

RESEARCH ARTICLE

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Key Points:

- We provide experimental evidence for the ecohydrological interactions within fairy circles in the Namib Desert
- Considerable heterogeneity in hydrological processes and soil properties exists between the gaps and edges of fairy circles
- Our results support the self-organization hypothesis of fairy circle formation attributed to scale-dependent antiphase biomass-water feedbacks

Supporting Information:

- Supporting Information S1
- Data Set S1

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Ecohydrological interactions within "fairy circles" in the Namib Desert: Revisiting the self-organization hypothesis

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Abstract Vegetation patterns such as rings, bands, and spots are recurrent characteristics of resource-limited arid and semiarid ecosystems. One of the most recognizable vegetation patterns is the millions of circular patches, often referred to as "fairy circles," within the arid grassland matrix extending over hundreds of kilometers in the Namib Desert. Several modeling studies have highlighted the role of plant-soil interactions in the formation of these fairy circles. However, little is known about the spatial and temporal variabilities of hydrological processes inside a fairy circle. In particular, a detailed field assessment of hydrological and soil properties inside and outside the fairy circles is limited. We conducted extensive measurements of infiltration rate, soil moisture, grass biometric, and sediment grain-size distribution from multiple circles and interspaces in the Namib Desert. Our results indicate that considerable heterogeneity in hydrological processes exists within the fairy circles, resulting from the presence of coarser particles in the inner bare soil areas, whereas concentration of fine soil occurs on the vegetated edges. The trapping of aeolian and water-borne sediments by plants may result in the observed soil textural changes beneath the vegetation, which in turn, explains the heterogeneity in hydrological processes such as infiltration and runoff. Our investigation provides new insights and experimental data on the ecohydrological processes associated with fairy circles, from a less studied location devoid of sand termite activity within the circles. The results seem to provide support to the "self-organization hypothesis" of fairy circle formation attributed to the antiphase spatial biomass-water distributions.

1. Introduction

Vegetation patterns, a recurrent characteristic of water-limited environments, are often manifested as spots [Couteron and Lejeune, 2001], bands [Leprun, 1999; Yizhaq *et al.*, 2005], stripes [White, 1971; Ludwig *et al.*, 1999], and rings [Sheffer *et al.*, 2007; Ravi *et al.*, 2008]. A multitude of field observations and mathematical models indicate that the key mechanisms responsible for the evolution of these patterns are the interactions among surface soil moisture, erosion processes, and vegetation [Ludwig *et al.*, 1999; Valentin *et al.*, 1999; Ravi *et al.*, 2007]. Vegetation patterns can be considered as indicators of abiotic processes (e.g., soil moisture, infiltration, and runoff), and hence, rapid changes in patterns are recognized as early warning signs of environmental changes such as desertification in dry lands [von Hardenberg *et al.*, 2001; Gilad *et al.*, 2004; D'Odorico *et al.*, 2007; Scanlon *et al.*, 2007]. Furthermore, analysis on the formation, structure, and growth of vegetation patterns and their interactions with hydrologic factors can improve our current understanding of important processes underlying the dynamics of water-limited ecosystems [Turner, 1989; Bestelmeyer *et al.*, 2006; Ludwig *et al.*, 2007].

One of the most recognizable vegetation patterns is the millions of circular patches within the arid grassland matrix extending over hundreds of kilometers along the eastern, interior margin of the coastal Namib Desert, from southern Angola to northern South Africa [van Rooyen *et al.*, 2004; Jankowitz *et al.*, 2008; Cramer and Barger, 2013; Juergens, 2013]. The circular patterns, often referred to as "fairy circles" (Figure 1), are manifested as circular barren gaps with mean diameter ranging from 3.7 m in the south to 34.6 m in the north [Juergens, 2013]. The bare patches are surrounded by a ring of grasses (e.g., *Stipagrostis giessii*, *S. ciliata*, *S. obtusa*, or *S. hochstetteriana*) and occur in sandy soils around the isohyet of 100 mm mean annual precipitation [van Rooyen *et al.*, 2004; Juergens, 2013; Tschinkel, 2012, 2015; Cramer and Barger, 2013]. The circles seem to appear and disappear in time, and their average life span is estimated to be around 41 years [Tschinkel,

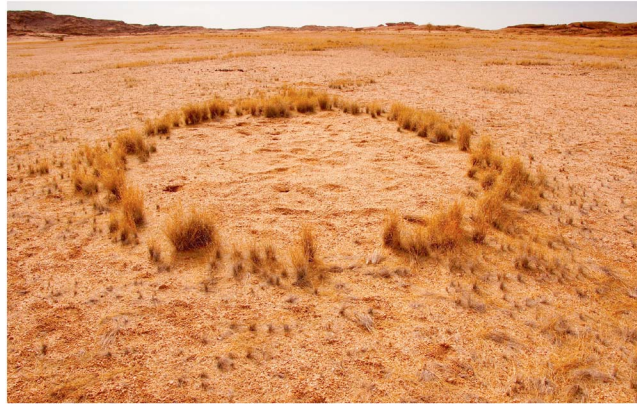


Figure 1. Fairy circles in the Namib Desert (photo credits: Lixin Wang).

2012]. Even though several hypotheses have been recently proposed to explain the formation and growth of fairy circles, from geochemical microseeps [Naudé *et al.*, 2011], activity of social insects like termites [Grube, 2002; Juergens, 2013], landscape-scale self-organization of vegetation [Cramer and Barger, 2013; Getzin *et al.*, 2015a], and a combination of some of the above-mentioned factors [Tarnita *et al.*, 2017], a comprehensive understanding of the abiotic and biotic processes that lead to the formation, growth, and die-off of these circular patterns is still lacking.

