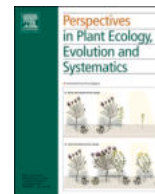


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Desiccation of undamaged grasses in the topsoil causes Namibia's fairy circles – Response to Jürgens & Gröngröft (2023)

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ABSTRACT

In a novel study, Getzin et al. (2022) have excavated 500 grasses at four regions of the Namib to systematically investigate the temporal process of how the young grasses die in fairy circles. Based on measurements of the root lengths, statistical testing, and comparative photo documentations the authors showed that sand termite herbivory did not cause the death of the freshly germinated grasses within fairy circles (FCs). Roots of those dead grasses were initially undamaged and even longer than those of the living grasses outside in the vegetation matrix, which is contrary to termite herbivory. The dying annual grasses within FCs had significantly higher root-to-shoot ratios than the vital grasses in the matrix, both of which can be attributed to the same grass-triggering rain event. This indicates that they died from water stress because the desiccating grasses invested biomass resources into roots, trying to reach the deeper soil layers with more moisture, but they failed.

Jürgens and Gröngröft (2023) commented on our research findings. Here, we shed light on their statements by investigating the existing data evidence on the Namib fairy circles, which includes a thorough literature review about the proposed termite-feeding mechanism, as well as describing the properties of soil water within and around the FCs. Our review shows that there is no single study to date that has demonstrated with systematic field evidence in the form of root measurements and data from several regions of the Namib that the green germinating grasses within the FCs would be killed by root herbivory of sand termites.

We emphasize that the top 10 cm of soil in the FCs is very susceptible to drying out. In this topsoil layer, the freshly germinated grasses with their 10 cm long roots die quickly after rainfall due to lack of water, because these small plants cannot reach and utilize the higher soil moisture content, which is only found in deeper soil layers below the dry topsoil. Based on 400 measurements of soil moisture during the rainy season 2024, we show that the topsoil in the FCs is significantly drier than in the matrix outside. Finally, we show that the soil physical conditions allow a very high hydraulic conductivity that supports the “uptake-diffusion feedback” during the first weeks after grass-triggering rainfall. During the first two weeks, the soil moisture at 20 cm depth ranged for several rainfall events between 9% and 18% within the FCs, hence way above the 6–8% threshold below which the hydraulic conductivity strongly declines. Even 20 days after rainfall, soil moisture was still above 8%. During this biologically active period, new grasses germinate after about five days, the large perennial grasses along the FC edge resprout and strongly draw water with their established root system at 20–30 cm depth, and the freshly germinated grasses in the FCs desiccate and die within 10–20 days. With our continuous soil moisture measurements, we argue that the quickly greening and competitively superior grasses on the FC edge, as well as the vital matrix grasses, draw soil water from the FCs. This rapid depletion of soil water and drying out of the topsoil leads to the death of the new grasses in the fairy circles.

1. Introduction

The fairy circles (FCs) of Namibia are a mysterious phenomenon for

quite a long time. The two theories about their origin that enjoyed most popularity are the sand termite hypothesis and the plant self-organization hypothesis (Sahagian, 2017). The sand termite

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hypothesis suggests that the species *Psammotermes allocerus* causes fairy circles by “foraging on the roots of freshly germinated grasses” (Jürgens, 2013). The plant self-organization hypothesis argues that the grasses within FCs die of plant water stress “arising from resource competition and facilitation” (Cramer and Barger, 2013) with “positive biomass-water feedbacks involving water transport towards growing vegetation patches” (Getzin et al., 2015a).

During the years 2020–2022, Getzin et al. (2022) undertook detailed fieldwork and they excavated about 500 grass individuals at four regions of the southern, central, and northern Namib to document for the first time systematically how the freshly germinating grasses die within FCs after grass-triggering rainfall. If termite herbivory were the cause, the roots of the dying grasses should be shorter according to Jürgens (2013, Fig. S9B) and show signs of biomass consumption, compared to the vital grasses in the matrix away from the FCs. However, Getzin et al. (2022) found the opposite: in the 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 inside the FCs than outside, and the roots were as long or even significantly longer as those of the surrounding matrix grasses outside of the FCs. Such long roots contradict the termite herbivory theory but indicate that drought stress caused grasses in the FCs to invest resources into roots to reach the percolating water in deeper soil layers (Cramer et al., 2017). Getzin et al. (2022) even showed for new emerging FCs at NamibRand Nature Reserve that the quickly dying grasses had undamaged roots.

Jürgens and Gröngroft (2023) published a comment on our paper with the title “Sand termite herbivory causes Namibia’s fairy circles – a response to Getzin et al. (2022)”. In that paper, the authors make four different statements. Here we make explicit reference to these statements.

2. Materials and methods

The study sites of the southern, central, and northern Namib and the methodology have been described in Getzin et al. (2022).

3. Results and discussion

In the following sections we discuss in detail the four statements of Jürgens and Gröngroft (2023).

3.1. The sand termite theory and proposed mechanism of root feeding on the green germinated grasses lacks fundamental field evidence

In their paper Jürgens and Gröngroft (2023) claim that “the fairy circle grasses die because of damage to roots due to sand termite herbivory”. To back up this statement, they wrote an incorrect sentence which is not supported by their mentioned references: “evidence for the statement that grasses in the bare patch of fairy circles get killed by localized herbivory at the roots has been provided by numerous publications (Jürgens, 2013), Vlieghe et al., 2014, Jürgens, (2015), Jürgens et al., (2015), Vlieghe, (2016), Vlieghe and Picker, (2019), Gunter et al. 2022a, 2022b, 2022c, Jürgens (2022), Jürgens and Henschel (2022).”.

