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RESEARCH ARTICLE

Microbial Factors May Contribute to the Persistence of Australian Fairy Circles

Liron Klipcan¹, Nina A Kamennaya^{2,3}, Naw Than Than Aye⁴, Ruth Van-Oss-Pinhasi¹, Ehud Meron^{5,6}, Shmuel Assouline⁷ and Hezi Yizhaq^{5*}

¹Gilat Research Center, Agricultural Research Organization: Volcani Center, M.P., Negev, 85280, Israel

²The Goldman Sonnenfeldt Schools of Sustainability and Climate Change, Ben-Gurion University of the Negev, Israel

³French Associates Institute for Agriculture and Biotechnology of Drylands, Ben Gurion University of the Negev, Israel

⁴Albert Katz International School for Desert Studies

⁵Department of Solar Energy and Environmental Physics, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Beer-Sheva 8499000, Israel

⁶Department of Physics, Ben-Gurion University of the Negev, Beer-Sheva 8410501, Israel

⁷Institute of Soil, Water and Environmental Sciences, Agricultural Research Organization: Rishon Letzion, Israel

Abstract

Fairy Circles (FCs) are roughly circular, spatially periodic barren patches occurring both along the southwestern African coast, spanning the Namib Desert (NFCs), and in the Pilbara region of Western Australia (AFCs). The origin of both NFC and AFC patterns is still debatable and a subject of ongoing research. Recently, it was argued that pathogenic soil microbes may contribute to ring formation of the *Triodia basedowii* grass which is the same grass species that forms the AFCs. We have analyzed, under controlled laboratory conditions, soil samples taken from different parts of AFCs (center, periphery and matrix) for microbiological activities by Lettuce germination experiments under different manipulations. In seven different circles, out of an average of 13, root lengths of germinated seeds were strongly inhibited in the samples taken from the center, and to a lesser extent, in the samples taken from the periphery and the matrix. Quantitative analyses of the soil microbial community from the FC center found no support to the hypothesis that phytotoxic effect was caused by soil crust cyanobacteria due their low abundance. However, in soil of the FCs it identified both heterotrophic bacteria and fungi that may contribute to the phytotoxic effect. Although our study was not done with seeds of *Triodia basedowii* it supports the idea that microbial activities in the soil may contribute to AFC persistence by inhibiting plant germination and development in the bare soil gaps in addition to the physical soil crusts resulting from weathering. This suggests that negative plant-soil feedback can act in concert with the main driver mechanism of the AFCs, the scale-dependent plant-water feedback.

*Corresponding author(s)

Hezi Yizhaq, Department of Solar Energy and Environmental Physics, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Beer-Sheva 8499000, Israel

Email: yiyeh@bgu.ac.il

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- Fairy circles
- Plant-soil feedback
- Phytotoxicity
- *Triodia basedowii*
- Germination experiments
- Fungi

Introduction

Fairy Circles (FCs) are roughly circular barren patches in grasslands, occurring in a narrow band ca. 100 km inland from the southwestern African coast, spanning the Namib Desert [1], and also in the Pilbara region of Western Australia (Figures 1,2) [2–5]. A recent work, based on remote sensing analysis [6], claimed that FC-like patterns are globally distributed and discovered 263 new sites of vegetation gaps, but more detailed field work is needed to understand the formative mechanisms (physical and ecological) at these new sites and to distinguish between

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FC-like patterns to true FCs. While there are multiple hypotheses for their origin, two currently prevail [7]. The first attributes their formation to pre-patterns formed by termite social dynamics [8–11] and the second to scale-dependent plant–water feedbacks that result in partial plant mortality and the formation of gap patterns, which, in turn, may provide habitats for termite populations [12–16]. Another class of processes that may possibly affect FC patterns, but so far has received little attention in this context, is negative plant–soil interactions, such as allelopathy and autotoxicity, which can either be direct, through the release of toxic materials, or mediated by microorganisms' phytotoxic activities [17–20]. Allelopathy has received much attention in the context of invasive exotic species [18,20,21], while autotoxicity causes great concern in crop systems, as it affects agricultural productivity [22]. More recently, autotoxicity has also been studied in the context of spatial patterning, mostly as a driver of vegetation ring formation [23,24] or fairy rings of mushroom-forming fungi [25]. It was shown that including autotoxicity in the models for vegetation patterns can lead to travelling waves solutions [24]. Additional negative plant–soil feedbacks could emerge from soil-borne microbiological pathogen populations [26]. The dominant process in all cases is the attempt of the biomass to escape areas with high concentration of toxic compounds. Interestingly, it was suggested

