See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/372321063

Long and Undamaged Roots of Dying Grasses in Namibian Fairy Circles Reject the Sand Termite Hypothesis – Response to Jürgens & Gröngröft (2023)

Preprint · July 2023

DD: 10.2133/ssm.4507988
CITATIONS
0
READS
79
2 authors, including:
Stephan Getzin
Helmholtz-Zentrum für Umweltforschung
54 PUBLICATIONS 2,743 CITATIONS
SEE PROFILE
SEE PROFILE

Some of the authors of this publication are also working on these related projects:



SpatioDiversity View project

Long and undamaged roots of dying grasses in Namibian fairy circles reject the sand termite hypothesis – Response to Jürgens & Gröngröft (2023)

Stephan Getzin^{1,2*} & Hezi Yizhaq³

¹Department of Ecosystem Modelling, University of Goettingen, Goettingen, Germany

²Gobabeb Namib Research Institute, Walvis Bay, Namibia

³Department of Solar Energy and Environmental Physics, Blaustein Institutes for Desert

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

*Corresponding author: stephan.getzin@uni-goettingen.de

Highlights

- The sand termite hypothesis lacks fundamental field evidence.
- Most parts of the inner fairy circles remain bare soil and grass death happens mainly at the inner periphery of the circles.
- The upper soil layer where grasses try to germinate is dry and not moister than the matrix.
- Field data show that water does move horizontally over many meters.
- The formation of circular grass rings in response to water stress is a universal phenomenon in the Namib but not limited to fairy circles.

Abstract

In a recent paper, Getzin et al. (2022) have systematically tested the plant self-organization hypothesis and the sand termite theory for their ability to explain the cause of Namibia's fairy circles (FCs). Based on about 500 excavated grasses from four regions across the Namib, the authors concluded that termite herbivory did not cause the death of the new grasses within FCs because the roots were initially undamaged and even longer than those of the vital grasses outside in the vegetation matrix. Benefitting from the good rainfall seasons in 2021 and 2022, the authors found several types of field evidence that plant water stress caused the grass death within FCs.

Jürgens & Gröngröft (2023) commented on our novel research findings using four statements.

Here we respond to these four points: 1) We highlight that the sand termite hypothesis cannot

challenge the detailed fieldwork results of Getzin et al. because no opposing systematic field evidence in the form of in-situ measurements, replicates, and statistical testing has been ever provided by Jürgens & Gröngröft to show that the green germinating grasses would be killed by sand termites via herbivory on the live roots. 2) Most parts of the inner fairy circles remain bare right from the beginning of the rains which cannot be explained with biomass consumption due to termite herbivory. Grass death happens mainly at the inner periphery of the circles. 3) Jürgens & Gröngröft (2023) do not take into account that the upper 10 cm of the soil is primarily relevant for the establishment and rapid death of the young grasses within the FCs. This upper soil layer is dry and not moister than the matrix. 4) Field data show that water does move horizontally over many meters, contrary to the merely theory-based statement of Jürgens & Gröngröft. Additionally, 5) we show that the formation of circular grass rings in response to water stress is a universal phenomenon in the Namib and not limited to fairy circles, which further supports the plant self-organization hypothesis.

Keywords

Desiccation, Namib Desert, Soil-water diffusion, Plant ring, Plant water stress, Root-shoot ratio

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 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 & Barger 2013) with "positive biomass-water feedbacks involving water transport towards growing vegetation patches" (Getzin et al. 2015a). Given that both of these hypotheses have never been systematically

investigated in-situ across the Namib Desert, Getzin et al. (2022) undertook detailed fieldwork and tested the two competing theories. For the first time, they excavated about 500 grass individuals at four regions of the southern, central, and northern Namib to document precisely how the freshly germinating grasses die within fairy circles 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, and the roots were as long or even significantly longer as those of the surrounding matrix grasses outside of the FCs. Such long roots entirely 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. Getzin et al. (2022) even showed for new emerging fairy circles at NamibRand Nature Reserve that the quickly dying grasses had undamaged roots.

Jürgens & Gröngröft (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 four statements of Jürgens & Gröngröft (2023) and add another perspective on plant self-organization in the Namib based on related grass and forb rings.