The core assumption of the sand termite hypothesis is that the “foraging on the roots of freshly germinated grasses” (Jürgens, 2013) would cause the FCs. However, field-based in-situ “evidence” that these green fresh *Stipagrostis* grasses “get killed by localized herbivory at the roots” has not been provided by systematic measurements in the above-mentioned studies. For example, all three cited publications with the author “Gunter” (Gunter et al., 2022a, Gunter et al., 2022b, Gunter et al., 2022c) deal with genetics of the sand termite but not with evidence for root herbivory. The book chapter with “Henschel” (which is correctly referenced as Henschel and Jürgens, 2022 but not “Jürgens and Henschel”) deals with general animal diversity of the Namib, addressing antelopes, rodents, and beetles but it does not show evidence

for root herbivory by sand termites. The papers of Jürgens (2015) and Jürgens et al. (2015) do not show any evidence for root herbivory by sand termites but repeat the so far unproven narrative that root herbivory would kill the grasses. The above mentioned reference “Jürgens 2022” does not exist. The authors probably mean volume 7 of “Biodiversity & Ecology”, which is a journal of the Division Biodiversity, Evolution and Ecology of Plants published by the University of Hamburg. But also in this book by Jürgens et al. (2022), there are no systematic measurements of root length or biomass to show with basic statistics that insect herbivory would have a negative effect on the roots and vitality of freshly germinated grasses. Vlieghe and Picker (2019) investigated the effects of temperature on the germination success of *Stipagrostis* grasses but this study did also not show any evidence for the claim that grasses “get killed by localized herbivory at the roots”. Thus, we clarify that all these cited studies do not show any systematic evidence for root herbivory on the green fresh grasses.

The only study that documented “foraging on the roots of freshly germinated” wheat seedlings is the one of Vlieghe et al. (2015), which Jürgens and Gröngroft (2023) incorrectly cited as “Vlieghe et al. (2014)”. These authors used laboratory trials to demonstrate that *Psammotermes allocerus* reduced the root length and root number of grown wheat seedlings. However, this is not direct evidence that sand termites would also kill the freshly germinated *Stipagrostis* grasses of the Namib because artificially grown wheat seedlings are different from *Stipagrostis* seedlings. For example, the dead and desiccated *Stipagrostis* seedlings within FCs often have a protective sand coating in form of a rhizosheath around their roots (Getzin et al., 2022). The firmly attached rhizosheath with its fine and dense sand particles can be expected to protect the grass roots from insect herbivory (Moore and Johnson, 2017). Moreover, as the termite expert Walter Tschinkel (2015) pointed out: “their experiments were carried out with wheat seedlings under starvation conditions”, hence the termites had no other choice than feeding on freshly germinated plants. In the Namib, however, sand termites behave as typical detritus feeders (Crawford and Seely, 1994) that “selectively grazes the outer grey layer of the stems of perennial *Stipagrostis* species” (Jacobson et al., 2015). Hence in-situ field evidence on the feeding behavior of sand termites in the Namib is in sharp contrast to this artificial laboratory experiment.

Vlieghe (2016) investigated also the grass roots of dead seedlings within FCs of NamibRand and showed that these were shorter than the roots of healthy grasses in the matrix. This comparison shows only that the already dead grasses experienced termite herbivory which led to measurable shorter roots, but it does not show the temporal process of killing the freshly germinated grasses. However, in a more process-oriented fieldwork at the same study site, Vlieghe (2016) compared the roots of the dying grass seedlings over a period of 16 days from freshly germinated green seedlings towards yellow, dead seedlings. The author reports “grasses on the FC showed the greatest degradation in colour at the end of the 16 days from healthy green to chlorosed yellow” while the grasses outside of the FC showed no such change in colour and “no deaths of seedlings in the matrix”. This significant change from a healthy green stage towards complete death of the seedlings within the FC did not result from subterranean root herbivory because “the number of roots and the root length did not differ” between the dead seedlings of the FC and the green vital seedlings of the matrix vegetation (Vlieghe, 2016, p. 53). These in-situ fieldwork results of grass excavations at NamibRand agree with our own study which focused on documenting the temporal process of seedling death during the first days and weeks after grass-triggering rainfall events (Getzin et al., 2022). Both studies also show that the main dynamics of grass desiccation and death in the FCs happen within just two to three weeks after rainfall. Consequently, if termite feeding on the dead grass roots is documented after this critical phase of grass desiccation, it will not reveal the true cause of the fairy circles but it will only show that sand termites feed on the dead grasses.

If termite herbivory would indeed systematically kill the freshly

germinating *Stipagrostis* grasses within all FCs of the Namib, then this would clearly reduce the root length and root number of the green grasses, and it could be easily measured and documented in the field during the first weeks after grass-triggering rainfall. However, such systematic data evidence based on root measurements, replicates across the southern to northern Namib, and based on statistical testing is absent. Neither Jürgens (2013) nor the new book of Jürgens et al. (2022) have ever provided such fundamentally relevant support for the core mechanism of the proposed sand termite hypothesis. Both of these publications show single pictures of isolated cases where the authors propose that root damage on some green grasses would have happened. But the consumption of root biomass and subsequent destruction of the young vital grass through termite herbivory would lead to a measurable reduced root length, as the artificial laboratory experiment of Vlieghe et al. (2015) on wheat seedlings has demonstrated, and as Getzin et al. (2022) have shown for root herbivory on long dead grasses. Furthermore, Crawford and Seely (1994) emphasized that “*Psammotermes* readily attacks comparatively large units of detritus” in the Namib, and Jacobson et al. (2015) have documented with pictures of detritus feeding sand termites that biomass consumption is clearly visible with the naked eye. Consequently, the proposed mechanism of “foraging on the roots of freshly germinated grasses” (Jürgens, 2013) would be measurable with a simple ruler, and does not require a microscope.

Such absence of systematic data evidence for the root-herbivory hypothesis cannot be substituted by other data such as demonstrating a correlation between the presence of sand termites and fairy circles. Likewise, showing above-ground sand sheetings around the stem base of dead grasses or soil dumps (Jürgens et al., 2022) implies only that sand termites consume the dead grass in the area but it does not show evidence for the core mechanism of the termite hypothesis, which is the killing of young green grasses via root herbivory. To sum up, we agree with Tschinkel (2015) who concluded “while termites can certainly be expected to feed on the dying grasses of any forming fairy circle, the evidence that termites cause fairy circles currently remains weak to absent”.