that pathogenic soil microbes may contribute to ring formation of *Triodia basedowii* grass (Figure 1d) which is the same grass species that form the Australian fairy circles (AFCs) [27]. Indeed, several studies of Namibian fairy circles (NFCs) have suggested that edaphic microorganisms, such as bacterial or fungal communities, are involved in the phenomenon. While it has been shown that FCs in Namibian sands or gravel harbor specific microbial taxa, it remains unclear whether they have a true phytopathogenic effect, and whether they are involved in FC maintenance (i.e. the stability of the bare soil in the gap) or whether they merely colonize a specific niche that is provided by the FCs [28,29].

The apparent spatial similarity between NFC patterns and AFC patterns (Figure 1a–c) has been attributed to the same general positive feedback that both systems share, a scale-dependent feedback between local vegetation growth and water transport to the growth location [15,30], albeit with different water transport mechanisms [2,16,31]. NFCs patterns form in deep aeolian sands, characterized by high water infiltration rates. The water-transport mechanism, in this case, is soil–water lateral diffusion towards denser and, thus, drier vegetation patches [5,31,32] and the soil water content is on average higher in the center than in the fairy circle periphery. By contrast, in Australia, the top soil layer is a barely permeable

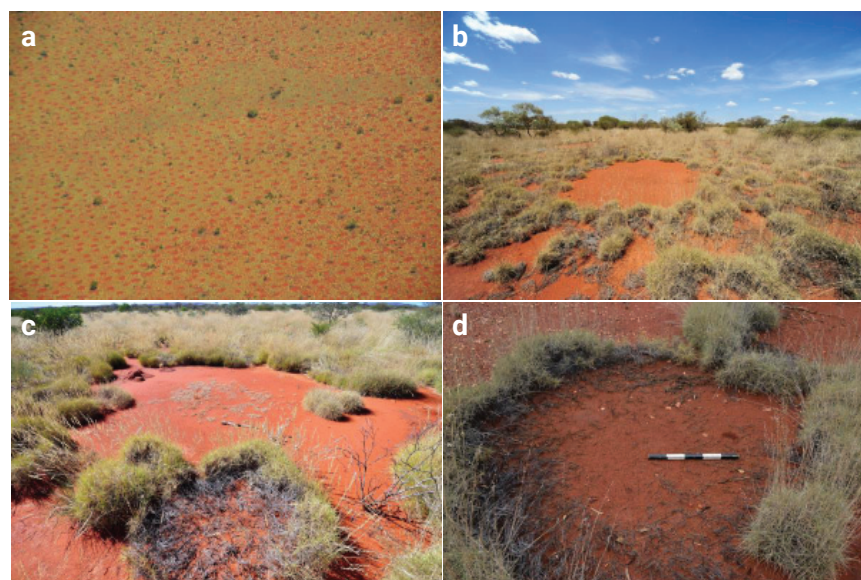


Figure 1 Example of a fairy circle pattern formed by the bunchgrass species *Triodia basedowii* E. (spinifex) near the town of Newman in Western Australia's Pilbara region. There are few cattle farms in the area with little impact on the natural vegetation. (a) Aerial image showing the regularly hexagonal spaced bare-soil gaps (the fairy circles) that form the pattern. (b, c) Closer looks at two fairy circles. Note the ring developed in the matrix. (d) Small-scale ring patches within the grass matrix caused by dieback of the plants in the center (the length of the scale bar is 50 cm). It was suggested that pathogenic soil microbes are involved in the ring formation of *Triodia basedowii* grass [27].

claypan that generates overland water flow towards denser vegetation patches at the gap edges (Figures 2a,3c) [2,3,14] and the soil water content in the center of the AFC is lower than in the periphery.

