	8.9	6.2	6.7	-3.9	-5.6	-6.0
7.5 weeks after 1st rainfall	15 Mar 2022	6.4	5.4	5.5	-2.5	-0.8	-1.2
10 weeks after 1st rainfall	01 Apr 2022	5.2	4.7	4.6	-1.2	-0.7	-0.9

we investigated over three years the growth of the *Stipagrostis* grasses immediately after the first rainfall events as well as slightly delayed some weeks later. This was a challenging task, as we had to follow the unpredictable locations of rain events across hundreds of kilometers along the Namib. Our observations on grass excavations, the infiltration measurements, and the continuous soil-moisture recordings from the dry to the wet season enabled us to provide deep insights into the origin and dynamics of Namibia's fairy circles.

4.1. Termite herbivory did not cause Namibia's fairy circles

Our first study region was the Kam-1 plot near the Kamberg in the central Namib, where we investigated the dynamics of FCs immediately after rainfall. Already eight to nine days after rainfall, when the matrix turned into a green layer, most FCs did not revegetate but they largely remained as bare-soil patches (Fig. 2b). This instant absence of grasses within FCs cannot be explained with herbivory by primary consumers such as termites (Juergens, 2013; Vlieghe et al., 2015) because there was no standing biomass for consumption. Moreover, we noticed that the few grasses that were able to germinate within the FCs started wilting already about a week after rainfall. By less than three weeks after rainfall, all grasses within FCs were desiccated and dead while the matrix grasses were still vital. Careful inspection of the grasses and of potential termite activity revealed that neither grass roots of the dead plants inside the FCs nor of the matrix outside of FCs showed any sign of termite damage as proposed by Juergens (2013), and no termite individuals or nests were found under or nearby the excavated grasses (Table 2). These results from 2020 are robust also in a temporal sense because in the more productive rainfall season 2022, when plant growth was much more vigorous, the dead grasses within the identical FCs showed again roots that were unaffected by termite herbivory and indistinguishable from the root characteristics of the vital matrix grasses (Fig. A.1).

This absence of termite herbivory was also confirmed for the Bra-4 plot near Brandberg, about 300 km further north (Figs. 3h, A.4c–f, Video A.2). While the grass roots of the Kam-1 plot had an equal length inside and outside of FCs, the dead FC grasses at Bra-4 had even significantly longer roots than the matrix grasses. These quantitative and visual data strongly contradict the proposed core mechanism of the termite hypothesis (Juergens, 2013) because a 100 % of all dead grasses within the FCs showed no sign of termite herbivory. Only in the plots Jag-1, Gar-1, and Bra-3, where grass-triggering rainfall occurred with about seven to more than eight weeks longer ago, root damage of the

dead grasses within FCs ranged between 18 % and 32 %. But the majority of desiccated grasses showed even in those plots no sign of root damage (Table 2, Figs. 3, A.4). Importantly, our results address not only mature FCs whose positions are stable for several decades (Tschinkel, 2012). The findings are also valid for the origin of “new” emerging FCs or “floaters in time” that may only appear in certain years, such as at NamibRand in the Jag-1 plot, which has been compared with drone and satellite imagery for different years (Fig. A.6). Therefore, our conclusions are generalizable for both, the maintenance of established FCs, as well as for the cause of new and re-appearing FCs.

In summary, we found no termites or their nests around the investigated grasses, and we also found no such termite activity during additional soil excavations, when we dug several trenches to install the soil-moisture sensors at NamibRand. Our results confirm the findings of most older and recent FC studies that termites or their underground nests have not been found in excavated fairy circles in many regions of the Namib (Theron, 1979; van Rooyen et al., 2004; Tschinkel, 2010, 2012; Picker et al., 2012; Cramer et al., 2017; Ravi et al., 2017; Meyer et al., 2020; Getzin et al., 2021a). For example, van Rooyen et al. (2004) excavated the FCs in the Hartmann's Valley, Marienfluss, Giribes Plains, Brandberg, Khan, Escourt Experimental Farm, Sesriem, Namib Guest Farm, and Rooiduin but “none of the trenches revealed any termite tunnels” and “the presence of termite nests beneath the circle has yet to be demonstrated”. In particular addressing the sand termite *P. allocerus*, Ravi et al. (2017) concluded “at present, empirical data on termite tunnel structures within fairy circles that may favor niche construction by sand termites are not yet available”. Given that *P. allocerus* termites specifically consume fungal-colonized litter of *Stipagrostis ciliata* grasses in the Namib (Jacobson et al., 2015) this does, of course, not exclude the possibility that the desiccated dead grasses may be attractive to termites (Crawford and Seely, 1994).

Overall, our data support our first hypothesis and contradict the core mechanism of the termite hypothesis because grass death in fairy circles was not induced by root herbivory. Consequently, termites are not a necessary prerequisite for the formation of FCs and we reject the termite hypothesis as a primary cause of the fairy circles.