1) The sand termite hypothesis lacks fundamental field evidence

In their paper Jürgens & Gröngröft (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 & Picker 2019, Gunter et al 2022a, 2022b, 2022c, Jürgens (2022), Jürgens & 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 publications with the author "Gunter" deal with genetics but not with evidence for root herbivory. The book chapter with "Henschel" deals with general animal diversity of the Namib but not with evidence for root herbivory by termites. The papers of Jürgens (2015) and Jürgens et al. (2015) do not show any evidence for root herbivory but merely repeat the unproven narrative that root herbivory would kill the grasses. Vlieghe & 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" (Jürgens & Gröngröft 2023). It is therefore surprising and highly misleading that these authors list all these studies, although they do not show any evidence for root herbivory.

The only study that documented "foraging on the roots of freshly germinated" wheat seedlings is the one of Vlieghe et al. (2015). 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 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, *Stipagrostis* seedlings often have a protective sand coating in form of a

rhizosheath around their roots (Getzin et al. 2022). 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 & 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 dead grasses experienced termite herbivory but it does not show the temporal process of killing the grass. 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 healthy, 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 results agree with our own study which focused on documenting the temporal process of seedling death during the first days and weeks after rainfall, showing that the roots of dying seedlings were undamaged and as long or even significantly longer than the roots of the vital matrix grasses (Getzin et al. 2022).

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, numerous replicates across the southern to northern Namib, and based on statistical testing is still absent. Neither Jürgens (2013) nor the new book of Jürgens et al. (2022) have ever provided such fundamentally relevant support for the sand termite hypothesis. Both of these publications merely show a few anecdotal 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 & 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 termite-herbivory mechanism of "foraging on the roots of freshly germinated grasses" (Jürgens 2013) is measurable, and does not require a microscope. However, the sand termite hypothesis lacks such fundamental field evidence based on in-situ root measurements across the Namib Desert.

Such absence of systematic data evidence cannot be substituted by other data such as demonstrating a mere correlation between sand termites and fairy circles. Likewise, showing aboveground sand sheetings around the stem base of dead grasses or soil dumps (Jürgens et al. 2022) is merely evidence 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. Opposing to the sand termite hypothesis, our data evidence has shown that the young dying grasses within FCs have undamaged and even significantly longer roots than the vital grasses outside in the matrix (Getzin et al. 2022). These young grasses started dying between eight to 20 days after rainfall and the reason for their death was plant-water stress and desiccation. 2) Most parts of the inner fairy circles remain bare soil and grass death happens mainly at the inner periphery of the circles

Jürgens & Gröngröft (2023) make the incorrect 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". First, their anecdotal video does not show the entire FC area, i.e. the center but rather the margins of the obviously large circle. Second, their own time lapse recording from the Marienfluss Valley shows in the right foreground a fairy circle where grasses start dying at the 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 this anecdotal evidence based on individual FCs, 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 even 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 (Fig. 2b). 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. The initial absence of grass vegetation for most parts of the FCs is due to a lack of water in the upper soil layer because the amount of rainfall in the seasons and plant-competitive interactions determine the size, appearance or disappearance of FCs and thus the amount of revegetation that may occur (Zelnik et al. 2015).

Below we show two more examples of FCs that have no grass germination in the interior FC area but grasses die at the inner edge (Fig. 1). The fact that grasses quickly die mainly near the inner periphery is due to the strong competition for water from the large perennial edge plants.

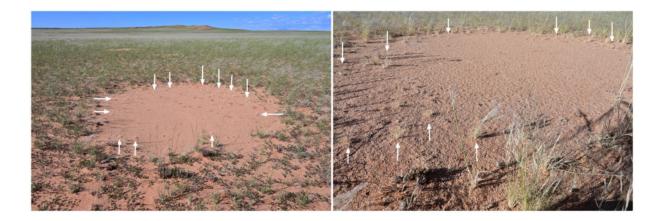


Fig. 1. Two FCs from the Kamberg area in the Namib-Naukluft Park, photographed on 7th March 2022. The inner area remains almost entirely devoid of vegetation right from the beginning of the rainy season while dead grasses are mostly near the edge (arrows), where they suffer from competition of the large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

3) The upper soil layer where grasses try to germinate is dry and not moister than the matrix

Jürgens & Gröngröft (2023) make the misleading 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.*" This claim is evidently incorrect, even based on their own data. Jürgens & Gröngröft (2023) do not take into account that the upper 10 cm of soil is primarily relevant for germination and survival of the young grasses, since Getzin et al. (2022) Table 2 shows that the median root length of young dead grasses within FCs is < 10 cm in the southern, central, and northern Namib. Consequently, moisture containing deeper layers of soil (i.e. \ge 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. Jürgens & Gröngröft's (2023) own moisture data (their Fig. 2B) 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 Gröngröft & Jürgens (2022), where five days after first good rains of 25 mm, when grasses start germinating, the moisture at 10 cm depth is lower within the FC than outside in the matrix (Fig. 2). For example, at "Half radius" where young grasses typically die, the soil moisture is only 5.2% but in the matrix it is 8.9% (Fig. 2). These data demonstrate that the relevant soil layer for grass germination is not "at any given time" moister in the biologically active season but it is even significantly drier, contrary to the statement of Jürgens & Gröngröft (2023).