3.2. Most parts of the inner fairy circles remain bare soil and grass death happens mainly at the inner periphery of the circles

Jürgens and Gröngroft (2023) make the statement “*Our own observations of the dieback of the grasses within the bare patch of fairy circles in Angola, Namibia, and South Africa equally show that the dieback always starts in the center of the bare patch*”. However, their own time lapse recording from the Marienfluss Valley shows in the foreground a fairy circle where grasses start dying at the inner edge and remain green in the center at variance with their claim. https://www.sasscalobservationnet.org/obs_webcam_obs.php?obs_id=A05.

In contrast to their claim, we have numerous photographs evidence

from many FC regions in Namibia showing that the majority of FCs do not have grass germination in the center at all. Some examples are provided in Getzin et al. (2022, their Figs. 2, 3, A1) and in that paper we highlighted “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. This instant absence of grasses within FCs cannot be explained with herbivory by primary consumers such as termites”, because if there is no standing biomass, then herbivory cannot have occurred. Below we show two more examples of FCs that have no grass germination in the central FC area but grasses die only at the inner edge (Fig. 1).

3.3. The freshly germinated grasses with their 10cm long roots die in fairy circles due to desiccation because they cannot reach the moister soil layers beneath the topsoil

Jürgens and Gröngroft (2023) make the claim that “*The soil beneath the dry topsoil of the bare patch of fairy circles contains an equal or, especially during the biologically active season, higher amount of moisture than the surrounding matrix at any given time. Thus the grasses in the bare patch of the fairy circles do not die due to soil drought.*”.

We agree with their statement that the topsoil is dry. But we do not agree with their claim that the fresh grasses “do not die due to soil drought” because the quick death of the freshly germinated grasses happens only in that dry topsoil of around 10–12 cm depth. Therefore, the higher soil moisture beneath that topsoil is irrelevant for the freshly germinated grasses. This has been shown with our systematic excavations of grass roots in fairy circles across the Namib Desert. Here the young grasses have roots only 10 cm long, which dry out within a few days of sprouting and show no signs of damage from sand termites (Getzin et al., 2022, Table 2, Figs. 2, 3, A1, A4). This upper topsoil layer is very susceptible to drying out and is not moister than the surrounding matrix. Jürgens and Gröngroft (2023) state that “water in the topsoil evaporates within a few days, thus developing an almost dry layer at the soil surface”. We agree that this topsoil dries out within a few days. Our systematic root measurements show that this is the reason why the young grasses with their 10 cm long roots die of desiccation. Jürgens and Gröngroft’s (2023) own moisture data (their Fig. 2 B) and the same data presented in Jürgens et al. (2023) show that for a typical rainfall event of 16.8 mm the soil moisture within the FC at 10 cm depth is much lower than the moisture in the matrix at 10 cm depth. The same finding is published by Gröngroft and Jürgens (2022), where five days after first good rain of 25 mm, when grasses start germinating, the moisture at 10 cm depth is lower within the FC than outside in the matrix. For example, at “Half radius” the soil moisture is only 5.2% but in the matrix it is 8.9%. Such differences between 5.2% and 8.9% are critical because the water conductivity strongly declines below 6–8% due to its threshold behavior.

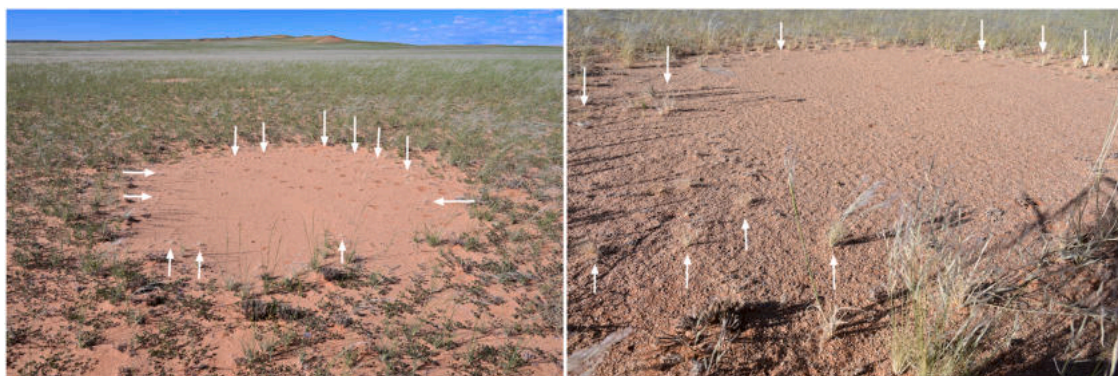


Fig. 1. Two FCs from the Kamberg area in the Namib-Naukluft Park, photographed on 7th March 2022. The inner area remains almost entirely devoid of vegetation right from the beginning of the rainy season while dead grasses are mostly near the edge (arrows), where they suffer from competition of the large peripheral grasses.

Our new measurements of soil water content during the rainy season 2024 at farm Rostock and at Kamberg also demonstrate that the topsoil is significantly drier within the FCs as compared to the matrix (Table 1, Fig. A.1). Using a mobile (TDR) moisture sensor with 12 cm long metal rods, we found that the differences in soil moisture were small but highly significant. Such differences are critical to the survival or death of grass seedlings because if they cannot grow with their roots quick enough to deeper soil layers, where the moisture is above the permanent wilting point of 2%, then grass seedlings cannot survive in this “death zone”. The fact that we found at farm Rostock lower soil moisture within the FCs already one day after rainfall, when no grasses were yet established, demonstrates that sand sorting processes may play an additional role in enforcing the FCs as a long-lived structure. The permanent winds along the Namib and the permanent presence of alive or dead grass stubbles around the FC edge may cause aeolian feedbacks and soil textural differences with coarser particles remaining within the FCs (Ravi et al., 2017, Yizhaq et al., 2024). While this may locally lead to faster loss of water and plant death within the FCs, it can only be a secondary effect because such differences in water infiltration do not occur consistently across the Namib FCs (Getzin et al., 2022).