4.2. The root-to-shoot ratios and the rhizosheath

The finding that the root-to-shoot ratios in the plots with most recent rainfall, Kam-1 and Bra-4, were significantly larger within FCs than outside shows that the grasses invested more resources into getting longer roots. Whereas low root-to-shoot ratios and a high biomass are

typical for the grasses around the FC periphery and thus indicate a less stressful environment, high root-to-shoot ratios within FCs indicate a highly water-stressed environment (Cramer et al., 2017). This effect resulting in very long roots was particularly noticeable in the Bra-4 plot where TDR-measured soil moisture within the FC was significantly lower than in the matrix. Obviously, the grasses within the FCs had too little water available for survival, ultimately causing their quick desiccation and death over the entire FC area (Fig. 3g, Video A.2).

This water stress has already been observed during fieldwork at NamibRand Nature Reserve, where von Hase (2010) “concluded that circle soils could dry out faster than roots manage to grow and that this may kill grass seedlings and keep circles bare”. While the author could not specify why the FC soils dry out faster, he argued that the fast moisture loss would cause grass seedlings to die before the end of the growing season and that differences in drought tolerance may be accentuated due to the lack of root hairs in plants grown on circle soils. Indeed, also in our plots such as in Kam-1 and to some extent in Bra-4, we found often grasses inside FCs with an incomplete or absent rhizosheath, as is also reported by Albrecht et al. (2001). A rhizosheath is thought to improve the drought tolerance of grass species in arid environments but the development and thickness of the rhizosheath may strongly vary between years, depending on environmental conditions such as the amount of fallen rainfall (Hartnett et al., 2013). This high plasticity in the development of the rhizosheath may explain why we often also found dead grasses within FCs with a fully developed rhizosheath (Figs. 3, A.1, A.4). Hence a lack of a rhizosheath cannot be the principal reason for the death of the grasses because even with a solid sand coating around the root hairs, the grasses still desiccated in the FCs.

4.3. Infiltration differences between fairy circles and matrix cannot explain the water stress

A potential explanation for the quick wilting is the assumption that infiltration rates would be faster within FCs due to coarser soil particles, hence the plants cannot reach the more quickly percolating water (Ravi et al., 2017). Similarly, Meyer et al. (2020) proposed a hydrophobicity effect within FCs, suggesting that infiltration rates were faster within FCs than in the matrix. However, their infiltration analysis was done in a laboratory and resulted in exceptionally long infiltration times that are not matching in-situ measurements. By contrast, Getzin et al. (2021b) demonstrated for the same three study plots as shown here Garub, Brandberg, and Giribes that infiltration can be either faster or slower within FCs than in the matrix or equal, which rejects mechanisms related to infiltration speed as a generalizable explanation for plant death within FCs.

Here, we further tested this general hypothesis on the speed of water percolation by comparing the infiltration rate between FC and matrix positions for 10 regions along the Namib Desert. Already Moll (1994) found slower infiltration rates in FCs than in the matrix at Kamberg and we found the same for the Kam-1 plot, albeit the small difference of 55 vs 53 s was not significant. At Rostock infiltration was significantly quicker in the matrix than in FCs, which thus cannot explain grass desiccation with faster infiltration rates within FCs (Fig. 4). The most striking finding, however, is that particularly on deep eolian sands such as at Jagkop, the Giribes, and in the Marienfluss, infiltration rates are very rapid within FCs but also in the matrix, ranging only from 28 to 46 s. This is because the coarse-grained sandy soils in these regions are very homogeneous. More importantly, of all Namibian FC regions, these three plots Jagkop, Giribes, and Marienfluss have periodically ordered FC patterns with the highest degree of spatial regularity (Getzin et al., 2019). Vegetation self-organization can explain this strong regularity because under these homogeneous sandy substrate conditions, where rain water can infiltrate equally across large areas, plant competition for soil moisture leads to spatially periodic FCs (Meron, 2012, 2016; Getzin et al., 2015a,b). In other words, the symmetry of this self-organized pattern is a direct consequence of the homogeneity of the substrate,

while at the same time, edaphic differences in infiltration cannot explain this pattern.

In line with this, abiotic gas in the form of hydrocarbon seepage, that has been proposed to cause the FCs (Naude et al., 2011), can also not account for this periodic pattern, because geologic anomalies are typically heterogeneously spread along the parent bedrock (Getzin et al., 2015a).

With regard to the spatial patterns of the FCs, it is also hard to picture how bacteria or fungi acting at the micro scale could explain the strongly regular distances between FC centers of about 15 m at the macro scale (Ramond et al., 2014; van der Walt et al., 2016).

4.4. Ecohydrological feedbacks can explain grass desiccation in fairy circles

One of the major explanations for strongly patterned dryland vegetation is that short-range positive biomass-water feedbacks lead locally to larger plant biomass but at the same time to negative long-range depletion of resources, and ultimately to periodically ordered bare-soil gaps (Rietkerk and van de Koppel, 2008; Borgogno et al., 2009; Deblauwe et al., 2011; Meron, 2012). Sophisticated fieldwork has demonstrated that such plant self-organization leads to vegetation gaps in African shrubland (Barbier et al., 2008) or to genuine fairy circles in Australian hummock grasslands (Getzin et al., 2016, 2021c). In the sandy substrates of the Namib, the uptake-diffusion feedback is the main pattern-forming feedback which is caused by a high rate of water uptake by the permanently transpiring grasses and by fast lateral soil-water diffusion, relative to biomass expansion (Zelnik et al., 2015; Cramer et al., 2017). This leads to antiphase spatial biomass-water distributions and explains, why the bare FCs store water deep underground mainly at depths of 30–100 cm (Kinast et al., 2014; Getzin et al., 2016).