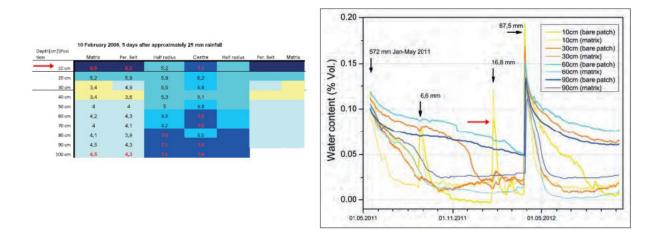


Fig. 2. These moisture data are taken from Gröngröft & Jürgens (2022). They show that after typical grass-triggering rainfall events of 16.8 to 25 mm, the soil moisture at 10 cm depth (red arrows) is lower but not equal or higher than in the matrix.

In order to understand moisture values at various soil depths, it is important to consider how the measurements were taken. Our own continuously recording moisture probes at NamibRand show higher moisture values than our spot measurements at the grasses using TDR rods. The continuously recording moisture probes were horizontally installed at 20 cm depth, which is below the upper soil layer where grass seedlings quickly die within FCs. Hence these measurements do not integrate over the upper soil layer above a depth of 20 cm and thus it is principally moister at 20 cm depth using these continuously recording sensors (Getzin et al. 2022, Table 3). In contrast, our TDR measurements

with vertically inserted metal rods that reflect the moisture deficiency from the upper 5-10 cm down to 20 cm, were taken directly at the desiccating grasses where water is lost through transpiration. These moisture data show, for example, for a FC at the Brandberg 35 days after rainfall, 3.8% volumetric water content inside the FC where all the grasses died, but with 4.4% significantly more moisture outside of the FC (Getzin et al. 2022, Table 2). At the Kamberg FCs, soil moisture was already after 19 to 20 days 1.9% inside the FCs versus 2.0% outside in the matrix. We have therefore written "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" (Getzin et al. 2022). Hence our TDR measurements reflect the entire moisture deficit in the upper 20 cm of soil, including the very dry 10 cm of top soil where grasses typically fail to survive. Our measurements from several regions of the Namib show that during the first weeks, when grasses are dying, the moisture in the upper 20 cm soil is below 5% and even near "the permanent wilting point at ca. 2 vol%" (cf. Jürgens & Gröngröft 2023). Thus, the low moisture values in the upper soil layer after typical rainfall events of 15 to 25 mm show strong plant-water stress to the young grasses with their circa 10 cm long roots, which kills them quickly. Given that the driest layer is the upper 10 cm of top soil, the water stress for the young grasses within FCs is even higher than revealed by our measurements based on the 20 cm long TDR rods. 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".

Furthermore, as we noted in our PPEES paper, "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" (Getzin et al. 2022). This is because these values are less relevant than the competitive interactions between neighboring plants for water (Cramer & Barger 2013). We have shown that with established matrix grasses shortly after rainfall, the moisture loss at 20 cm depth within the FC is three times faster than without the water-demanding surrounding

grasses. It must have been the matrix grasses and particularly the large peripheral plants that used up the FC water because there were no grasses growing within the FC that could have been responsible for the fast water loss (Getzin et al. 2022).

It is also important to note that the *Stipagrostis* grasses in the Namib only start growing after a minimum rainfall event of around 12 mm (Jacobson 2017). But they do not germinate when a rainfall event is only 6-8 mm. In both cases, the upper soil would be wet, but subtle differences in soil moisture and the rain intensity decide whether the germination and survival of seedlings occurs. For example, Fig. 2 shows a rainfall event of 6.6 mm which results in 8% volumetric soil-water content at 10 cm depth. But even though this moisture appears relatively high in terms of absolute values, grasses would not germinate.