Detailed field work has shown that soil hardness and clay content were higher inside the AFCs and in large bare-soil areas than in the matrix. When compared to the matrix soil with protective grass cover, the almost three times higher clay content in FCs and large bare-soil areas derives from multiple abiotic weathering processes, such as intense rainfall events, particle dispersion, surface heat, evaporation, and mechanical crust building that inhibit plant growth in both areas [3,5,14]. These results have been confirmed with long-term data on rainfall and soil-moisture in AFCs. In the unprotected bare soil in the FC interior, only few major rainfall events, in combination with extreme surface heat, are sufficient to establish a nearly impermeable soil crust [13]. Despite the effects of mechanical weathering, microbial activity can also enforce the crust building over the long term. For example, the Australian Outback experiences regular wildfires every few decades, and biological and cyanobacterial soil crusts are known to recover after four to six years [33]. Therefore, the formation of biological soil crusts may well be involved in the stability of the AFC system.

Here, we propose that microbially induced negative plant-soil feedback can contribute to stabilization of the AFC patterns. We have analyzed, under controlled laboratory conditions, soil samples taken from AFC area near the town of Newman in Australia, and present indirect evidence for the possible existence of a microbial factor that can exert phytotoxic effects and inhibits plant germination and grass development inside the circular barren patch in AFCs. However, more experiments with the local seeds of *Triodia basedowii* are needed to confirm this proposal.

Materials and Methods

Sample collection

Soil samples were collected from 13 AFCs in Western Australia near Newman in the Pilbara region (Figure 3a) [2], a hot desert with the aridity index (AI) of ~ 0.09 (the ratio between annual precipitation to potential evapotranspiration). Samples were collected from the upper 3 cm of the soil layer, from the FC center (C samples), from the FC periphery (P samples), and from the area outside the FC that is covered with vegetation (matrix: M samples; Figure 3b). The soil properties and mineralogy can be found in [2]. The clay and silt contents are higher in the FC

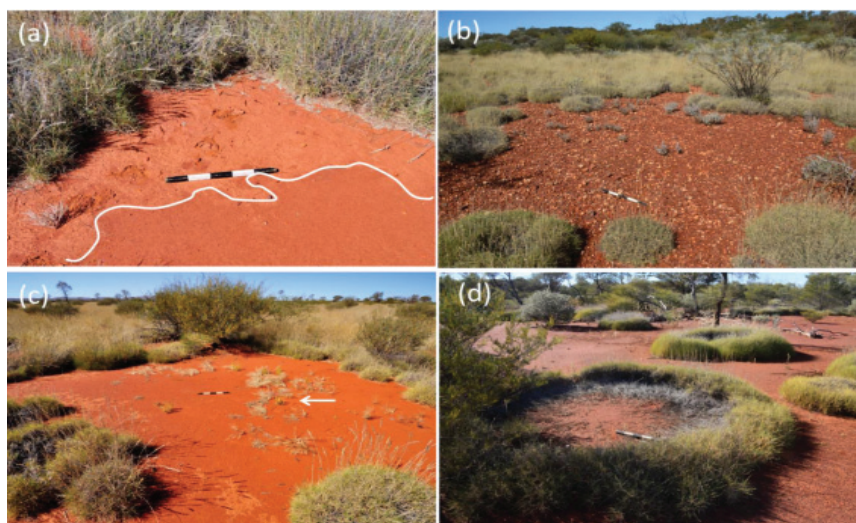


Figure 2 More pictures of the vegetation patterns in the study site.

- The area near the edge of a fairy circle. The white curve delineates the area where water accumulates in heavy rains and available for plants, from the harder clay surface (the more reddish area in the bottom). See also the schematic illustration in figure 3c.
- Unusual fairy circle covered with small stones and pebbles. The formation of the stone covered fairy circles is still unknown.
- The white arrow indicates new established grasses at the bare soil. These new grasses are very small and may not persist for a long time.
- A large ring of *Triodia basedowii* grass. Note the gray dead grass in the inner belt. Rings can be found in the matrix and usually smaller than the fairy circles (scale bar is 0.5 m).