Generally, the upper topsoil layer of 10 cm depth dries out fastest. Our own new measurements of 10 FCs at Sesriem show that the upper topsoil is consistently about four times drier than the upper 20 cm of soil during the dry season, which demonstrates the great susceptibility of the topsoil layer to drying out (Fig. 2). Additionally, our new measurements from 2024 at Kamberg show that the topsoil is also three times drier than the upper 20 cm during the rainy season when the quickly resprouting plants on the FC edge strongly draw water from the FC (Table 1, Fig. A.1). All moister soil layers below the upper 10–12 cm of the topsoil are irrelevant for the quickly desiccating and dying grasses within the FCs because these small grasses cannot reach or utilize the water of those deeper soil layers. Getzin et al. (2022, their Table 2) have shown that the median root length of young dead grasses within FCs is around 10 cm in the southern, central, and northern Namib (Fig. 3). Consequently, moisture containing in deeper layers of soil ≥ 20 cm depth do not directly reflect the moisture deficiency that leads to the desiccation and quick death of the young grasses within the upper 10 cm of soil. Due to their small size and biomass, the young grasses transpire far less than the large perennial grasses along the FC periphery that start photosynthesis soon after rainfall, giving them a superior competitive advantage over the freshly germinated grasses. Hence, the small new grasses within the FCs have no water-drawing ability as the large perennial edge plants and the vital matrix grasses. Therefore, they quickly die after germination. In summary, the higher moisture levels beneath the dry topsoil that are addressed by Jürgens and Gröngroft (2023) are of no benefit to the freshly germinated grasses within the FCs because they cannot utilize

Table 1

Volumetric soil water content (SWC in %) measured during the rainy season 2024 with a mobile (TDR) moisture sensor with 12 cm long metal rods for the topsoil and for the upper 20 cm of soil. For the fairy circles (FCs) at farm Rostock, the data were only gathered for the topsoil but at two different days. For the FCs at Kamberg in the Namib-Naukluft Park, the data were only gathered at one day but compared for a soil depth of 12 and 20 cm. Significant differences between the means of the samples were investigated with two-sided *t*-tests.

Type of measurement	FC	Matrix	<i>t</i> -test <i>p</i> -value
Rostock:			
10 FCs, 5 × in FC (N = 50), 5 × in matrix (N = 50)			
SWC in 12 cm topsoil, 1 day after rain (26 Jan 2024)	4.9	5.3	0.0168
SWC in 12 cm topsoil, 17 days after rain (11 Feb 2024)	1.6	1.8	0.0005
Kamberg:			
10 FCs, 5 × in FC (N = 50), 5 × in matrix (N = 50)			
SWC in 12 cm topsoil, 2–3 weeks after rain (15 Feb 2024)	1.0	1.3	0.0000
SWC in upper 20 cm of soil, same day (15 Feb 2024)	3.1	3.4	0.0001

that higher soil moisture.

Even our TDR measurements with vertically inserted 20 cm long metal rods reflect the moisture deficiency from the upper 10 cm down to 20 cm, because they were taken directly at the desiccating grasses where water is lost through transpiration. These moisture data show for a FC at the Brandberg 35 days after rainfall that the volumetric water content was 3.8% inside the FC where all the grasses died, but there was with 4.4% significantly more moisture outside of the FC (Getzin et al., 2022, their Table 2). At the Kamberg FCs, soil moisture resulting from a single rainfall event was already after 19–20 days 1.9% inside the FCs versus 2.0% outside in the matrix. At Garub, soil water was with only 4% again lower inside the FC than the 5% outside in the matrix. While all these measurements from 2020 to 2021 have been taken after the death of the grasses when the plants had been already desiccated, they show that there is a moisture deficiency inside the FCs, contrary to the claim of Jürgens and Gröngroft's (2023). In addition, our new data from 2024 at Kamberg show that the upper 20 cm of the soil was two to three weeks after several rainfall events significantly drier in the FCs as compared to the matrix (Table 1). Our recorded data evidence for plant water stress also agrees with similar results of von Hase (2010) who found for grass death at NamibRand: “The fast moisture loss would bring about soil desiccation faster than roots can grow, thereby causing grass seedlings to die before the end of the growing season”.

3.4. The hydraulic conductivity is very high during the active growth and competition phase of the grasses and therefore enables the uptake-diffusion feedback

Jürgens and Gröngroft (2023) make the claim that “The “uptake–diffusion feedback” in the sandy soils of fairy circles is very low”. They further write “The unsaturated hydraulic conductivity is strongly related to the water content of the soils: with ongoing desiccation, the conductivity reduces by orders of magnitude”. The authors show a threshold value of 6–8% volumetric soil moisture, below which the hydraulic conductivity is very low. This shown threshold is 8% for the FC and 6% for the perennial belt and matrix plants. Gröngroft and Jürgens (2022) also write “the strong reduction in conductivity starts at approximately 6–8 vol %”.