Our continuous soil-moisture recordings along the transect at NamibRand provide an informative perspective for our third hypothesis, which states that ecohydrological feedbacks are the drivers of the vegetation pattern. Between February 2020 and April 2021, we were able to witness how strong rainfall in January 2021 converted bare soil into a dense layer of tall and vital grasses. The key observation after the major rainfall was that the new matrix grasses, which have a maximal root length of 20 cm (Fig. 3), strongly depleted the soil water at a depth of 20 cm by – 4.5 % within one week from 31st January to 7th February. At the same time, the grasses around the FC periphery depleted their soil water a bit less by – 3.1 % because they benefitted from being closest to the FCs and thus from tapping that water to reduce it by – 2.2 %. Within the next 2.5 weeks the strongly vital grasses depleted the SWC in the matrix only from 6.1 % to 5.0 % and thus only by – 1.1 %. The grasses directly around the FC periphery acted in a similar way. Given that the grasses are permanently transpiring under the strong heat, this small loss in soil moisture cannot have sustained their demand for water. While we have not directly measured lateral water flow, our data suggest that these matrix grasses have drawn the water from the FCs and induced water stress to the desiccating grasses within the circles because the soil water within FCs dropped sharply from 9.8 % to 6.5 %, and thus with – 3.3 % at a rate that was three times higher than in the vegetated matrix.

This proposed feedback mechanism is even more supported by our data from the 2022 rainy season. Two weeks after the first rainfall event, and thus without the presence of large matrix grasses, the SWC at 20 cm depth dropped only by – 1.4 % and – 1.2 % within the FC and matrix, respectively. But later in the rainy season, when matrix grasses were fully established, the SWC dropped after the second major rainfall event very strongly by – 6.0 % in the matrix but also by – 3.9 % in the unvegetated FC (Table 3). Why would the SWC within the FC drop now suddenly at a magnitude that is 2.8 times higher than before? We argue that this strong decline in soil water within the FC is due to the uptake-diffusion feedback, whereby the transpiring grasses strongly pull laterally water from their surroundings because soil water in these coarse

sands at NamibRand does diffuse relatively quickly over distances of more than 7 m (Cramer et al., 2017).

For several reasons, this strong temporal difference in the magnitude of water loss from the FC cannot be explained by abiotic conditions: The drop in soil water started from similar levels of about 12.5–12.8 % the week before, hence the absolute change in SWC cannot be affected by such pre-existing moisture levels. Contrary to the first main rainfall event on 21st January, there were several smaller rain events around the 7th/8th and 12th/13th of February (cf. Fig. 5b) just before the second major rainfall event on 14th February 2022. We would therefore expect that the soil would be more moisture-saturated over its entire vertical profile after the second rainfall event, hence the drop in SWC within the FC should be lower than after the first rain event. However, the opposite occurred which we attribute to the uptake-diffusion feedback of the matrix grasses. The weather conditions at those times can also not explain this strong drop in soil water: During the week 28th January–4th February after first rainfall, when SWC only dropped by – 1.4 % within the FC, mean average temperature and wind speed were 25.7 °C and 8.5 km/h, respectively, about 7 km away at Keerweder weather station (<https://www.wunderground.com/dashboard/pws/IHARDAPR2/table/2022-04-29/2022-04-29/monthly>; data accessed on 29th August 2022). But during the week 21st–28th February, when SWC strongly dropped by – 3.9 % within the FC, mean average temperature and wind speed were only 24.8 °C and 4.4 km/h, respectively. Hence, also these weather data could hardly account for e.g. a presumed stronger evaporation, as the wind speed and air temperature were even lower, when water loss within the FC was highest. Finally, the relatively strong loss in FC water cannot be explained with, for example, presumed hotter soil-surface temperatures because FC soils at NamibRand were in a recent study consistently 2 °C cooler than matrix soils at both the surface and at 15 cm depths (Vlieghe and Picker, 2019). Consequently, those authors concluded that the circle soil temperature is unlikely to limit grass germination and seedling growth.

Overall, we identify the ecohydrological feedback effects and lateral soil-water diffusion, that is actively induced by the matrix grasses, as the most likely mechanism being responsible for the plant-water stress within the fairy circles and ultimately for the quick death of the grasses within the FCs.