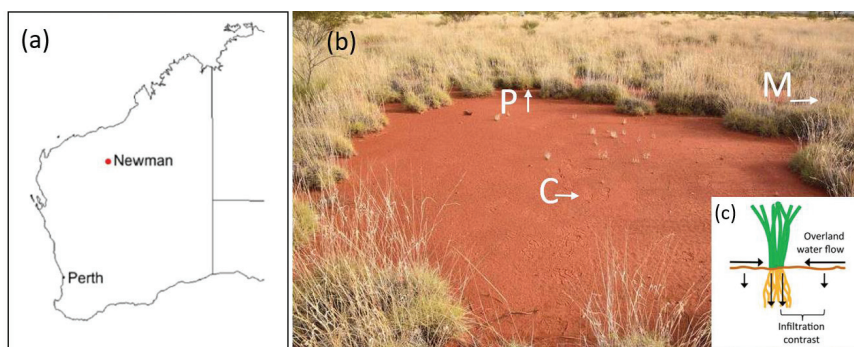


Figure 3 a). A schematic map of western Australia showing the location of the study site near Newman about 1000 km from Perth.
b). The locations of the sampling sites, the fairy circle center (C), the fairy circle periphery (P) and the matrix (M). The inset.
c). shows a schematic illustration of the infiltration feedback from the center towards the periphery due to the low infiltration of the hard soil in the center [2].

center (18.13% and 38.88%) than in the periphery (12.10% and 23.89%) and in the matrix (6.53% and 13.86%).

The phytotoxicity assay

To assess soil type effects on germination and root elongation, lettuce (*Lactuca sativa*) plants were used as a model which are frequently used to establish phytotoxic activities in novel phytotoxic molecules [34]. The assay consisted of placing 10 g of dry soil from the control (soil from Negba, Israel's Negev Desert), and the C, P, and M samples in Petri dishes, wetting it with 2 ml of sterile water, and placing seven lettuce seeds in the soil in each Petri dish. All Petri dishes were closed with lids after seeding and placed in a controlled growth room at 25°C with a 16/8 h light/dark cycle. After five days of growth, the seedling root lengths were measured. Similar experiments were performed in the presence of 0.5% glucose or Antibiotic Antimycotic Solution (Sigma) and with autoclaved soil. Descriptive statistics, plotting, and hypothesis testing were done using Prism 8 software (GraphPad Software Inc.).

Filter paper bioassay with soil water extract

For this, 3 gr of each AFC soil sample was mixed with 6 ml water and incubated for 120 min. The liquid phase was collected after spindown (1500 rpm) and filtered with 0.45 µm syringe filter. The aqueous extracts were used in Petri dish bioassays to assess their effect on lettuce growth. Whatman no. 1 filter paper (Whatman) in Petri dishes was treated with 1.0 ml of a soil water extract. Ten lettuce seeds were placed on the moist paper filter in each Petri dish. After 5 days in a controlled environment (25°C at a 16/8

h light/dark cycle), the root lengths of experimental and control plants were measured.

Soil surface microscopy

Soil crust from FC center was imaged at bright-field and epifluorescent imaging modes with a long-focus 5×/0.12 objective. Chlorophyll fluorescence was imaged with E4 filter system (Leica). Micrographs were recorded using DFC 7000 T microscope camera (Leica).

Determination of chlorophyll content of the soil

To estimate the abundance of photosynthetic organisms at the C soil surface, chlorophyll *a* and *b* content was determined in soil samples. Chlorophyll was extracted in three replicates from 0.5 g of mechanically ground soil using MgCO₃-saturated 99% (v/v) ethanol. Following heat-extraction at 80°C for 5 min, the extract was cleared of particles by centrifugation and collected. The second extraction was performed in the same manner. Extracts were combined, and chlorophyll *a* and *b* concentrations was determined spectrophotometrically at 665 and 750 nm using 50 Bio UV-Vis spectrophotometer (Cary).

Flow cytometric enumeration of bacteria

One gram of C sample soil was suspended in 25 ml of 0.22 µm-filtered 0.85% (w/v) NaCl solution and homogenized for 10 min by vortexing at maximum speed. The suspension was centrifuged for 10 min at very low speed to pellet large soil particles. Extracted cells were fixed for 2h with 1% (w/v) paraformaldehyde at 4°C and stained with of SYBR Green I at room temperature in the dark for 30 min.