Unfortunately, Jürgens and Gröngroft (2023) do not account for our unpublished soil moisture data from NamibRand, where we recorded continuously every 30 minutes the moisture within and around FCs at 20 cm depth. These measurements show (Getzin et al., 2022, their Table 3 and Fig. 5b) that during the first two weeks after grass-triggering rainfall, the volumetric soil water content ranges typically between 9% and 18% within the FCs. It was thus way above the threshold which causes a decline in the conductivity. Even 20 days after rainfall, soil moisture was still above 8% for all grass-triggering rainfall events in 2021 and 2022 (Fig. 4a). When grasses start growing, the conditions for the uptake-diffusion feedback and horizontal water flow are thus met. Especially, the quickly regreening and resprouting perennial grasses on the FC periphery start drawing water soon after rainfall. These large perennials have their roots primarily distributed at 20–30 cm depth (Fig. A.1, Cramer and Barger, 2013, Jürgens, 2013, Cramer et al., 2017, Ravi et al., 2017). It is this moist layer with a high soil moisture content and hydraulic conductivity, where the grasses actively draw the water with the uptake-diffusion feedback. With this biomass-water feedback and associated concentration gradients in soil moisture, the grasses also deplete the topsoil, which dries out fastest and which contains the young dying grasses that cannot reach sufficiently moister soil layers below their 10 cm long roots. All these processes of intensive plant competition for water, the sprouting of new grasses four to five days after rainfall, and finally the desiccation and death of the new grasses after 10–20 days, happen during the time period when soil water conductivity at a depth of 20 cm is always very high (Fig. 4a).

While Getzin et al. (2022) have not provided direct evidence for this water drawing by the grasses at the periphery and matrix, their

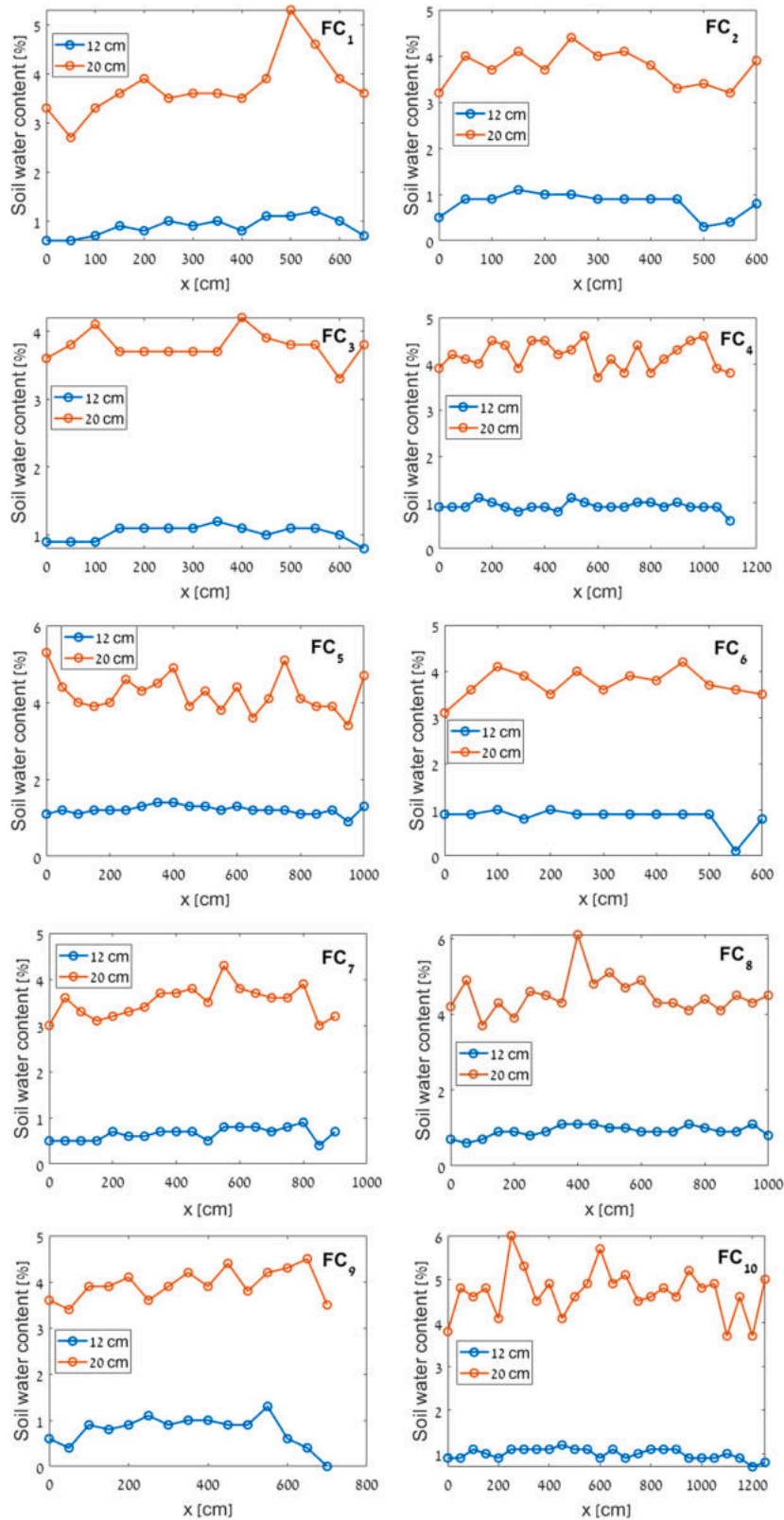


Fig. 2. Volumetric soil water content at the topsoil versus 20 cm depth, measured with a mobile (TDR) moisture sensor in 10 fairy circles (FCs) near Sesriem during the dry season in August 2023. The data represent a cross section where 0 cm is the FC edge on one side and the end of the x-axis is the FC edge on the opposing side. We took a measurement every 50 cm.