It becomes also clear that the absolute values of volumetric soil-water content, as measured at 20 cm depth in FCs (which may appear high) tell us little about the true water stress for the struggling grasses within FCs because such values do not reveal how much more moisture would be there if there wouldn't be matrix grasses in the surrounding. Only the relative loss of soil water compared between FCs and matrix can reveal the competitive stress exerted by the surrounding grasses. Our individual TDR measurements were done directly next to the grasses in FCs and matrix, and in the three plots Kam-1, Bra-4, and Gar-1 the soil water was lower at those desiccating grasses than at the vital matrix grasses. This is further indication that the grasses died of water stress.

For Namib fairy circles, evidence in support of the short-range positive biomass-water feedback has been provided with fieldwork (Cramer et al., 2017; Ravi et al., 2017) as well as with pattern-process inference using aerial image analysis and process-based modeling (Tlidi et al., 2008; Getzin et al., 2015a, 2015b; Zelnik et al., 2015). In a previous ecohydrological study near the same study plot Jag-1 at NamibRand, it has been demonstrated with stable isotope labeling that water in these homogeneous sands moves horizontally over 7.5 m within a short time (Cramer et al., 2017). The typical matrix positions investigated here are only a few meters away from the soil-moisture sensors of the FCs and are thus well within the reach to tap the FC water. Given the strong concentration gradients in soil water between the depleted upper matrix soils and the FC soils, we argue that strong diffusion processes are key to understanding the pattern-forming feedbacks in this environment. In this regard, the uptake-diffusion feedback destabilizes the uniform vegetation to induce so-called Turing patterns (Turing, 1952; Kinast et al., 2014). This ecohydrological mechanism explains the

long-distance negative feedbacks where plants actively deplete water resources at a spatially periodic wavelength and thus cause Turing-like dryland vegetation patterns such as the fairy circles.

5. Conclusions

Here, we argue that the periphery and matrix grasses are actively modifying the soil moisture of the fairy circles and thus act as “ecosystem engineers”, similar to the grasses that form the fairy circles in Australia via self-organization (Getzin et al., 2021c). By forming periodic vegetation-gap patterns and preventing other grasses to establish within the fairy circles, the matrix grasses benefit from the additional water resource supplied by the FCs. In homogeneous sands of the Namib Desert, the extremely regular, spatially periodic packing of the fairy circles allows for the highest density of vegetation gaps with water supply to the grasses, which is crucial for plant survival in this extremely resource-poor environment. With our study, we provide empirical support for the causal explanation that the emergent fairy circle pattern and its relative permanence is critical for the optimal functioning of the ecosystem to capture, store and recycle limited resources (van Rooyen et al., 2004). From our detailed investigations we conclude that plant water stress and associated ecohydrological feedbacks cause the grass desiccation within fairy circles and thus induce this striking vegetation-gap pattern along the Namib Desert.

CRedit authorship contribution statement

S.G., H.Y. and K.W. conceptualized the study and designed the methodology; S.G., H.Y. and S.H. collected the data; S.G., H.Y. and S.H. analyzed the data; S.G., H.Y. and K.W. wrote the paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2022.125698.

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Appendix A

Supplementary data for

Perspectives in Plant Ecology, Evolution and Systematics

Plant water stress, not termite herbivory, causes Namibia's fairy circles

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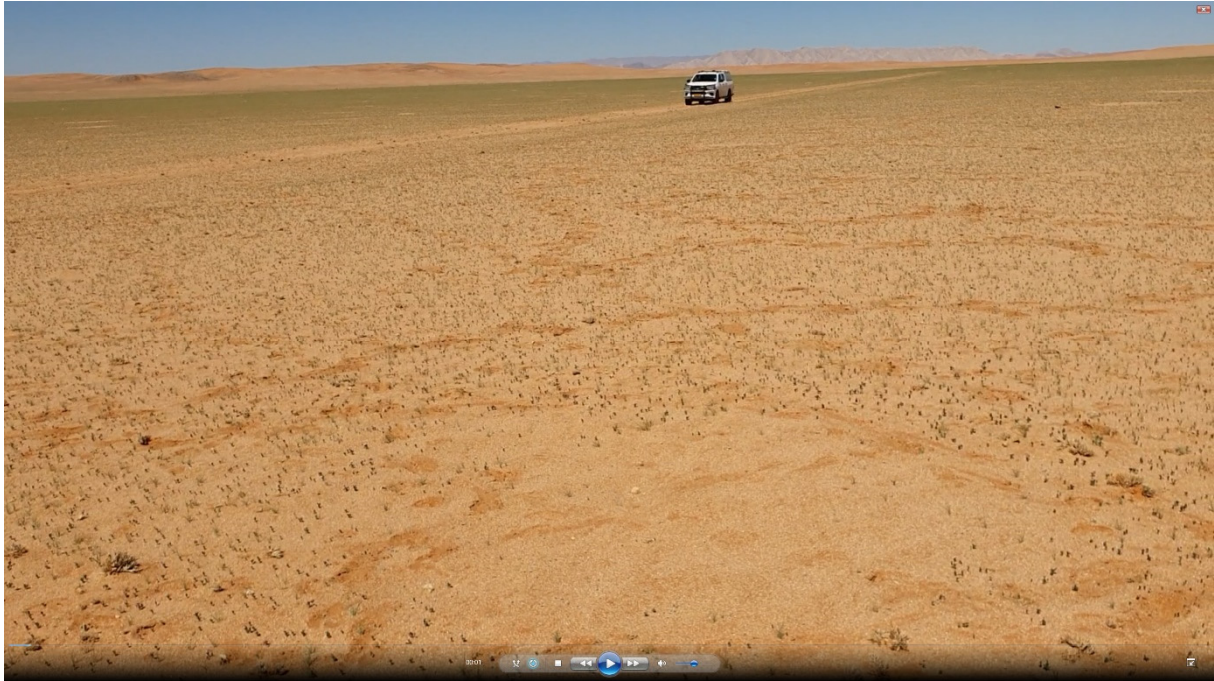
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Research, Ben-Gurion University of the Negev, Be'er Sheva, Israel