The SYBR Green-stained particles in the soil extract and in the negative control solution were enumerated using FACSCalibur flow cytometer; data was acquired and processed using the Cell Quest software (Becton Dickinson). Sample duplicates were counted three times each.

Microscopic identification and scaling of fungal hyphae

To estimate the abundance of fungi in the C sample soil, 0.01–0.015 g of soil sample was suspended in 300 µl of sterile double distilled water and smeared on a microscope slide for analysis. Fungal hyphae

were located microscopically using bright field and epifluorescent (DAPI-ET filter system) imaging modes (LMD 7.0, Leica). Biovolume of hyphae were calculated based on the hyphae length and average thickness [35]. Counts were performed in triplicates.

Results

We first observed that the leaves of germinated plants from the C samples were more chlorotic than those from the M samples (Figure 4a). In the second experiment, we added 0.5% glucose to increase the metabolic response. All samples exhibited some seed germination and elongation inhibition, compared

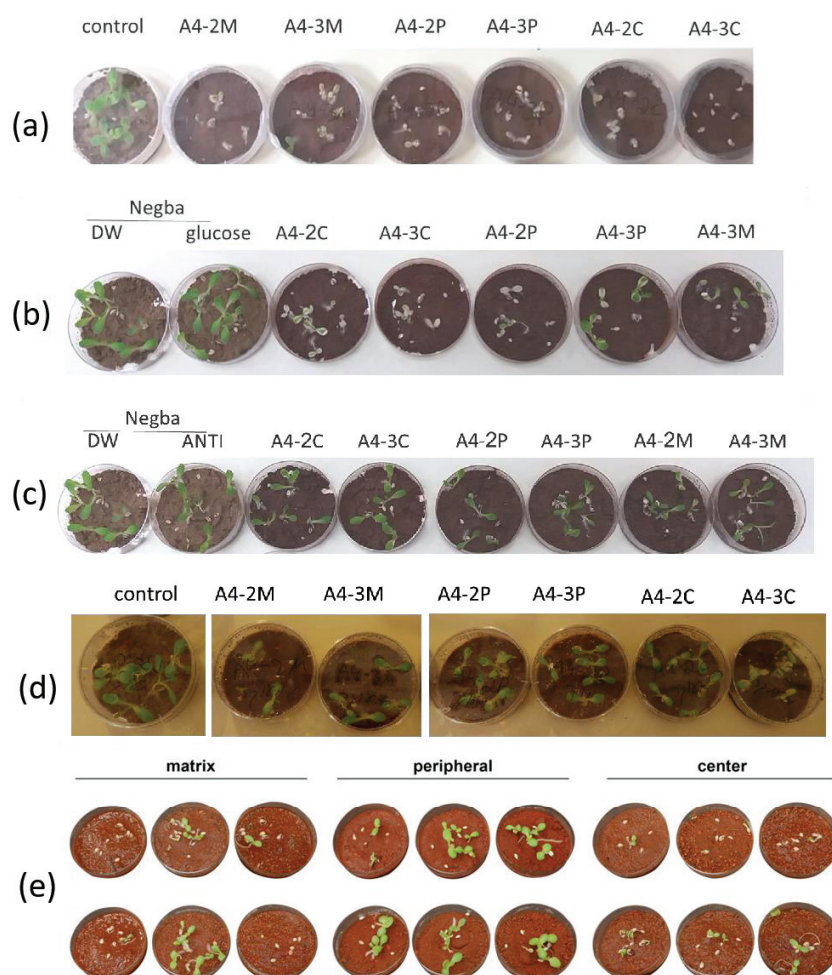


Figure 4 : a). Lettuce germination experiments with soil samples from two different FCs. Soil from Negba, southern Israel Negev, was used as a control.
b). Lettuce germination experiments with soil samples from two different FCs in the presence of 0.5% glucose. Soil from Negba was used as a control. The DW is the control soil with distilled water.
c). Lettuce germination experiments with soil samples from two different FCs and soil from Negba in the presence of antimycotic and antibacterial moieties.
d). Lettuce germination experiments with soil samples from two different FCs and soil from Negba after autoclaving.
e). Results (in more details) from lettuce germination experiments with soil samples from two different AFCs in the presence of 0.5% glucose.

to the control soil (Figures 4b,4e). Although not all samples demonstrated a precise phytotoxic pattern, a statistical analysis revealed that in seven different circles, out of an average of 13, root lengths of germinated seeds were strongly inhibited in the C samples, and to a lesser extent, in the M and P samples (Figure 5a).

