

Table 3

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

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

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

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

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

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

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

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

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

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

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