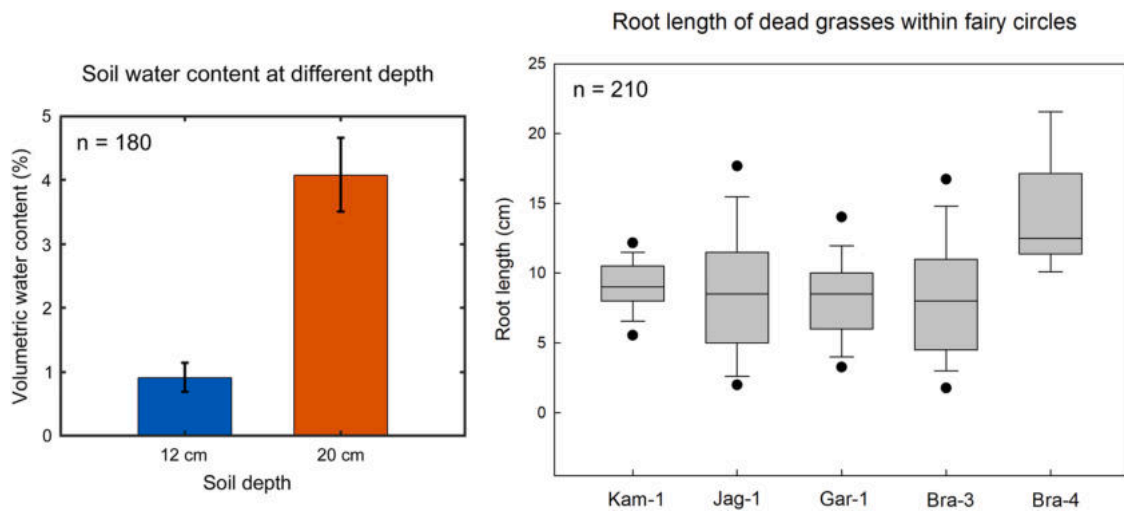


Fig. 3. Volumetric soil water content at different soil depth, summarized for all measurements shown in Fig. 2 (left). The soil water content is four times lower in the uppermost 12 cm of soil, as compared to 20 cm depth. It is in this quickly drying topsoil layer where young grasses desiccate and die with their roots that are about 10 cm long (right). The plot names from Kam-1 to Bra-4 refer to the survey published by Getzin et al. (2022).

recording of soil moisture in and around the FCs showed that with the active and vigorous grass growth around the FCs, the soil moisture dropped very strongly in the unvegetated FCs. But this did not happen before, without the presence of vigorous grass growth in the matrix. Additionally, the data also show that the decline of soil water content within one week is much stronger in the vegetation matrix than in the unvegetated FCs. For example, in 2021 the soil water content dropped within one week from 12.0% to 9.8% within the FC but from 10.6% to 6.1% in the matrix. The same was recorded in 2022, when soil water dropped from 12.8% to 8.9% within the FC but from 12.7% to 6.7% in the matrix (Getzin et al., 2022, their Table 3). Hence, the strong transpiration of grasses in the matrix resulted in an almost twice as high depletion of soil water at 20 cm depth, which demonstrates how strongly the grasses pull water.

Fig. 4b shows more than 10 m long biomass gradients around FCs. In such desert environments, biomass increases proportionally with the availability of soil moisture towards the FCs. Jürgens et al. (2015, their Fig. 2) have measured the soil moisture about 8 km away from where Fig. 4b with the halos was photographed in Iona National Park in Angola. Their data show a significant decline in soil water content ($p < 0.01$) from the periphery of the FC up to 24 m into the matrix, which corresponds to the typical biomass gradients in that area. Their selected fairy circle (GPS location: -16.918600°S; 12.362910°E) shows in Google Earth imagery from 2013 biomass gradients of more than 10 m away from the edge of the circle and a halo was also present in 2018. Additionally, their measured soil water content at 15 cm depth ranged mainly between 8% and 12% which allows a very high hydraulic conductivity and thus long-distance water diffusion. Hence, the high lateral mobility of soil water after rainfall events and associated concentration gradients in soil moisture are well illustrated by these halos around the FCs, which serve as circular water reservoirs. Cramer et al. (2017) have shown that the grasses around the FC periphery have a circa 10-fold higher total biomass than the matrix grasses, as well as a 2.3-fold higher shoot-to-root ratio, which they interpret as a result of a less water-stressed environment near the FC because the large grasses invested biomass more into shoots than into roots. This interpretation is in line with our results of finding higher root-to-shoot ratios of dying water-stressed grasses in the FCs. The study of Cramer et al. (2017), which was conducted at NamibRand where we recorded the soil moisture continuously (Fig. 4a), found also that coarse roots of peripheral grasses had a length of 33 cm, and with increasing distance from the FCs the matrix grasses had root lengths of 24 cm and 21 cm, respectively. This demonstrates that these grasses around the FCs draw soil moisture

primarily at a depth where the water conductivity remains high during the biologically active period (Fig. 4a). The biomass gradients shown in Fig. 4b also indicate that the grasses near the FCs likely facilitate each other because their higher canopy volume (cf. Cramer et al., 2017) provides more shade and thus less evaporation of soil water. This facilitation of grass growth decreases with increasing distance from the FCs, because the less water is available, the higher the cost of facilitation compared to competition for resources. Hence, the positive effects do not compensate anymore the unavoidable costs of sharing resources between neighboring individuals (Kéfi et al., 2016).

With regard to the ecohydrological feedback it is also essential to note that the “fast lateral soil water diffusion” is “relative to biomass expansion” as the studies of Zelnik et al. (2015) and Getzin et al. (2022) have written. This is key for understanding the pattern-forming feedback induced by the high rate of water uptake by the permanently transpiring grasses. The uptake-diffusion feedback was supported by another fairy-circle study which was lead-authored by the soil-hydrology expert Sujith Ravi. Using measurements on hydraulic conductivity and grain-size distributions in matrix vegetation and FC centers, the authors stated “the center infiltrates more water and could serve as source to provide water to plants at the edges through interflow (or soil water diffusion)” and “our results provide experimental evidence to demonstrate that heterogeneity of soil-hydrological processes exists within a fairy circle and highlight the potential role of ecohydrological interactions in the formation of fairy circles. The fairy circles selected for our experiments lacked any sign of sand termite activity or disturbance due to foraging animals” (Ravi et al., 2017).