To establish that the AFC sample results were linked to the soil's microbiological activity, we investigated the effect of adding an antibacterial and antimycotic solution, containing penicillin, streptomycin, and amphotericin B, to the samples. These tests showed that the presence of bacterial and/or fungal inhibitors reduced the toxic effects (Figures 4c,5b). In an additional experiment, we autoclaved the soil samples, to kill most soil biota, and repeated the assays described earlier; the inhibition in germination and root elongation was substantially reduced, and all samples behaved similarly (Figure 4d). Thus, the results suggest that a soil microbiological activity inhibits germination of Lettuce seeds, especially for soil taken from the center of the fairy circle.

To delineate whether the inhibition is directly

caused by the microorganisms or whether certain secreted compounds are responsible for it, we tried to isolate chemical compounds from the soil samples, using water extraction. As a control, we also used soil sampled from Israel's Negev Desert (Negba) and applied the same assay to it. Water extracts from the AFC samples exhibited more phytotoxic properties than extracts from the Negev soil; however, the data were not statistically significant (Figures 5c, 6).

Microscopic observation of soil revealed that the surface of the C sample soil was covered with a greenish layer (Figure 7) potentially formed by pigment-containing cyanobacteria or eukaryotic algae, which could inhibit seed germination. However, concentrations of the primary photosynthetic pigments, i. e., chlorophyll a and b, were only 0.05–0.1 µg/g and 0.03–0.06 µg/g, respectively, suggesting chemical origin of the greenish layer. Microscopic examination confirmed negligible abundance of chlorophyll-containing cells in the soil surface (data not shown).

To assess the abundance of bacteria, present in the soil, we used flow cytometry to enumerate

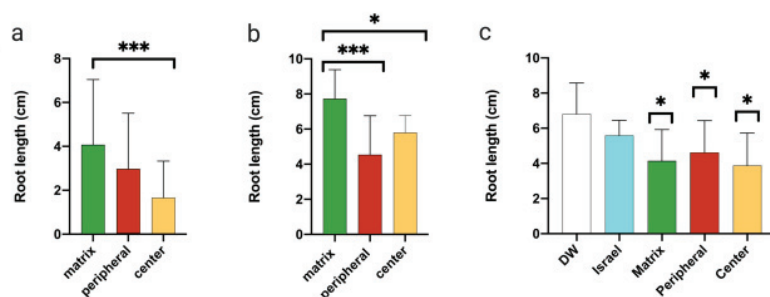


Figure 5 a). Statistical analysis of lettuce root lengths from seven AFCs treated with glucose.
b). Statistical analysis of lettuce root lengths from seven AFCs treated with an antibacterial/antimycotic reagent.
c). Statistical analysis of root lengths from AFC water extracted experiment.

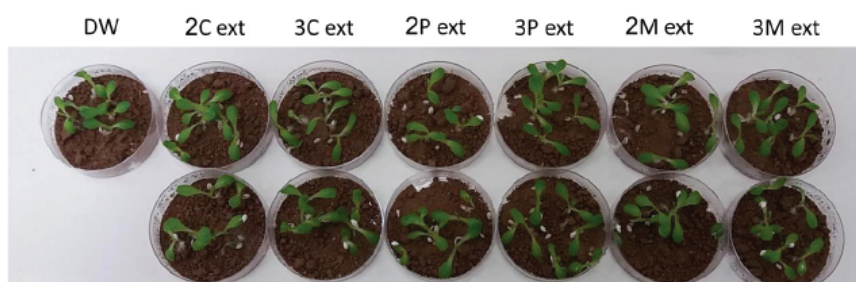


Figure 6 Lettuce germination experiments with water extraction from AFCs soil added to the Negev soil (Negba). The average root length is shown in figure 3c. There is no significant change in the color of the leaves of germinated plants between the different samples (C, P, and M).

bacteria-size DNA-containing particles that could be dissociated from mineral particles and debris. The number of bacteria-like particles counted was $1.5\text{--}2.5 \times 10^6$ cells per 1 g of C sample soil.