One hypothesis is that the fairy circles are self-organizing emergent vegetation patterns arising from the interplay of local scale positive feedbacks (between the vegetated edges of the circular gaps) and long-range negative feedbacks (between the gaps and the surroundings) [Cramer and Barger, 2013; Getzin *et al.*, 2015a]. The competition for scarce resources is thought to explain not only ring formation but also spacing of adjacent circular gaps [Cramer and Barger, 2013; Getzin *et al.*, 2015a]. Positive feedbacks exist between vegetation and soil moisture, leading to transport of water to vegetated patches [Cramer *et al.*, 2016], mostly through soil water diffusion toward the root zone. This process enhances the vegetation growth in areas where soil moisture is available and inhibits vegetation at farther distances where moisture is limited [Kinast *et al.*, 2014]. The severe competition for available moisture may create the central bare areas in the grass patches, as observed in several studies [Bonanomi *et al.*, 2005; Sheffer *et al.*, 2007; Ravi *et al.*, 2008]. Once formed, the bare patches can percolate more rainfall and act as water reservoirs, which the plants along the edges can access during dry seasons [Cramer and Barger, 2013; Getzin *et al.*, 2015a]. In dryland systems, the spatial distribution of hydrological processes such as infiltration, runoff, and sediment transport [Bhark and Small, 2003; Ravi *et al.*, 2007] are closely linked to heterogeneities in vegetation and soil properties, which may be enhanced by positive feedbacks between the vegetation and surface soil moisture [Bhark and Small, 2003; Ravi *et al.*, 2007; Eldridge *et al.*, 2015]. The resulting landscape is characterized by areas of enhanced plant productivity (the ring edges) surrounding areas of nutrient-depleted bare soil interspaces or gaps (the ring centers) [Ludwig *et al.*, 2005; Puigdefabregas, 2005].

A contesting hypothesis proposes that the fairy circle patterns are created and maintained by social insects, with specific reference to termites [Moll, 1994; Becker and Getzin, 2000; Juergens, 2013; Vlieghe *et al.*, 2015] and ants [Becker, 2007; Picker *et al.*, 2012]. The bare patches are argued to be the product of ecological engineering [Juergens, 2013] of the sand termite *Psammotermes allocerus* in particular [Moll, 1994; Juergens, 2013; Vlieghe *et al.*, 2015]. *Psammotermes allocerus* termites are suggested to engage in niche construction that ensures reliable soil moisture availability [Juergens, 2013; Juergens *et al.*, 2015] under the specific abiotic conditions where the fairy circles occur. The bare patches are subsequently colonized by satellite fauna [Vlieghe *et al.*, 2015] and maintained by a combination of herbivory and chemical inhibitions of plant growth [Juergens *et al.*, 2015] that results in similar landscape vegetation patterns [Tarnita *et al.*, 2017] through self-perpetuating feedback loops, as was suggested for the self-organizing vegetation model.

Even though several modeling studies have highlighted the role of small-scale ecohydrological feedbacks (plant-soil-water interactions) in the development of large-scale self-organized patterns such as the Namibian fairy circles, little is known about the spatial and temporal variabilities of hydrological and soil processes inside a fairy circle. In particular, detailed experimental research of soil and hydrological properties inside and outside the fairy circles are limited. To address these knowledge gaps, here we report findings from infiltration experiments, soil moisture and biometric measurements, and soil grain size analysis from multiple fairy circles in the Namib Desert to provide experimental evidence for the ecohydrological interactions within fairy circles and discuss the implications of our findings on the “self-organization hypothesis” for fairy circle formation.

2. Materials and Methods

The study site was located in the hyperarid central Namib Desert, near Mirabib about 95 km from the coast (23°31'33"S, 15°11'52"E). Rainfall follows an east-west increasing gradient from the coast inland (<10 mm at the coast and ~60 mm 100 km from the coast [Hachfeld and Jürgens, 2000; Henschel and Seely, 2008]). Although fog is characteristic of the Namib Desert [Olivier, 1995], it rarely penetrates 70–75 km [Hachfeld and Jürgens, 2000]. The region is characterized by an extremely arid climate, with mild winters and hot summers. The mean annual rainfall is 70–80 mm. For the experiments and soil sampling, we selected similar sized fairy circles (*Stipagrostis ciliata* along edges) at three sites along a ~20 km area, which were similar in terms of climate, topography, soil type, and vegetation distribution. The infiltration experiments and soil sampling were conducted during the winter (July–August) of 2015. The selected circles were approximately uniformly shaped, ~5 m in diameter, and separated by 10–20 m of grass matrix. At each site, we conducted in situ infiltration experiments, as well as soil moisture and biometric measurements.

Infiltration rates were measured by using two different methods—using a mini disk infiltrometer and a dual-head infiltrometer. The mini disk infiltrometer (Decagon Devices, WA, USA) measures the amount of water infiltrating into the soil in a given time interval. This infiltrometer, with an adjustable suction, is ideal for measuring the variability of unsaturated hydraulic conductivity within the bare center and edges, or the periphery, because of its small footprint (measuring area of 5 cm diameter porous stainless steel disk) and very small water requirement for its operation (135 mL). More than 200 infiltration experiments were performed on the bare inside, on the edge, and in the vegetated matrix outside of 9 randomly selected fairy circles at the three sites (three circles from each site). The infiltration data were used to calculate the unsaturated hydraulic conductivity (K at that suction) following the method of Zhang [1997], which is ideal for dry soils.

The saturated hydraulic conductivity was measured in the center and in the matrix outside of nine fairy circles (three from each site) by using a novel dual-head infiltrometer technique. Due to the larger footprint of this instrument compared to the mini disk infiltrometer, it could not be used to measure infiltration at the vegetated edges. This instrument (Decagon Devices, WA, USA) calculates saturated hydraulic conductivity by using a modified two-ponding head approach proposed by Reynolds and Elrick [1990] for the analysis of steady flow from a ponded one-dimensional infiltration in a single ring. The infiltrometer can produce variable hydraulic conductivity conditions without varying the water depth by using air pressure to create different pressure heads. It maintains the steady water levels and measures infiltration rates through two complete pressure cycles. The data are collected by a control unit that performs the calculations to determine field saturated hydraulic conductivity. The instrument is fully automated and has an infiltration rate range of 0.003 to 115 cm h⁻¹ with a resolution of 0.0003 cm h⁻¹ and an accuracy of ±5%.

Volumetric soil moisture was measured by using a 15-cm-long soil water content reflectometer (CS655, Campbell Scientific Inc., UT, USA) connected to data logger (CR1000, Campbell Scientific Inc., UT, USA). Soil moisture measurements (five replicates in the top 15 cm) were made at the center and outer edge of each circle. The height, top width, and basal perimeter of 240 plants on the periphery and matrix between the fairy circles at two sites were also measured. The basal perimeter was used to calculate the basal area of the plants. Soil samples (top 5 cm) were collected from the center, periphery, and from the vegetated interspace soil between fairy circles.