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The images and videos of this Appendix are available in high resolution in the link below

<https://data.mendeley.com/datasets/4m3c54btmk/1>



Video A.1. Short movie of the excavation of grass at the Kam-1 plot near the Kamberg. The movie was recorded about a week after the grass-triggering rainfall event that occurred on 4th March 2020. The footage demonstrates that the few germinated grasses inside the fairy circle died already within this short time after rainfall, but root damage by termites was absent and thus cannot explain the cause of the desiccating grasses.

Download movie here: <https://data.mendeley.com/datasets/4m3c54btmk/1>

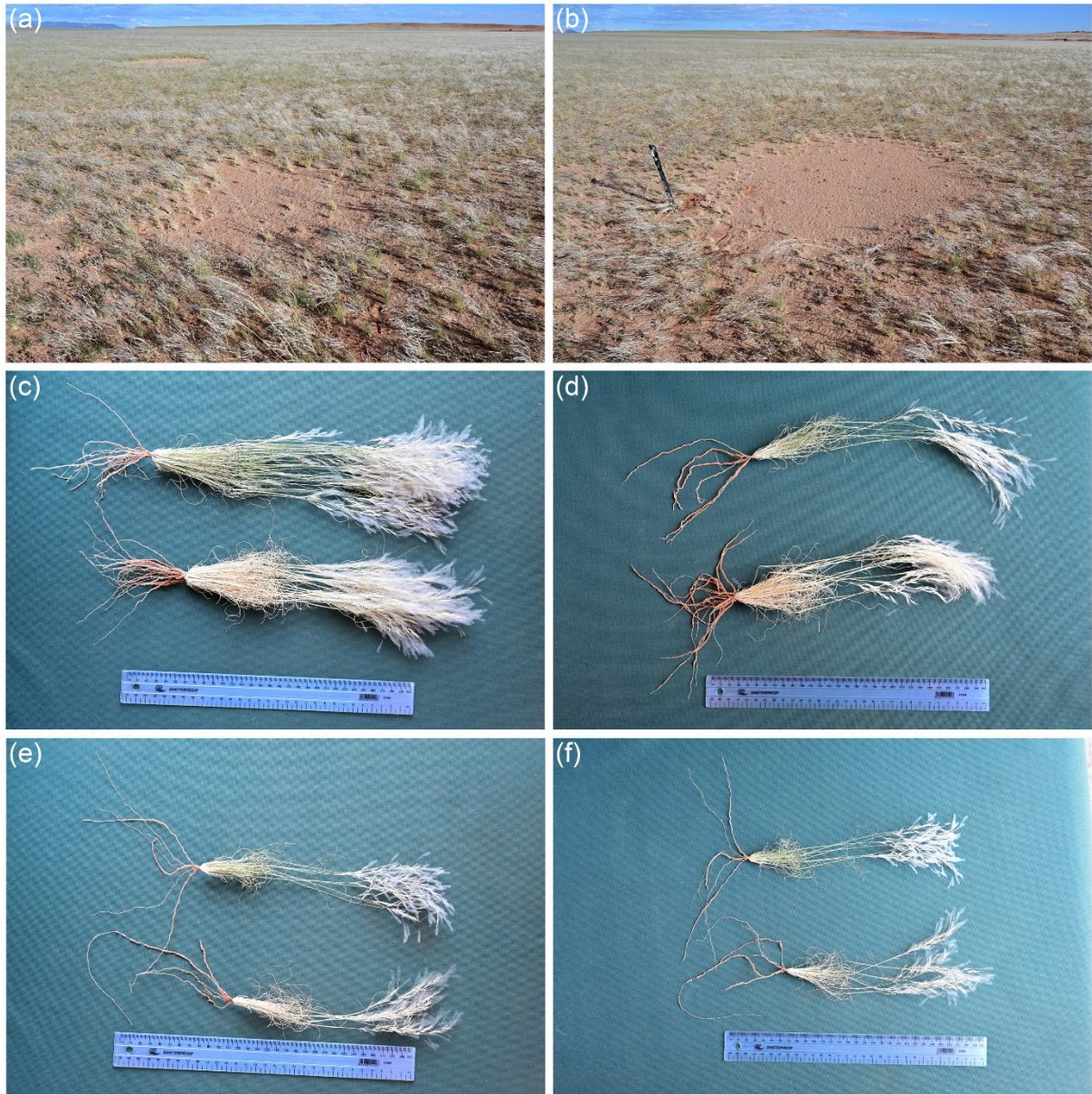


Fig. A.1. Grass excavations at the Kam-1 plot undertaken in March 2022. This plot received only low rainfall during a singular event in March 2020, but two years later vigorous grass growth was present. Grasses were excavated within and around the same FCs, two examples shown in (a) and (b), that have been examined and