In summary, absolute soil moisture values need to be carefully interpreted, as they not necessarily directly reflect the water stress for the plants and as only the moisture deficit in the most upper soil layer is relevant for the quick death of the young grasses with their commonly 8-10 cm long roots (Getzin et al. 2022, Table 2).

4) Field data show that water does move horizontally over many meters

Without data evidence, Jürgens & Gröngröft (2023) make the claim that "*The "uptake –diffusion feedback*" *in the sandy soils of fairy circles is very low*".

This statement is primarily based on theory. The authors have not provided field data to substantiate their claims whereas empirical evidence to the contrary was published by Cramer et al. (2017). These authors showed that water moves horizontally up to 7.5 m within a short period. Cramer et al. (2017) also used control measurements made in a nearby circle where no pulse was supplied and they adjusted for variation in water content based on this control. Consequently, the increase in soil-moisture at 7.5 m distance is not due to an artifact but a true measurement resulting from the irrigation event. This empirical data evidence 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).

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 has been overlooked by Jürgens & Gröngröft (2023) but it is key to understanding the pattern-forming feedback induced by the high rate of water uptake by the permanently transpiring grasses.

Regarding lateral water diffusion, the soil needs to be wet to some extent in order to enhance water flow. Hence, if Jürgens & Gröngröft (2023) refer to "low unsaturated hydraulic conductivities" that would restrict water flow to very small amounts, then this rather applies up to their given threshold of 6-8% volumetric soil-water content. Gröngröft & Jürgens (2022, p. 191) write "the top-soil layer needs to be wetted by rainfall to more than approximately 8 vol% before a capillary flow in deeper horizons is possible". Indeed, these values exceeding 6-8% volumetric soil-water content are typically occurring after grass-triggering rainfall events in the Namib. The continuous soil-moisture measurements of Getzin et al. (2022, Table 3) show that one to two weeks after grass-triggering rainfall, when grasses start to germinate and redistribute soil water via their transpiration, the volumetric soil-water content ranges typically between 8-13% at 20 cm depth. Hence when grasses start growing, the conditions for the uptake-diffusion feedback and horizontal water flow are met. But as shown above, water may quickly become scarce in the upper soil layer where grasses fail to establish or to survive.

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. 3). 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.

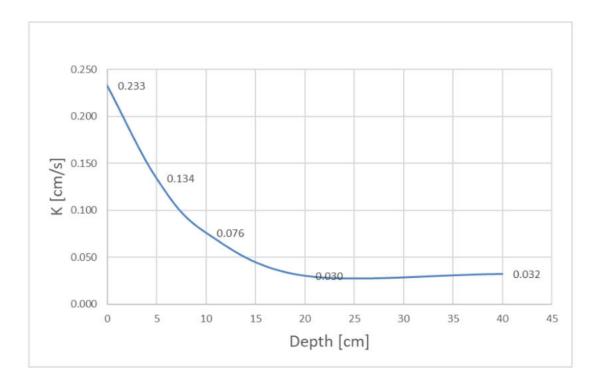


Fig. 3. The hydraulic soil conductivity decreases with depth in sandy soils.

These 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. 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 dimension is actually more complex than described by Jürgens & 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 a function of soil depth.

In any case, 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.

5) The formation of circular grass rings in response to water stress is a universal phenomenon in the Namib but not limited to fairy circles

The self-organization hypothesis is strongly supported by the fact that many different grass and forb species do form circular rings along the Namib where water is principally limiting the growth of vegetation. 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 cm to > 100 cm (Getzin et al. 2021). Even within the same study plots where fairy circles exist, e.g. in the NamibRand Nature Reserve, these plants, including *Stipagrostis ciliata*, form such rings. Similar to fairy circles, the rings have large peripheral plants because these grasses outcompete the plants from the interior of the rings so that they have exclusive access to the moisture within the rings (Fig. 4). Using 20 cm-long rods of a TDR, Getzin et al. (2021) measured the soil-water content in 15 *Schmidtia* rings on 14 February 2021, three days after the last rainfall event. Volumetric water content was with 3.6% far lower inside the rings than the 5.3% outside and about 0.5 m away from the rings. This indicates that the edge plants formed a ring to deplete the soil moisture from the interior. At the same time, excavations of these rings have shown that there was no termite activity or their nests that would have killed the grasses (Fig. 4).