The grain size distributions of the soil samples were determined by using two particle size analyzers: laser diffraction (for sieved samples) and optoelectronic (for unsieved samples) units. The soil samples were air-dried and sieved by using a 2 mm sieve and split into 2 g subsamples by using a riffle sampler (Humboldt Mfg. Co., IL, USA). The subsamples were treated with bleach (24 h) to remove organic matter before the laser-diffraction grain size analysis. The particle size analyzer (LS 13320, Beckman Coulter, Inc., CA, USA) measures the size distribution of particles suspended in a liquid by using the principles of light scattering. The instrument provides a dynamic measurement range of 0.017 to 2000 μm. The particle size characteristics of air-dried unsieved samples were analyzed by using the Camsizer (Retsch Technology GmbH, Haan, Germany) optoelectronic particle size analyzer, which comprehensively characterizes dry free-flowing bulk materials by digitally imaging and quantifying several size and shape parameters of thousands of particles in each sample. The instrument has a measurement range of ~0.04 mm to 8 mm (+5φ to -3φ).

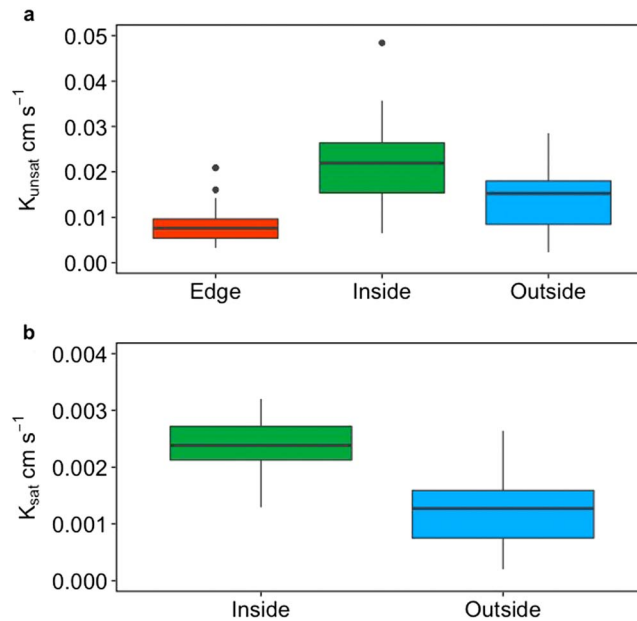


Figure 2. Hydraulic conductivity values (a) K_{unsat} using mini disk infiltrometer and (b) K_{sat} using a dual-head infiltrometer. Each box plot shows the median (solid line); the box enclosure, which represents the interquartile range (first and the third quartiles); and the whiskers, which represent the variability outside the upper and lower quartiles (1.5 times or more the range of variation above the third quartile or more below the first quartile).

In December 2016, we revisited the same site to quantify the abundance of termites and other social insects within the fairy circles as well as evidence of other social insects within the surrounding vegetated matrix. We excavated a soil cube of 0.125 m³ soil in the center of six fairy circles and smaller 0.016 m³ cubes on the periphery to examine termite presence and activity within the fairy circles. We also examined the grasses on the periphery for signs of termite activity (sand termite casts and harvester termite soil dumps) and surveyed four 50 m transects within the vegetated matrix for soil dumps of *Hodotermes mossambicus* harvester termites. The excavations in the centers of circles and along the edges also allowed us to observe plant root distribution.

Statistical tests (one-way analysis of variance (ANOVA), R ver. 3.2.4, 2016) were conducted to test the significance of the differences in hydraulic conductivity, particle size distribution, and soil

moisture between the inside, outer edges of the fairy circles, and interspaces of the fairy circles.

3. Results

The results from the infiltrometer experiments show that the saturated (K_{sat}) and unsaturated (K_{unsat}) hydraulic conductivities were consistently higher inside the fairy circles compared to the interspaces between the circles (Figure 2). The dual-head infiltrometer measurements indicated that the K_{sat} average values were 0.0024 m³ s⁻¹ and 0.0012 m³ s⁻¹ within the circle and in the interspaces, respectively ($F = 14.98$, $p = 0.0012$). The mini disk infiltrometer was used to quantify the spatial variability of infiltration (K_{unsat}) within a fairy circle (including the bare center and vegetated edge). K_{unsat} values varied within the rings, with lower infiltration at the edges compared to the bare centers of the grass circles (Figure 2). The average K_{unsat} values were 0.0214, 0.0084, and 0.014 m³ s⁻¹ for center, edge, and interspaces, respectively ($F = 53.79$, $p < 0.001$).

The volumetric soil moisture content was significantly higher in the middle of the circles compared to the edges and interspaces (Figure 3), with average values of 0.8, 0.4, and 0.6 % for inside the circles, along the edges, and interspaces, respectively ($F = 32.62$, $p < 0.001$).

The grain size analyses of the sieved soil samples showed difference in fines between the center and the edges of the fairy circle (Figure 4), with greater mean and median (D_{50}) grain diameters in the center. The median grain diameters for the sieved samples were 123.8 μm, 127.4 μm, and 179.4 μm for the interspaces, edges, and interiors, respectively. Statistical test showed significant difference in median grain diameter between the center, edges, and interspaces ($F = 57.37$, $p < 0.001$) for both the sieved and unsieved samples. However, Tukey honest significance difference post hoc tests showed that the grain size distribution between the edge and interspaces was not significant ($p = 0.60$). The mean grain diameters also demonstrated a similar trend ($F = 59.47$, $p < 0.001$) (Figure 4). Granulometric analyses of the unsieved soil samples showed, however, significant differences between median diameter (D_{50}) grain sizes from the edges and interspaces ($F = 11.56$, $p < 0.001$). The D_{50} for the unsieved samples were 318.8 μm, 229.2 μm, and 337.4 μm for the interspaces, edges, and inside, respectively. The relationship between mean and sorting