GPS-recorded in 2020. Grasses were dead within the FCs and these wilted plants occurred primarily at the inner edges of the FCs (a,b). Various sizes of still vital and greenish matrix grasses (upper plants in c-f) have been compared to the dead grasses from within the FCs (lower plants in c-f). The root morphology of the dead FC grasses is indistinguishable from the roots of the vital matrix grasses and signs of termite herbivory are completely absent.

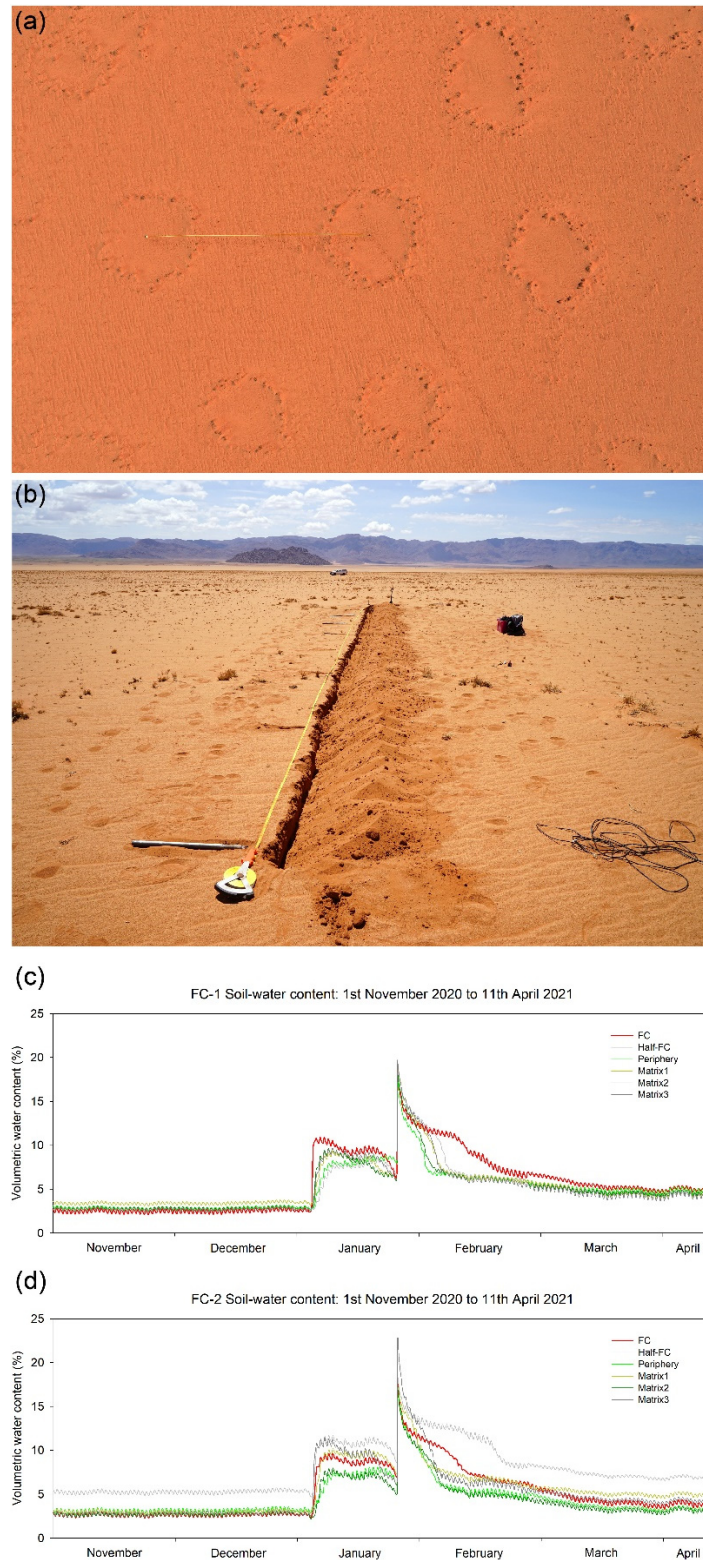


Fig. A.2. Data loggers at the Jag-1 plot. The two FCs selected for continuous soil-moisture measurements (see yellow measuring tape) are part of a hexagonal arrangement, where one FC has six nearest neighbors with equal distances from each other (a). Twelve soil-moisture sensors were installed at 20 cm depth along a transect connecting the two FCs (b). No grass cover existed during the drought in 2020, making this setup ideal to study the effects of active grass growth on the soil-water distribution before, during, and at the end of the rainy seasons (c,d).