To determine the abundance of fungi in the soil, we identified fungal hyphae microscopically and scaled them to calculate their biovolume. In 0.01 g of surface soil layer we counted 15–20 long (> 1 mm) fungal hyphae (Figure 8) and many shorter hyphae and hyphal fragments. The calculated total fungal biovolume in 1 g of C sample soil was 0.011–0.016 mm³.

Discussion

The phenomenon of phytotoxic activity's spatial organization has previously been demonstrated in several plant species [36,37]. For example, cherry tree (*Prunus serotina*) seedlings experience high mortality in soil collected beneath conspecific adults but exhibit low mortality in the same soil collected far from adult

trees. Intriguingly, a particular soil pathogen (a fungus of the genus *Pythium*) that lives on mature cherry tree roots is responsible for the phytotoxic effect [26]. Similarly, cyanobacterial toxin microcystin was shown to inhibit germination and root elongation and development in pea (*Pisum sativum*), maize (*Zea mays*) and durum (*Triticum durum*) [38].

Microbial growth and related allelopathic effects may also depend on environmental conditions, such as temperature variability near plants, water and nutrient availability, and soil texture [39]. For example, high-temperature environments, e. g. hot deserts, were shown to harbor relatively high abundance of soil-born potential fungal plant pathogens [40]. Furthermore, such environments with particularly low plant biomass were predicted to have relatively diverse communities of fungal pathogens [41]. It was demonstrated, under controlled laboratory conditions, that drying and rewetting of soil collected around shrubs showing allelopathic effects triggered

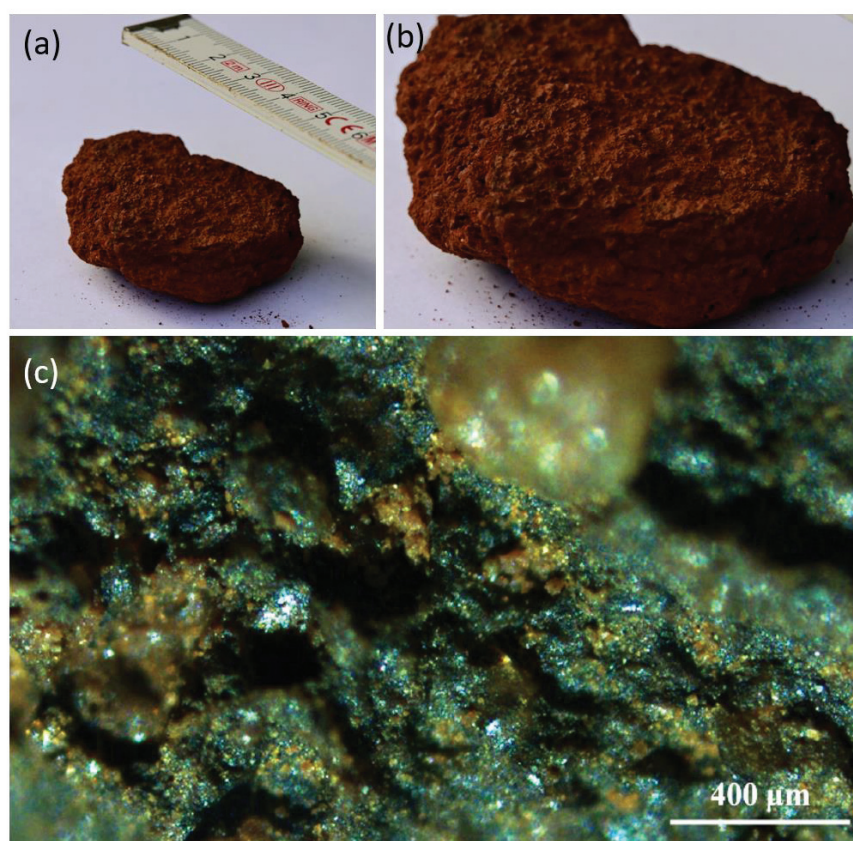


Figure 7 a). A sample of the hard physical crust from AFC center and a close. b). Shows the texture of the crust. c). A true-color micrograph of the C sample soil surface imaged at bright-field mode using a 5x long-focus objective. The green layer visible on surface of the soil sample can be formed by chlorophyll-containing microorganisms, e. g., cyanobacteria and algae, or from chemical weathering on the soil minerals.