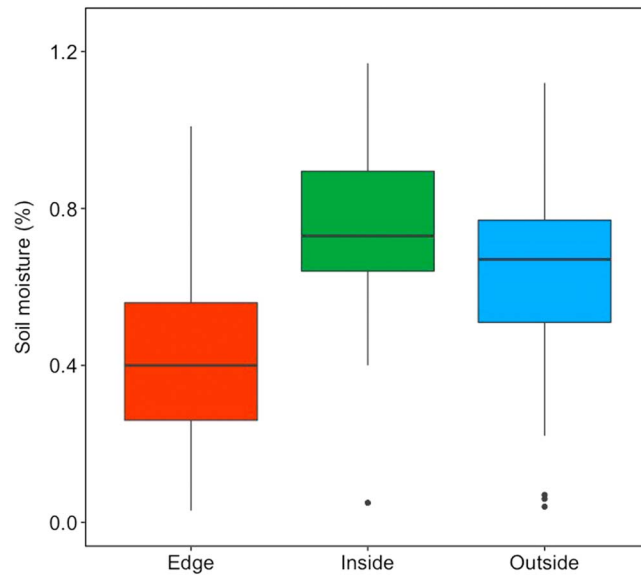


Figure 3. Volumetric soil moisture values at center, edges, and interspaces. Each box plot shows the median (solid line); the box enclosure, which represents the interquartile range (first and the third quartiles); and the whiskers, which represent the variability outside the upper and lower quartiles (1.5 times or more the range of variation above the third quartile or more below the first quartile).

e.g., nests, tunnel networks, or foraging cast remains within the centers or along the vegetated edges of circles. The results indicate that the sand termite species *Psammotermes allocerus* were absent or occur at a very low density in the area we investigated. We did find soil dumps at the exit of foraging holes of the harvester termite *Hodotermes mossambicus* within the periphery of two fairy circles.

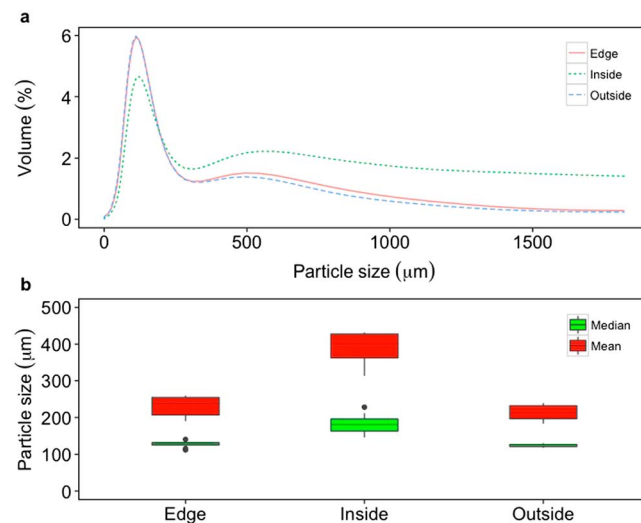


Figure 4. (a) Soil grain size distribution and (b) the mean and median grain size of soil samples from the ring edges, ring inner areas, and the interspaces (sieved samples < 2 mm). The box plot (Figure 4b) shows the median (solid line); the box enclosure, which represents the interquartile range (first and the third quartiles); and the whiskers, which represent the variability outside the upper and lower quartiles (1.5 times or more the range of variation above the third quartile or more below the first quartile).

(ϕ size scale; Figure 5) is typical for active transport systems (improved sorting with decreasing grain diameter).

Grass biomass was highest at the periphery of the circles compared to the grass biomass in the interspace matrix, indicating that grasses along the edges benefit from the circles (Figure 5). Statistical analysis (one-way ANOVA) indicated significant differences in height ($F=212.4$, $p < 0.001$), width ($F=276.3$, $p < 0.001$), and basal area ($F=211$, $p < 0.001$) between the grasses along the edges and from the interspaces between circles. None of the circles selected for our experiments contained any sign of disturbance by fossorial or foraging animals, e.g., lizards, rodents, suricates, or ants, nor did we observe signs of surficial or subsurface termite activity.

When we revisited the sites to specifically investigate termite presence and grass root growth attributes, we did not find any indication of sand termite activity, e.g., nests, tunnel networks, or foraging cast remains within the centers or along the vegetated edges of circles. The soil excavations furthermore showed that all live root growth was toward the bare interior of the fairy circles. The maximum root length of the grasses along the edges was 15 cm, with an average length of 5.9 cm. Much longer root lengths toward the inner areas were observed during our earlier field visit (20–30 cm) in July 2015. No live roots were observed deeper into or in the centers of the fairy circles.

4. Discussion

Our results indicate considerable heterogeneity in soil hydrological properties between the bare center, vegetated edge of the circle (Figure 1), and the vegetated matrix between circles (interspaces). The infiltrometer measurements indicate that infiltration rates (and hydraulic conductivities) are significantly higher inside the fairy circles compared

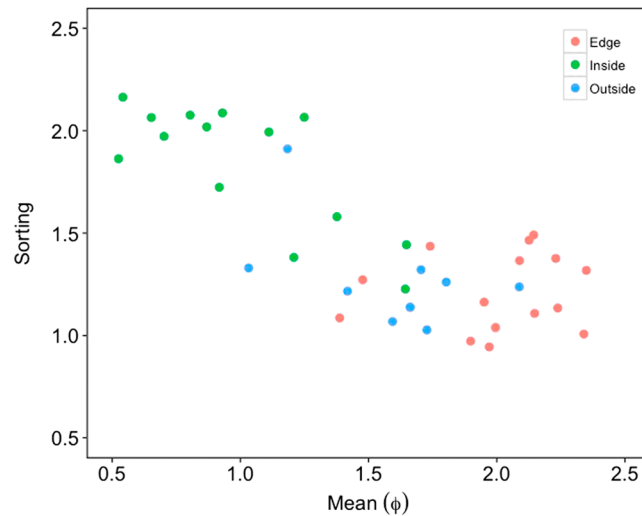


Figure 5. Sorting and mean of grain size (ϕ) of soil samples (unsieved) from the ring edges, interiors, and the interspaces. The improved sorting with decreasing particle diameter clearly separates the ring edges from the winnowed interiors.

to the edges and the interspaces (Figures 2 and 3). Soil texture directly affects infiltration; hence, the spatial variability of hydraulic conductivity can be explained by the differences in the soil grain sizes between the center and edges of the circles (Figure 4). Sorting and mean grain size of unsieved samples from the periphery, interiors, and vegetated matrix show a common trend of improved sorting with decreasing particle diameters at ring edges (Figure 5). More water infiltrates the inside of the circular patches and may therefore provide water to plants along the edges through surface runoff or interflow. The higher grass biomass along the edges of the circles in comparison to the interspaces indicates that the grasses benefit from circular-pattern formation (Figure 6).