The logic reason for the grasses to form a ring is that a circle has the smallest circumference-to-area ratio. This optimizes their water usage inside the gap 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). Likewise, *Stipagrostis* grasses form fairy circles because the circular shape optimizes their access to water, because in the long run, the large peripheral plants with deep-reaching roots benefit from the moisture stored at deeper soil layers below 20 cm.



Fig. 4. Not only *Stipagrostis* grasses form circles but also annual grass species like *Schmidtia kalahariensis* form rings along the Namib, where the large peripheral plants benefit from the additional soil water supplied by the ring's interior. No termites or their nests were found in such rings, as our excavations have shown.

4. Conclusion

The response paper of Jürgens & Gröngröft (2023) is misleading, because Getzin et al. (2022) have for the first time, systematically tested the termite herbivory hypothesis, and all their data, comparative images and video material rejects termites as a causal factor. Ten years after Jürgens (2013) published the sand termite hypothesis for the first time, and recently his book (Jürgens et al. 2022), the authors do not provide yet any relevant data evidence in terms of root measurements, replicates and statistics to show that sand termites would indeed cause the FCs via "foraging on the roots of freshly germinated grasses".

Finding a correlation between termites and fairy circles is easily achieved or documented. This applies also to the Australian FCs (Walsh et al. 2023). But "partial correlation with aboveground or underground termite (or ant) signs does not imply causation and ... such mere correlation needs to be carefully interpreted" (Getzin et al. 2019). This is because the actual mechanism of the formation of fairy circles is the only relevant process but it is not correlation (Getzin et al., accept in principle). Not only in Australia can we document a systematic absence of termites from FCs, also in Namibia we find often a large absence of sand termites throughout the range where fairy circles exist (Ravi et al. 2017). To the contrary, Jürgens & Gröngröft (2023) highlight "a presence of sand termites at Namibrand" or a correlation between sand termites and FCs elsewhere in Namibia. However, this over-emphasized correlation is irrelevant for the proposed causal mechanism of root herbivory because our fieldwork revealed that "no termite individuals or nests were found under or nearby the excavated grasses". Our careful investigations of the dying plants within fairy circles revealed that these excavated grasses died due to desiccation but not due to termite herbivory on the roots, even though sand termites may be present elsewhere in the area. In any case, scientific progress rests always on data evidence in the form of measurements, replicates and statistical testing. Such data have been previously collected by Getzin et al. (2022), showing that the grasses within fairy circles do not die due to termite herbivory, but due to plant water stress.

Acknowledgements

This manuscript has benefitted from fruitful discussions with Kerstin Wiegand, Katrin M. Meyer, Mike Cramer and Jeremy Midgley. We are grateful to the German Research Foundation (DFG) for supporting this study (Grant no. 433057155).

References

- Cramer, M.D., Barger, N.N., 2013. Are Namibian "fairy circles" the consequence of self-organizing spatial vegetation patterning? PLoS ONE 8, e70876.
- Cramer, M.D., Barger, N.N., Tschinkel, W.R., 2017. Edaphic properties enable facilitative and competitive interactions resulting in fairy circle formation. Ecography 40, 1210-1220.
- Crawford, C.S., Seely, M.K., 1994. Detritus mass loss in the Namib Desert dunefield: influence of termites, gerbils and exposure to surface conditions. J. Afr. Zool. 108, 49–54.
- Getzin, S., Wiegand, K., Wiegand, T., Yizhaq, H., von Hardenberg, J., Meron, E., 2015a. Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia. Ecography 38, 1-11.
- Getzin, S., Wiegand, K., Wiegand, T., Yizhaq, H., von Hardenberg, J., Meron, E., 2015b. Clarifying misunderstandings regarding vegetation self-organization and spatial patterns of fairy circles in Namibia: a response to recent termite hypotheses. Ecol. Entomol. 40, 669–675.
- Getzin, S., Yizhaq, H., Muñoz-Rojas, M., Wiegand, K. & Erickson, T. E., 2019. A multi-scale study of Australian fairy circles using soil excavations and drone-based image analysis. Ecosphere, 10(2), e02620.
- Getzin, S., Yizhaq, H., Tschinkel, W.R., 2021. Definition of "fairy circles" and how they differ from other common vegetation gaps and plant rings. J. Veg. Sci. 32, e13092.
- Getzin, S., Holch, S., Yizhaq, H., Wiegand, K., 2022. Plant water stress, not termite herbivory, causes Namibia's fairy circles. Perspectives in Plant Ecology, Evolution and Systematics, 57, 125698.
- Getzin, S., Yizhaq, H., Muñoz-Rojas, M., Erickson, T. E., accept in principle. Australian fairy circles and termite linyji are not caused by the same mechanism. Nature Ecology and Evolution.