Another important point is that soil is not homogenous and roughly consists of two layers with different hydraulic properties as shown in the book of Jürgens et al. (2022, their Fig. 7.5.6). The lower soil layer is more compacted and contains finer grains than the upper layer. Our own preliminary results in sandy environment show that the hydraulic conductivity decreases with soil depth (Fig. 5). In an experiment at the Secher Sands 15 km south of Beer Sheva in Israel (115 mm mean annual rainfall), we used a minidisk infiltrometer to measure the unsaturated hydraulic conductivity in excavated holes at various soil depths. These preliminary results demonstrate that especially in the upper 10 cm of soil, where new grass seedlings in fairy circles compete for moisture but fail to survive, the hydraulic conductivity is highest, even though this layer dries out fastest. The higher hydraulic conductivities in the upper soil layers can enhance lateral water diffusion especially in intense pulses of rain when the lower soil layer becomes saturated. Thus, the equation of water flow through an unsaturated porous medium in one

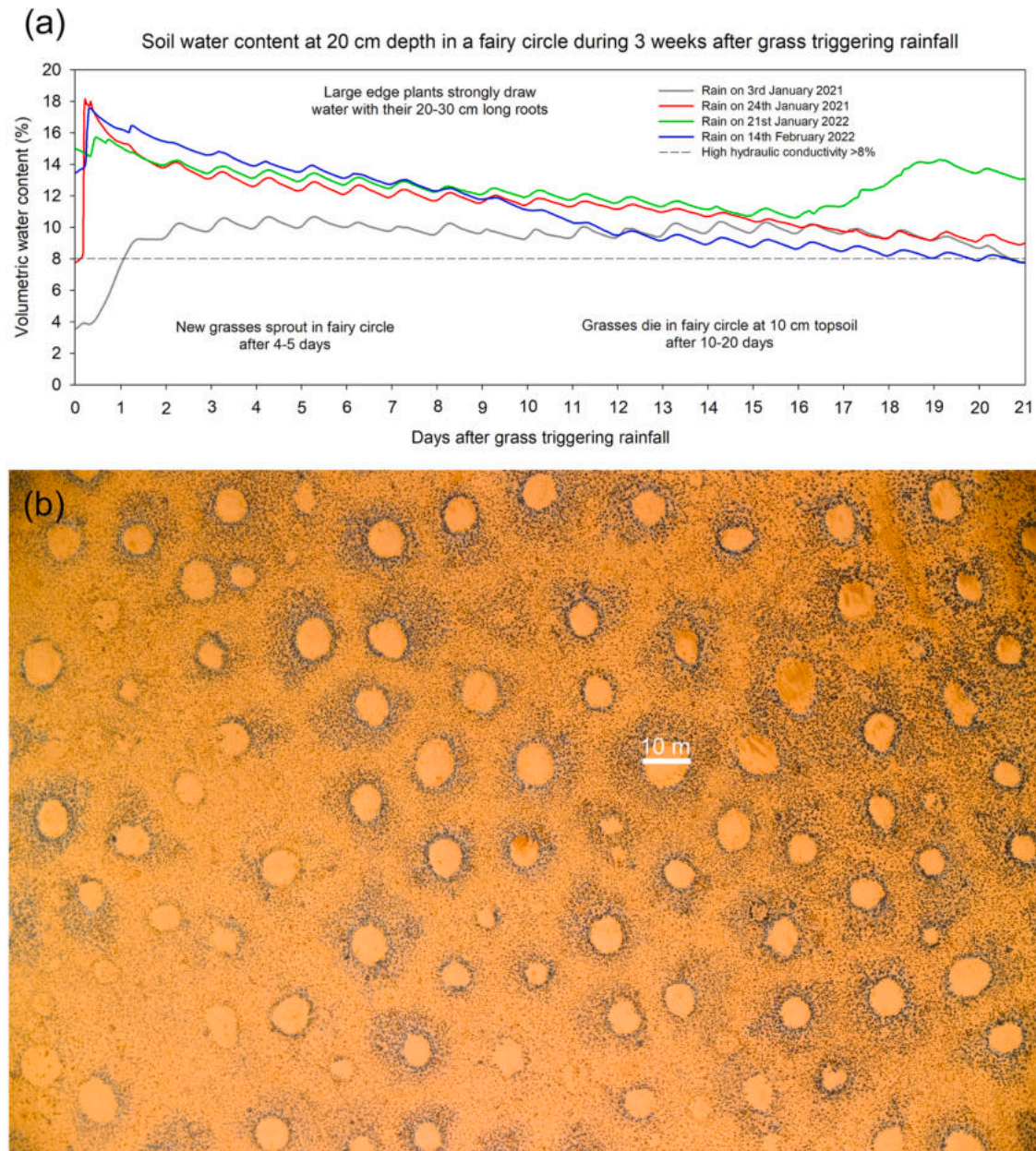


Fig. 4. Shown are four typical grass-triggering rainfall events at NamibRand Nature Reserve, demonstrating that soil moisture at 20 cm depth was always above the 8% threshold during the active growth and death phase of the grasses (a). Fig. 4b from Iona National Park in Angola (16.986729°S; 12.398526°E) shows the typical halos of declining grass biomass with distance from the water source. These biomass gradients extend for many meters. The biomass gradients in this sandy desert illustrate that the FCs are a critical source of moisture for the matrix plants (Fig. 4b is modified after Getzin et al. 2015b).

dimension is actually more complex than described by Jürgens and Gröngröft (2023). The formula incorporating soil depth is as following:

$$v = -k_u(x) \frac{\delta\psi}{\delta x}$$

where the unsaturated hydraulic conductivity $k_u(x)$ is also a function of soil depth.