Significant differences in median grain diameters for unsieved samples between the fairy circle edges and the interspaces between the circles for unsieved samples only indicate that the interiors of the circles are characterized by a higher fraction of particles greater than 2 mm. The lower hydraulic conductivity in the interspaces (compared to ring center) may also be the result of soil crusts (physical and biological), a common characteristic of dryland ecosystems [Singer and Shainberg, 2004; Belnap, 2006]. In fact, in our study sites, soil crusts were observed in the interspace matrix between the circles and not in their bare centers. In this study, we used the K_{unsat} calculated by using data from the mini disk infiltrometer, as an indicator of the rate of initial water entry into the soil. The higher K_{unsat} values compared to K_{sat} (for the centers and interspaces) seems counterintuitive but

can be explained by the high suction exerted by extremely dry soil profiles during the initial stages of water infiltration.

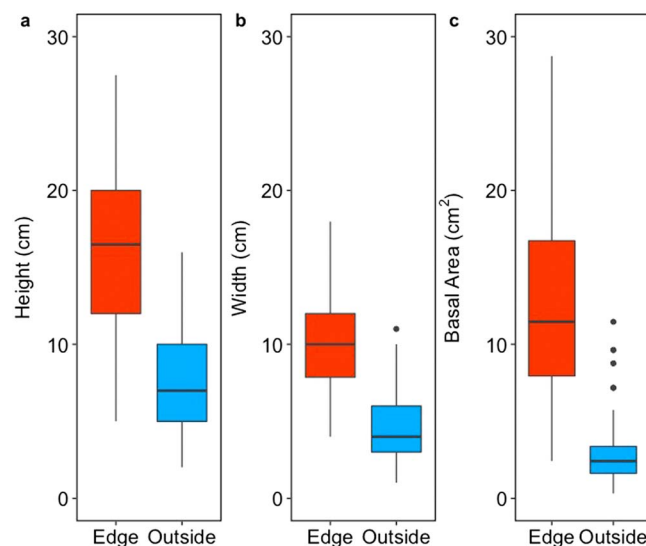


Figure 6. Biometric measurements ((a) height, (b) top width, and (c) basal area) of grasses at the ring edges and the matrix. Each box plot shows the median (solid line); the box enclosure, which represents the interquartile range (first and the third quartiles); and the whiskers, which represent the variability outside the upper and lower quartiles (1.5 times or more the range of variation above the third quartile or more below the first quartile). The solid black points represent the outliers.

Our results generally support the “self-organization theory” of circle formation attributed to scale-dependent biomass-water feedbacks (Figure 7). Competition for water resources may initiate the fairy circles, leading to the bare central areas. The fine soil particles in the center areas of the ring are redistributed to the vegetated edges by the winnowing action of hydrological-aolian transport processes (Figure 7). Aolian processes, which dominate in these arid environments, create and maintain the heterogeneity in soil and nutrient distribution within the ring by removal of fine soil (and nutrients) from the bare central areas and redistribution onto the grasses along the edges due to sediment trapping

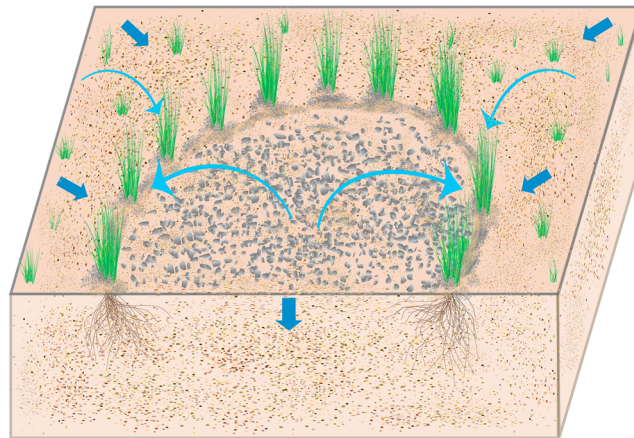


Figure 7. A conceptual framework for fairy circle development. The straight blue arrows indicate hydrological processes (infiltration and runoff from interspaces) that dominate during wet seasons, and the curved blue arrows indicate aeolian processes (fine sediment deposition and erosion) that dominate in dry seasons.

by vegetation [Ravi *et al.*, 2007, 2011; Field *et al.*, 2010]. Such sediment-vegetation feedback loops may explain the higher nutrient concentration in the grass edges compared to central areas with coarser soils of fairy circles, as reported by other studies [Cramer and Barger, 2013]. Low moisture retention and the presence of dry and hot (due to absence of vegetation) coarse topsoil in the center areas may prevent the recolonization of vegetation, thereby stabilizing the bare patches [Getzin *et al.*, 2015a]. The competing explanation of increased termite activity within the circles [Juergens, 2013; Juergens *et al.*, 2015] and soil turnover by secondary colonization by fossorial animals [Vlieghe *et al.*, 2015] would have maintained or increased the fine grain fractions.

The heterogeneity in soil and nutrient distribution results in the heterogeneity of hydraulic conductivity and soil moisture within the fairy circles. The center infiltrates more water and could serve as source to provide water to plants at the edges through interflow (or soil water diffusion) [Cramer *et al.*, 2016], although this process is expected to be slow, particularly in relatively dry soils. In areas with low precipitation, larger areas are needed to harvest the water required to survive low moisture conditions, which could explain the presence of larger circular patches in areas with low precipitation [Cramer and Barger, 2013]. Recent experimental evidence by Cramer *et al.* [2016] confirmed the high mobility of water and nutrients at fairy circles in sandy soils. That study illustrated hydrological and nutritional connectivities of over 7 m between the bare center, the periphery of the circle, and the vegetated matrix [Cramer *et al.*, 2016]. As would be expected, field observations based on root excavations at our sites and elsewhere [Cramer *et al.*, 2016] suggest denser root biomass toward the center of the fairy circles where grasses on the periphery exploit greater moisture availability, even though the roots are of limited length (15–30 cm) compared to the size of the fairy circles (~5 m in diameter).

The major difference between the fairy circles in this study on Namib gravel plain and those on deep sand substrates is soil texture and sequent soil hydraulic conductivity. The soil hydraulic conductivity on the gravel plain is 1 order of magnitude lower than that in sand within the Namib Desert [Li *et al.*, 2016], indicating a stronger interflow component in gravel plain. However, despite its desert armor of small pebbles, the gravel plain substrates consist of >95% sand. The results from this study should therefore apply to fairy circles in deep sand areas as well. Moreover, the heterogeneity in soil grain size distribution may benefit grasses immediately following rainfall events, where the fine soil under vegetation can hold more water at the surface (even by fog interception) and the coarse inner areas may infiltrate more water, thereby partitioning the available water for current and future use (Figure 7).