Video A.2. Short movie of the excavation of grasses at the Bra-4 plot at Brandberg, about 35 days after grass-triggering rainfall. The movie from 5th April 2021 demonstrates that the excavated dead grasses inside the fairy circle have very long and undamaged roots. Hence, termite herbivory can be excluded as the cause of the grass death within the FC.

Download movie here: <https://data.mendeley.com/datasets/4m3c54btmk/1>

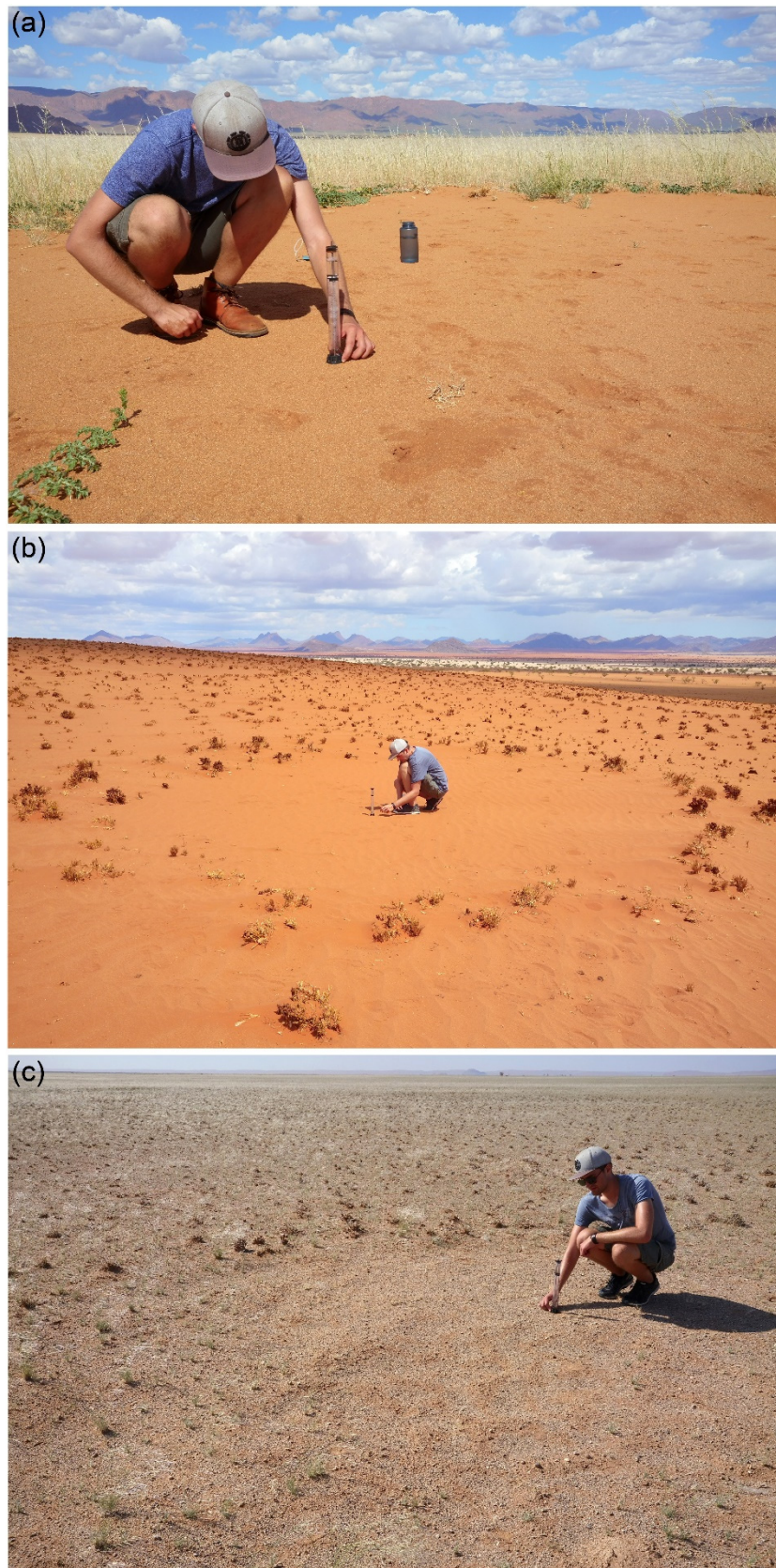


Fig. A.3. Examples of infiltration measurements inside fairy circles in various regions of Namibia. Infiltration times of 60 ml water were very short on deep and homogeneous sands such as at Jag-1, NamibRand Nature Reserve (a) or at Mar-1 in the Marienfluss Valley (b). In less sandy substrates such as at Tso-1 of the Tsondab Valley, infiltration times were much longer (c).



Fig. A.4. Additional examples of grass excavations undertaken in 2021 at Garub (a,b) and Brandberg (c-f). Grass death inside FCs at Gar-1 occurred despite the fact that most roots were undamaged and were covered by an intact rhizosheath (a,b). Also at Brandberg in the Bra-3 plot, the grasses died inside the FCs (upper plants in c,d) although the roots were undamaged. In the Bra-4 plot, the dead grasses from within the FCs (upper plants in e,f) had on average longer roots than the vital green grasses of the matrix (lower plants in e,f).