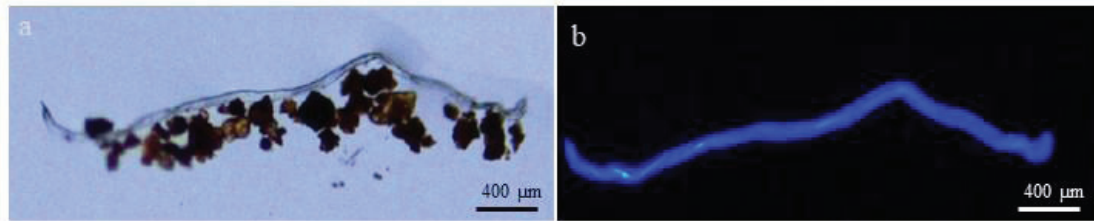


Figure 8 A non-branched fungal hypha associated with soil particles is visualized at 5× magnification: (a) at a bright-field imaging mode the hypha is semi-transparent and at an epifluorescent imaging mode with UV excitation it fluoresces blue (b).

soil toxicity, eventually reducing lettuce germination and development [42]. Such toxicity effects are probably related to a flush of microbial activity due to the rewetting. It seems plausible that drying and wetting cycles which are dominant climatic events in the Pilbara region [13], could potentially trigger the growth of specific microorganisms, e.g. fungi, that exert inhibitory effects on plant germination inside the FCs. These inhibitory effects may help to explain the potentially higher stability of AFCs and the lack of observations reporting on FC recovery (i.e., FC disappearance by germination and growth inside the bare soil), in contrast to NFCs [16,43], despite the occasional occurrence of wet years.

It is also possible that germination suppression around established plant canopies may result from the synergistic effects of plant exudates. Interestingly, the predominant Australian FC bunchgrass, *Triodia basedowii* E. Pritz, belongs to a genus with other species (*Triodia* sp. nov.) demonstrating a strong autotoxic effect and suppressed conspecific germination [44].

Another possible implication of our findings is related to the multi-scale nature of patterns observed in Namibian and Australian FCs—large-scale FC patterns and small-scale patterns within the vegetation matrix. In NFCs, the small-scale pattern often consists of spots [9,31], whereas in AFCs, it consists mostly of rings (Figure 1d) [2]. Vegetation rings have commonly been explained by negative plant-soil feedbacks [23,45] and by plant-water scale-dependent feedbacks [46–51]. In the latter case, rings generally break up into spots as they expand and approach other vegetation patches, forming a spot pattern [52]. The indications reported here for the presence of negative plant-soil feedbacks are, therefore, consistent with the observations of rings in the AFC matrix [27], which in the absence of scale-dependent plant-water feedback at this scale, do not converge to a small-scale spot pattern.

Conclusion

In summary, although our germination experiments have been done with Lettuce seeds and not with the local *Triodia basedowii* E. seeds that form the AFCs, they support the idea that microbial activities in the soil may contribute to FC persistence and stability in Australia by inhibiting plant germination in the bare soil gaps. Importantly, this inhibition in the C samples was reproduced under laboratory conditions, indicating a robust characteristic of the AFC soil. Quantitative analyses of the soil microbial community from the FC center found no support to the hypothesis that the phytotoxic effect was caused by cyanobacteria due to their low concentration but identified both bacteria or fungi in the soil of FCs that may contribute to the phytotoxic effect in the fairy circle center. However, further studies are needed to confirm this conjecture.

Our results highlight the need to study in depth the combined effects of plant-water and negative plant-soil interactions, both empirically, using field and controlled laboratory experiments with *Triodia basedowii* E. seeds, and theoretically, using mathematical models for water-limited vegetation such as the model used to describe the AFCs [2] with a coupling between biomass and toxicity [53,54].

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