The hypothesis that, at the local scale, fairy circles result from self-organized vegetation patterns [Fernandez-Oto *et al.*, 2014] is reinforced by fairy circle-like or ring patterns produced by grasses in other arid and semiarid regions [Danin and Orshan, 1995; Sheffer *et al.*, 2007; Ravi *et al.*, 2008; Getzin *et al.*, 2016]. Recent field observations on fairy circle-like patterns indicate similar and even opposite biomass-water relationships, emerging from different mechanisms of moisture transport to vegetation [Getzin *et al.*, 2016]. The direction and magnitude of vegetation-soil moisture feedbacks, leading to transport of water to vegetated patches, depend on the soil texture, the presence of physical or biological soil crusts, and the possible soil microtopography development as a result of the fine sediment accumulation beneath the vegetation canopies due to hydrological-aeolian processes [Borgogno *et al.*, 2009; Ravi *et al.*, 2010]. For example, soil water diffusion in porous sandy soils (antiphase spatial biomass-water

distributions) dominates in the case of Namibian fairy circles [Cramer and Barger, 2013; Getzin et al., 2016], while overland flow (runoff) toward vegetation in finer soils (in-phase spatial biomass-water distributions) dominates in case of circular gaps or ring patterns observed in North America and Australia [Ravi et al., 2008; Getzin et al., 2016]. The ring-like vegetation patterns observed in North America and Australia seem to progress from spots and are generally smaller in diameter (4–6 m) compared to the fairy circles. As noted by Ravi et al. [2008], below a critical ring diameter, the deposition of fine sediments by grass canopy trapping may result in increased concentration of finer soils (and more runoff) inside the circular patches. Grass along the edge absorbs part of the momentum of the airflow by the mechanism of drag partitioning and shelters the inner areas leading to deposition of fine sediments. However, in the case of large circular patches as the Namibian fairy circles, aeolian erosion dominates in the inner areas. As the size of the ring increases over a threshold diameter, the intraring area is no longer protected by the surrounding grass canopy. At this stage, wind shear velocity recovers to its initial values upwind of the outer vegetated edges and fine particles are eroded from the inner areas of the circular patches [Ravi et al., 2008]. Observations based on high-resolution satellite images indicate that the initial size of Namibian fairy circles appears close to their final sizes rather than progressing from spots [Tschinkel, 2012; Getzin et al., 2015b], while smaller circular structures that may develop are temporary [Juergens, 2015].

We demonstrate the existence of short-range ecohydrological feedbacks, in combination with abiotic processes like aeolian redistribution of sediments, which support recent studies on the development of fairy circles [Cramer and Barger, 2013; Fernandez-Oto et al., 2014; Getzin et al., 2015a, 2016]. Even though theories based on social insects like sand termites can explain the vegetation loss in the center and regularity of patterns [e.g., Juergens, 2013, 2015], they do not explain the occurrence of extremely ordered, large-scale homogeneous patterns of the fairy circles [Getzin et al., 2015b]. Getzin et al. [2015b] argued that insect nest distributions are generally less ordered and heterogeneous due to nest aggregation, interspecific competition, and spatial variability of dispersal. Both the very large-scale homogenous patterns and the narrow range of climatic conditions and soil characteristics [Cramer and Barger, 2013] within which fairy circle patterns occur are difficult to reconcile with faunal-mediated ecosystem engineering [Getzin et al., 2015b]; thus, some attempts tried to reconcile faunal and floral mechanisms for patterned landscapes [Juergens, 2015; Tarnita et al., 2017]. A central issue to the debate is the demonstrated strong correlation between the occurrence of fairy circles and the 70–120 mm isohyets [Cramer and Barger, 2013; Getzin et al., 2015b], while no regional-scale correlation has been observed between the distribution of fairy circles and the ecosystem engineering species *Psammotermes allocerus* that have been proposed as the causal agent [Moll, 1994; Juergens, 2013]. We acknowledge that this observed correlation between fairy circles and a narrow climatic zone, defined by mean annual precipitation (MAP), does not eliminate the role of termites or support the self-organization hypothesis. However, the occurrence of fairy circles in a narrow range that overlaps with the typical rainfall requirement for self-organized gap pattern generation in dryland vegetation and the observed distribution changes and disappearance of fairy circles with increasing rainfall (over MAP of 150 mm) strengthen the self-organization hypothesis [Cramer and Barger, 2013; Getzin et al., 2015a]. Moreover, the fairy circles we examined were devoid of the termite species *Psammotermes allocerus*.

We have not found such a ubiquitous presence of sand termites at fairy circles as was suggested by Juergens [2013] when carrying out ad hoc searches throughout the fairy circle range. In addition, we also did not find any circular phenomena resembling fairy circles at specific locations where *Psammotermes allocerus* nests were visible and where both the vegetation and local abiotic conditions approximate that of the Namib Desert margin, e.g., in the southern Kalahari and on sand sheets in southern Namibia. If *Psammotermes allocerus* is the causal agent, then it would be expected that its foraging and intraspecific competitive behavior would have resulted in the development of similar circular phenomena wherever local conditions are suitable, rather than only in a specific part of its range. Despite the suggestion that *Psammotermes allocerus* may abandon the centers of fairy circles [Juergens et al., 2015] after initially establishing conditions [Vlieghe et al., 2015] that results in its growth, the ecosystem-engineer hypothesis rests on the proposition that the sand termites will still exploit the higher moisture source in the center [Juergens, 2013]. At present, empirical data on termite tunnel structures within fairy circles that may favor niche construction by sand termites are not yet available.

5. Conclusions

Our results seem to provide support to the self-organization theory of fairy circle formation attributed to scale-dependent biomass-water feedback loops in *Stipagrostis* grasses. Our investigation provides new insights and data on ecohydrological processes and substrates associated with fairy circles, from a less studied location. We acknowledge that our results do not provide an explanation for the origin and evolution of fairy circles in the Namib Desert. However, 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. Further, studies from other arid and semiarid regions have demonstrated fairy circle-like pattern formation in the absence of animal stimuli. Integrated long-term monitoring of hydrological-aeolian processes and vegetation dynamics, at different spatial and temporal scales and at different locations, is required to develop a comprehensive understanding of the fairy circle evolution.