Fig. A.5. Continuous soil-moisture measurements from dry to rainy season at Jagkop. This image shows the download of the data on 25th February 2021, when the grasses were still vital and at full bloom.

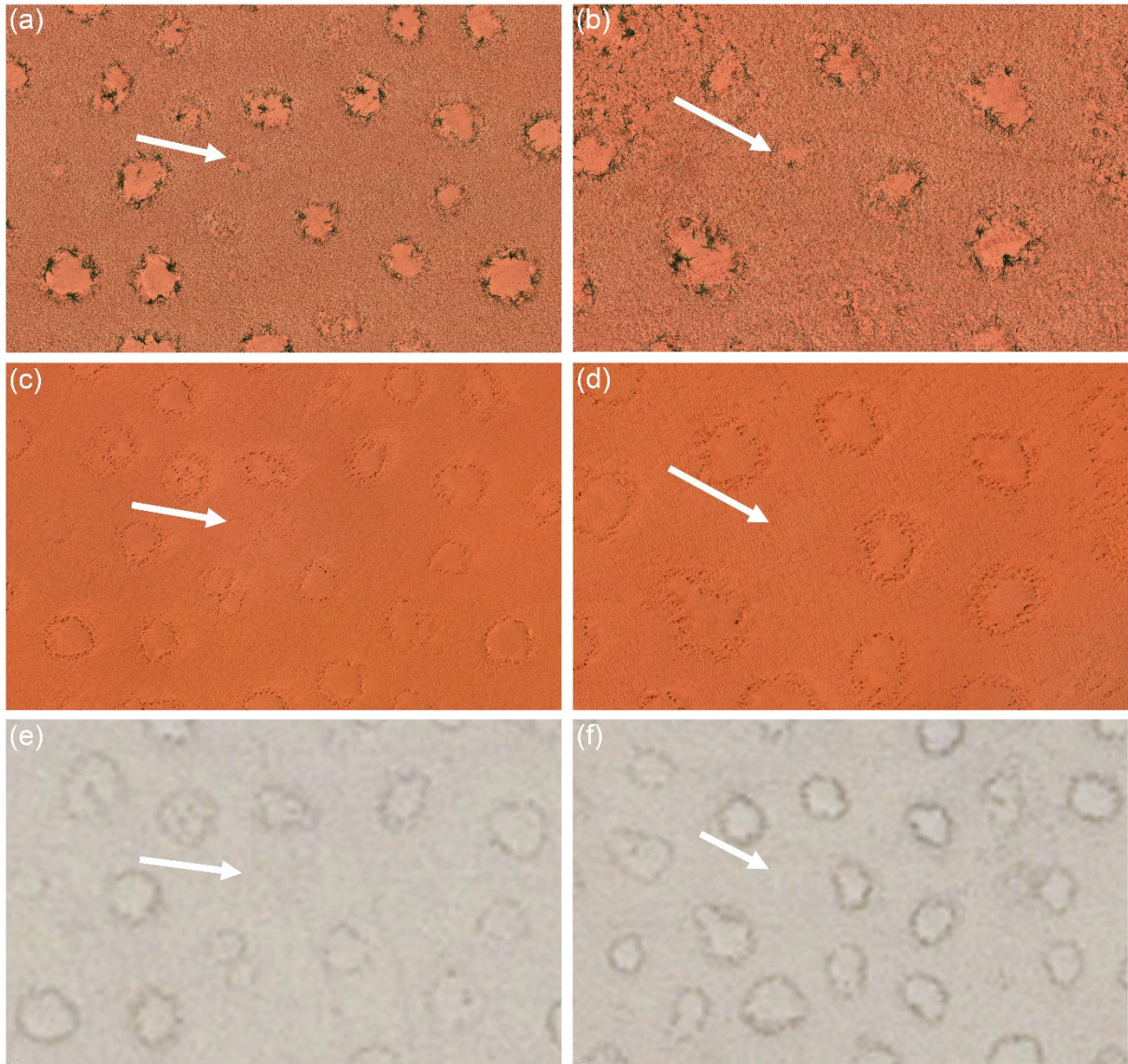


Fig. A.6. Examples of two FCs where grass excavations have been done in the Jag-1 plot. The drone images in (a) and (b) have been taken on 23rd February 2021, hence two days prior to the grass excavations. Comparisons with drone images of the same locations from 15th February 2020 (c,d) and with Google satellite imagery from 1st August 2016 (e,f) were used to specifically identify new emerging FCs that are different from the long-lived mature FCs in the surrounding. The arrows in (a) and (b) point to such exemplary FCs, where grass excavations have been undertaken. The dark green vegetation around the FC periphery is the Tsamma melone (*Citrullus lanatus*) that appeared temporarily after rainfall. Those two examined FCs were not visible as typical FCs in the years 2020 (c,d) or 2016 (e,f), hence they only appeared in the field season 2021.