3.5. Future outlook, abiotic drivers, and plant facilitation

More systematic experiments (e.g. Cramer et al., 2017, Ravi et al., 2017) and numerical simulations of water flow along the FC from the center to the matrix are needed to fully understand the process of lateral diffusion (e.g. by HYDRUS software) and its dependence on soil texture and heterogeneity. More research is also necessary to fully understand

the importance of phenotypic plasticity of grasses and how the soil water diffusion affects the pattern and distribution of individual grasses as well as of fairy circles under varying drought conditions (Bennett et al., 2023). This new study of Bennett et al. showed that lateral water diffusion in the sandy soils of the Namib and associated biomass-water feedbacks were able to explain all the empirically observed large-scale patterns of the fairy circles, as well as the small-scale distribution of individual grasses between the circles. The patterns of the individual plants thereby reflect optimal spacing distances that lower the plant environmental stress (Trautz et al., 2017).

Our fieldwork on related Australian FCs has also shown that high-vitality grasses were systematically more strongly associated with FCs than low-vitality grasses, because the grasses benefit from the FC water. High-vitality grasses also had highly aggregated patterns at short scales being evidence of positive feedbacks and facilitation whereby the roots

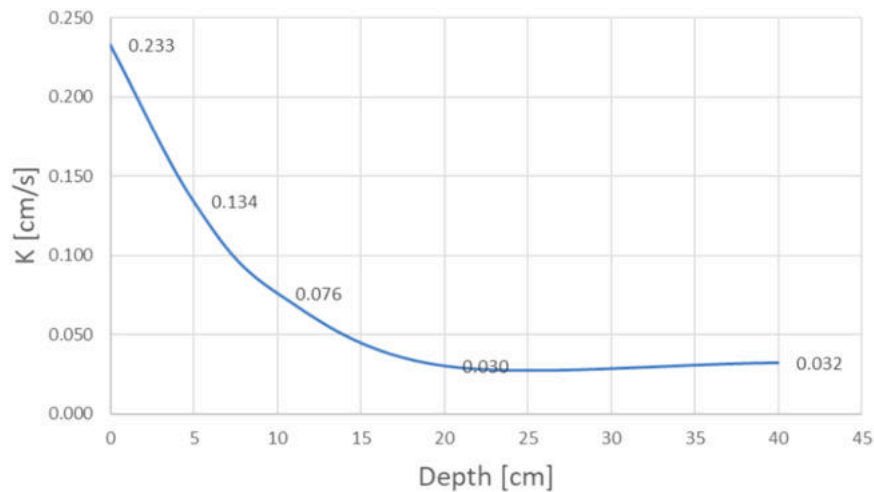


Fig. 5. The hydraulic conductivity decreases with depth in sandy soils.

of the grasses near FCs enhance water infiltration. This helps arriving wind-dispersed seeds to germinate and emerging seedlings to survive. By contrast, negative feedbacks being indicative of competition occurred at larger scales (Getzin et al., 2021b). The study showed further that the *Triodia* grasses in Australia act as ‘ecosystem engineers’ that modify their hostile, abiotic environment, leading to vegetation self-organization. Hence, according to this theory the Australian FCs with their spatially periodic patterns result from scale-dependent feedbacks and a Turing-instability mechanism.

Also, other studies have recently highlighted the importance of the Turing mechanism and Turing patterns which represent a spatially optimized self-organization structure for water acquisition (Ge, 2023). Another well-known self-organized gap pattern, resulting from combined facilitative and competitive plant interactions and scale-dependent feedbacks can be found in Niger (Barbier et al., 2008). Recently, Guirado et al. (2023) have shown by remote sensing analyses that circular vegetation gaps in grasslands that may resemble FCs on the ground are globally widespread (their study includes 263 sites). According to their predictive model, these gaps are mainly found on sandy soils with a very low soil moisture and a low nutrient content, and in hot regions that are characterized by a high precipitation seasonality and a low mean annual precipitation ranging between 100 and 300 mm. These authors identified abiotic drivers as the main determinants of the occurrence of such vegetations gaps on a global scale.

The circular shape of the fairy circles, of related vegetation gaps, and of plant rings deserves more future research to understand their formation and spatio-temporal dynamics. The logic reason for the grasses to form a ring is that a circle has the smallest circumference-to-area ratio of all geometric shapes. This optimizes their water usage inside the circle and keeps the competing grasses from the matrix effectively outside (Getzin et al., 2015b, 2022). Ring formation in arid environments is a common phenomenon and it helps plants to better survive in water deprived systems (Sheffer et al., 2011, Yizhaq et al., 2019, 2022, Yizhaq and Stavi, 2023). Also in the Namib, several annual grass and forb species are forming rings. We are currently studying how these annual grass species like *Schmidtia kalahariensis* or annual forbs like *Crotalaria podocarpa* or *Limeum argute-carinatum* form after rainfall spontaneously rings with diameters of 20 to > 100 cm (Getzin et al., 2021a).

4. Conclusion

With this response paper and literature review we reiterate that all our collected data, comparative images and video material contradict the hypothesis that sand termites would be a causal factor because the grasses die in an undamaged state (Getzin et al., 2022). We agree with

previous studies that classified sand termites of the Namib as detritus feeders (Crawford and Seely, 1994, Jacobson et al., 2015). Only the causal mechanism is ultimately important to explain the origin of the fairy circles in Namibia as well as in Australia (Getzin et al., 2024). Scientific progress rests always on data evidence in the form of systematic measurements, replicates and statistical testing. Such data have been previously collected by us, showing that the green fresh grasses within fairy circles do not die due to termite feeding on the roots, but due to desiccation in the uppermost topsoil. This, however, does not mean that plant self-organization is necessarily the sole factor being responsible for the grass desiccation. Additional factors like phytopathogenic microbes may also contribute to the maintenance of FCs (van der Walt, 2016). But we identify plant self-organization as the most likely working hypothesis (Getzin et al., 2015a,b, Bennett et al., 2023), because it accounts for all the empirical observations such as the unique, spatially periodic pattern regularity of FCs, the large distances between FCs or the vanishing of FCs at moister climatic regions above 150 mm mean annual rainfall.

CRedit authorship contribution statement

Hezi Yizhaq: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – review & editing. **Stephan Getzin:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing.

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.2024.125780](https://doi.org/10.1016/j.ppees.2024.125780).

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