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References

- Becker, T. (2007), The phenomenon of fairy circles in Kaokoland (NW Namibia), *Basic Appl. Dryland Res.*, *1*, 121–137.
- Becker, T., and S. Getzin (2000), The fairy circles of Kaokoland (north-west Namibia)—Origin, distribution and characteristics, *Basic Appl. Ecol.*, *1*, 149–159.
- Belnap, J. (2006), The potential roles of biological soil crusts in dryland hydrologic cycles, *Hydrol. Process.*, *20*(15), 3159–3178, doi:10.1002/hyp.6325.
- Bestelmeyer, B. T., J. P. Ward, and K. M. Havstad (2006), Soil-geomorphic heterogeneity governs patchy vegetation dynamics at an arid ecotone, *Ecology*, *87*(4), 963–973.
- Bhark, E. W., and E. E. Small (2003), Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico, *Ecosystems*, *6*(2), 185–196, doi:10.1007/s10021-002-0210-9.
- Bonanomi, G., F. Giannino, and S. Mazzoleni (2005), Negative plant-soil feedback and species coexistence, *Oikos*, *111*(2), 311–321.
- Borgogno, F., P. D'Odorico, F. Laio, and L. Ridolfi (2009), Mathematical models of vegetation pattern formation in ecohydrology, *Rev. Geophys.*, *47*, RG1005, doi:10.1029/2007RG000256.
- Couteron, P., and O. Lejeune (2001), Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model, *J. Ecol.*, *89*(4), 616–628.
- Cramer, M. D., and N. N. Barger (2013), Are Namibian “fairy circles” the consequence of self-organizing spatial vegetation patterning?, *PLoS One*, *8*(8), e70876, doi:10.1371/journal.pone.0070876.
- Cramer, M. D., N. N. Barger, and W. R. Tschinkel (2016), Edaphic properties enable facilitative and competitive interactions resulting in fairy circle formation, *Ecography*, *39*, 001–011.
- D'Odorico, P., K. Caylor, G. S. Okin, and T. M. Scanlon (2007), On soil moisture-vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems, *J. Geophys. Res.*, *112*, G04010, doi:10.1029/2006JG000379.
- Danin, A., and G. Orshan (1995), Circular arrangement of *Stipagrostis ciliata* clumps in the Negev, Israel and near Gokaeb, Namibia, *J. Arid Environ.*, *30*(3), 307–313.
- Eldridge, D. J., L. Wang, and M. Ruiz-Colmenero (2015), Shrub encroachment alters the spatial patterns of infiltration, *Ecohydrology*, *8*(1), 83–93.
- Fernandez-Oto, C., M. Tliidi, D. Escaff, and M. G. Clerc (2014), Strong interaction between plants induces circular barren patches: Fairy circles, *Philos. Trans. R. Soc. London A Math. Phys. Eng. Sci.*, *372*(2027), doi:10.1098/rsta.2014.0009.
- Field, J. P., J. Belnap, D. D. Breshears, J. C. Neff, G. S. Okin, J. J. Whicker, T. H. Painter, S. Ravi, M. C. Reheis, and R. L. Reynolds (2010), The ecology of dust, *Front. Ecol. Environ.*, *8*(8), 423–430, doi:10.1890/090050.
- Getzin, S., K. Wiegand, T. Wiegand, H. Yizhaq, J. von Hardenberg, and E. Meron (2015a), Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia, *Ecography (Cop.)*, *38*(1), 1–11, doi:10.1111/ecog.00911.
- Getzin, S., K. Wiegand, T. Wiegand, H. Yizhaq, J. Von hardenberg, and E. Meron (2015b), Clarifying misunderstandings regarding vegetation self-organisation and spatial patterns of fairy circles in Namibia: A response to recent termite hypotheses, *Ecol. Entomol.*, *40*(6), 669–675, doi:10.1111/een.12267.
- Getzin, S., et al. (2016), Discovery of fairy circles in Australia supports self-organization theory, *Proc. Natl. Acad. Sci. U.S.A.*, *113*(13), 3551–3556, doi:10.1073/pnas.1522130113.
- Gilad, E., J. von Hardenberg, A. Provenzale, M. Shachak, and E. Meron (2004), Ecosystem engineers: From pattern formation to habitat creation, *Phys. Rev. Lett.*, *93*(9), 098105.
- Grube, S. (2002), The fairy circles of Kaokoland (Northwest Namibia)—Is the harvester termite *Hodotermes mossambicus* the prime causal factor in circle formation?, *Basic Appl. Ecol.*, *3*(4), 367–370, doi:10.1078/1439-1791-00138.
- Hachfeld, B., and N. Jürgens (2000), Climate patterns and their impact on the vegetation in a fog driven desert: The Central Namib Desert in Namibia, *Phytocoenologia*, *30*(3/4), 567–589.
- Henschel, J. R., and M. K. Seely (2008), Ecophysiology of atmospheric moisture in the Namib Desert, *Atmos. Res.*, *87*(3), 362–368, doi:10.1016/j.atmosres.2007.11.015.
- Jankowitz, W. J., M. W. Van Rooyen, D. Shaw, J. S. Kaumba, and N. Van Rooyen (2008), Mysterious circles in the Namib Desert, *South Afr. J. Bot.*, *74*(2), 332–334, doi:10.1016/j.sajb.2007.10.010.
- Jürgens, N. (2013), The biological underpinnings of Namib Desert fairy circles, *Science*, *339*(6127), 1618–1621.
- Jürgens, N. (2015), Exploring common ground for different hypotheses on Namib fairy circles, *Ecography (Cop.)*, *38*(1), 12–14, doi:10.1111/ecog.01232.
- Jürgens, N., K. E. P. Vlieghe, C. Bohn, B. Erni, F. Gunter, J. Oldeland, B. Rudolph, and M. D. Picker (2015), Weaknesses in the plant competition hypothesis for fairy circle formation and evidence supporting the sand termite hypothesis, *Ecol. Entomol.*, *40*, 661–668.
- Kinast, S., Y. R. Zelnik, G. Bel, and E. Meron (2014), Interplay between Turing mechanisms can increase pattern diversity, *Phys. Rev. Lett.*, *112*(7), 78,701, doi:10.1103/PhysRevLett.112.078701.