- Gröngröft, A., Jürgens, N., 2022. Soil moisture and hydrology of fairy circles. In: Schmiedel, U. & Finckh, M. (Eds.) Fairy Circles of the Namib Desert. – Ecosystem engineering by subterranean social insects. Biodiversity & Ecology, 7, 185-198.
- Jacobson, K.M., 1997. Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. J. Arid Environ. 35, 59-75.
- Jacobson, K., van Diepeningen, A., Evans, S., Fritts, R., Gemmel, P., Marsho, C. et al., 2015. Non-rainfall moisture activates fungal decomposition of surface litter in the Namib Sand Sea. PLoS ONE 10, e0126977.
- Jürgens, N., 2013. The biological underpinnings of Namib Desert fairy circles. Science 339, 1618-1621.
- Jürgens, N., 2015. Exploring common ground for different hypotheses on Namib fairy circles. Ecography 38, 12–14.
- Jürgens, N., et al., 2015. Weaknesses in the plant competition hypothesis for fairy circle formation and evidence supporting the sand termite hypothesis. Ecol. Entomol. 40, 661–668.
- Jürgens, N. et al., 2022. Fairy Circles of the Namib Desert: Ecosystem Engineering by Subterranean Social Insects. University of Hamburg, 374 pp.
- Jürgens, N., Gröngröft, A., 2023. Sand Termite Herbivory Causes Namibia's Fairy Circles A response to Getzin et al. (2022), Perspectives in Plant Ecology, Evolution and Systematics 60, 125745. https://doi.org/10.1016/j.ppees.2023.125745
- Jürgens, N., Gröngröft, A., Gunter, F., 2023. Evolution at the arid extreme: the influence of climate on sand termite colonies and fairy circles of the Namib Desert. Phil. Trans. R. Soc. B 378: 20220149. https://doi.org/10.1098/rstb.2022.0149
- Ravi, S., Wang, L., Kaseke, K.F., Buynevich, I.V., Marais, E., 2017. Ecohydrological interactions within "fairy circles" in the Namib Desert: Revisiting the self-organization hypothesis. J. Geophys.
 Res. Biogeosci. 122, 405-414.

- Sahagian, D., 2017. The magic of fairy circles: Built or created? J. Geophys. Res. Biogeosci. 122, 1294-1295.
- Sheffer, E., Yizhaq, H., Shachak, M., Meron, E., 2011. Mechanisms of vegetation-ring formation in water-limited systems. J. Theor. Biol. 273, 138–146.
- Tschinkel, W.R., 2015. Experiments testing the causes of Namibian fairy circles. PLoS ONE 10, e0140099.
- Vlieghe, K., Picker, M.D., Ross-Gillespie, V., Ernie, B., 2015. Herbivory by subterranean termite colonies and the development of fairy circles in SW Namibia. Ecol. Entomol. 40, 42–49.
- Vlieghe, K., 2016. The ecology of Namibian fairy circles and the potential role of sand termites (*Psammotermes allocerus Silvestri*) in their origin. PhD dissertation. University of Cape Town.
- Vlieghe, K., Picker, M., 2019. Do high soil temperatures on Namibian fairy circle discs explain the absence of vegetation? Plos One 14, e0217153.
- von Hase, F., 2010. Can Soil Factors of Namibian Fairy Circles Explain the Absence of Vegetation from them? (B.Sc. Thesis). Faculty of Science, Department of Biological Sciences, University of Cape Town, South Africa.
- Walsh, F., Bidu, G.K., Bidu, N.K. et al., 2023. First Peoples' knowledge leads scientists to reveal 'fairy circles' and termite linyji are linked in Australia. Nature Ecology and Evolution 7, 610-622.
- Yizhaq, H., Stavi, I., Swet, N., Katra, I., 2019. Vegetation ring formation by water overland flow in water-limited environments: Field measurements and mathematical modelling. Ecohydrology 12, e2135.
- Yizhaq, H., Al-Tawaha, A.R.M.S., Stavi, I. 2022. A first study of *Urginea maritima* rings: A case study from southern Jordan. Land 11, 285.

Zelnik, Y.R., Meron, E., Bel, G., 2015. Gradual regime shifts in fairy circles. PNAS 112, 12327–12331.