- Leprun, J. C. (1999), The influences of ecological factors on tiger bush and dotted bush patterns along a gradient from Mali to northern Burkina Faso, *CATENA*, 37(1–2), 25–44.
- Li, B., L. Wang, K. F. Kaseke, L. Li, and M. K. Seely (2016), The impact of rainfall on soil moisture dynamics in a foggy desert, *PLoS One*, 11(10), e0164982, doi:10.1371/journal.pone.0164982.
- Ludwig, J. A., D. J. Tongway, and S. G. Marsden (1999), Stripes, strands or stipples: Modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia, *CATENA*, 37(1–2), 257–273.
- Ludwig, J. A., B. P. Wilcox, D. D. Breshears, D. J. Tongway, and A. C. Imeson (2005), Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes, *Ecology*, 86(2), 288–297, doi:10.1890/03-0569.
- Ludwig, J., R. Bartley, A. Hawdon, B. Abbott, and D. McJannet (2007), Patch configuration non-linearly affects sediment loss across scales in a grazed catchment in North-east Australia, *Ecosystems*, 10(5), 839–845.
- Moll, E. J. (1994), The origin and distribution of fairy rings in Namibia, *Proceedings of the 13th Plenary Meeting AETFAT*, edited by J. H. Seyani and A. C. Chikuni, pp. 1203–1209, National Herbarium and Botanical Gardens, Malawi.
- Naudé, Y., M. W. van Rooyen, and E. R. Rohwer (2011), Evidence for a geochemical origin of the mysterious circles in the Pro-Namib Desert, *J. Arid Environ.*, 75(5), 446–456, doi:10.1016/j.jaridenv.2010.12.018.
- Olivier, J. (1995), Spatial distribution of fog in the Namib, *J. Arid Environ.*, 29(2), 129–138, doi:10.1016/S0140-1963(05)80084-9.
- Picker, M. D., V. Ross-Gillespie, K. Vieghe, and E. Moll (2012), Ants and the enigmatic Namibian fairy circles—Cause and effect?, *Ecol. Entomol.*, 37, 33–42.
- Puigdefabregas, J. (2005), The role of vegetation patterns in structuring runoff and sediment fluxes in drylands, *Earth Surf. Process. Landforms*, 30(2), 133–147.
- Ravi, S., P. D'Odorico, and G. S. Okin (2007), Hydrologic and aeolian controls on vegetation patterns in arid landscapes, *Geophys. Res. Lett.*, 34, L24523, doi:10.1029/2007GL031023.
- Ravi, S., P. D'Odorico, L. Wang, and S. Collins (2008), Form and function of grass ring patterns in arid grasslands: The role of abiotic controls, *Oecologia*, 158(3), 545–555, doi:10.1007/s00442-008-1164-1.
- Ravi, S., D. D. Breshears, T. E. Huxman, and P. D'Odorico (2010), Land degradation in drylands: Interactions among hydrologic-aeolian erosion and vegetation dynamics, *Geomorphology*, 116(3–4), 236–245, doi:10.1016/j.geomorph.2009.11.023.
- Ravi, S., et al. (2011), Aeolian processes and the biosphere, *Rev. Geophys.*, 49, RG3001, doi:10.1029/2010RG000328.
- Reynolds, W. D., and D. E. Elrick (1990), Ponded infiltration from a single ring: I. Analysis of steady flow, *Soil Sci. Soc. Am. J.*, 54(5), 1233, doi:10.2136/sssaj1990.03615995005400050006x.
- Scanlon, T. M., K. K. Caylor, S. A. Levin, and I. Rodriguez-Iturbe (2007), Positive feedbacks promote power-law clustering of Kalahari vegetation, *Nature*, 449(7159), 209–212.
- Sheffer, E., H. Yizhaq, E. Gilad, M. Shachak, and E. Meron (2007), Why do plants in resource-derived environments form rings?, *Ecol. Complex.*, 4(4), 192–200.
- Singer, M. J., and I. Shainberg (2004), Mineral soil surface crusts and wind and water erosion, *Earth Surf. Process. Landforms*, 29(9), 1065–1075.
- Tarnita, C. E., J. A. Bonachela, E. Sheffer, J. A. Guyton, T. C. Coverdale, R. A. Long, and R. M. Pringle (2017), A theoretical foundation for multi-scale regular vegetation patterns, *Nature*, 541(7637), 398–401.
- Tschinkel, W. R. (2012), The life cycle and life span of Namibian fairy circles, *PLoS One*, 7(6), e38056.
- Tschinkel, W. R. (2015), Experiments testing the causes of Namibian fairy circles, *PLoS One*, 10(10), e0140099, doi:10.1371/journal.pone.0140099.
- Turner, M. G. (1989), Landscape ecology: The effect of pattern on process, *Annu. Rev. Ecol. Syst.*, 20(1), 171–197, doi:10.1146/annurev.es.20.110189.001131.
- Valentin, C., J. M. d'Herbes, and J. Poesen (1999), Soil and water components of banded vegetation patterns, *CATENA*, 37(1–2), 1–24.
- van Rooyen, M., G. Theron, N. van Rooyen, W. Jankowitz, and W. Matthews (2004), Mysterious circles in the Namib Desert: Review of hypotheses on their origin, *J. Arid Environ.*, 57(4), 467–485, doi:10.1016/S0140-1963(03)00111-3.
- Vlieghe, K., M. D. Picker, V. Ross-Gillespie, and B. Erni (2015), Herbivory by subterranean termite colonies and the development of fairy circles in SW Namibia, *Ecol. Entomol.*, 40, 42–49.
- von Hardenberg, J., E. Meron, M. Shachak, and Y. Zarmi (2001), Diversity of vegetation patterns and desertification, *Phys. Rev. Lett.*, 87(19), 198101.
- White, L. P. (1971), Vegetation Stripes on sheet wash surfaces, *J. Ecol.*, 59(2), 615–622.
- Yizhaq, H., E. Gilad, and E. Meron (2005), Banded vegetation: Biological productivity and resilience, *Phys. Stat. Mech. Appl.*, 356(1), 139–144.
- Zhang, R. D. (1997), Determination of soil sorptivity and hydraulic conductivity from the disk infiltrometer, *Soil Sci. Soc. Am. J.*, 61(4), 1024–1030.