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MACROFUNGAL ECOLOGY IN THE NAMIB DESERT: A FRUITFUL OR FUTILE STUDY?

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Namibia: driest country in southern Africa

Namibia defies the imagination of those who mistakenly envision Africa as a continent of dense tropical forests (Fig. 1). Only a paltry 10% of Namibia receives annual rains above 550 mm, supporting a dryland forest ecosystem. Most of this country (twice the size of California) is arid to semi-arid savanna and desert; hence Namibia's reputation as the driest country in southern Africa (Seely & Jacobson, 1994).

Namibia's climate is characterized by a strong gradient in annual rainfall. While virtually no rain falls at the coast, an average of 300 - 400 mm falls annually on the highlands in the center of the country. Two interacting factors ensure that western Namibia - the Namib Desert - is one of the driest places on earth (Fig. 2). Namibia's summer thunderstorms typically originate in the Indian Ocean, east of the African continent. As the storm systems move west across this large hot landmass, their potential for providing much needed moisture to the western edge of the continent dimin-

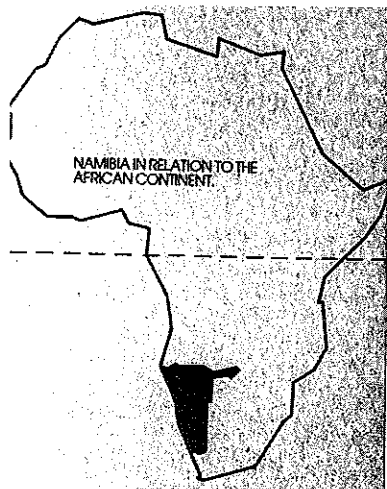


Fig. 1: Namibia: driest country in southern Africa

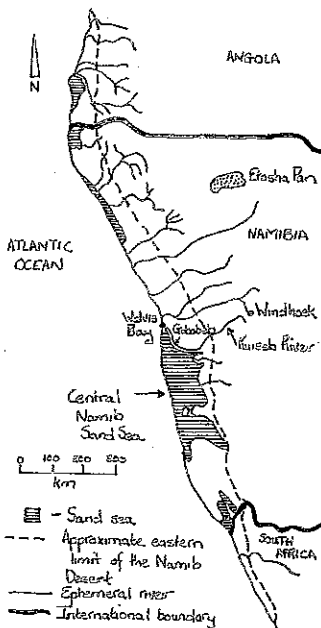


Fig. 2: Sand seas and ephemeral rivers of the Namib Desert.

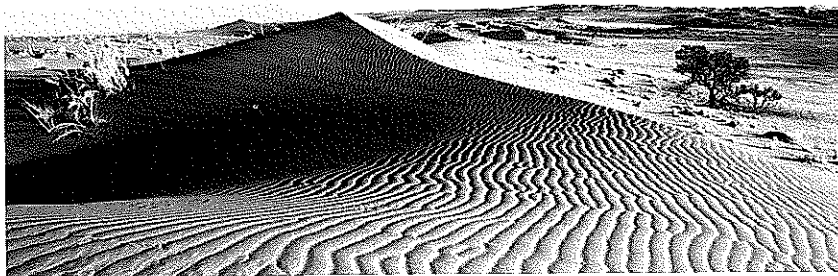


Fig. 3: Prime fungal habitat in the Namib Desert. Grass species inhabiting various aspects of the dune slopes, as well as *Acacia erioloba* trees at the dune base, provide the organic material upon which fungal decomposers depend.

ishes. In addition, the cold Benguela current offshore of Namibia cools the atmosphere along the coast, preventing the development of turbulence that would lead to thunderstorms. A common experience in the Namib Desert is to see huge cumulo-nimbus clouds building to the east over the inland escarpment in the early afternoon. As they begin to push westward over the desert fringe, however, they meet the cool dry westerly winds from the coast and these majestic clouds break apart and eventually disappear.

Cool, dry westerly winds don't always blow, however, and the warm moist air masses from the Indian Ocean occasionally reach western Namibia. The result is spectacular thunderstorms, often preceded by massive sand storms rolling across the desert. Although short-lived, these episodic storms and their intense rainfall have helped to shape the diverse landscapes of western Namibia.

Diverse habitats of the Namib Desert

The Namib Desert is recognized as the coastal portion of southwestern Africa, from northern South Africa to southern Angola (incorporating all of western Namibia), where rainfall is less than 100 mm (Fig. 2). Within this arid region are a variety of habitats characterized by their unique topography and substrates. The awe-inspiring dunefields (Fig. 3) for which the Namib Desert is best known, are only one part of this rich landscape. Vast gravel plains, dotted with isolated mountains, are home to the bizarre gymnosperm, *Welwitschia mirabilis* Hook. f. and numerous other endemic plants (Fig. 4) (Jacobson *et al.*, 1993). To the north, the desert features splendid vistas with volcanic mesas and deep canyons, not unlike the desert southwest of the United States.

Throughout the Namib, ephemeral rivers - those which flow only during summer months as a result of rains over the inland escarpment - cross the desert on their way to the sea (Figs. 2 & 5). These riverbeds receive tremendous but short-lived bursts of seasonal flood water, supporting comparatively lush riparian forests (Jurgens *et al.* In press). These linear oases, traversing the desert landscape, provide essential dry season refuges for a diversity of wildlife unrivalled by any other desert region in the world. Elephant, black rhino, giraffe and oryx, among others, move seasonally from the riverbeds to the adjacent desert, making use of the diverse

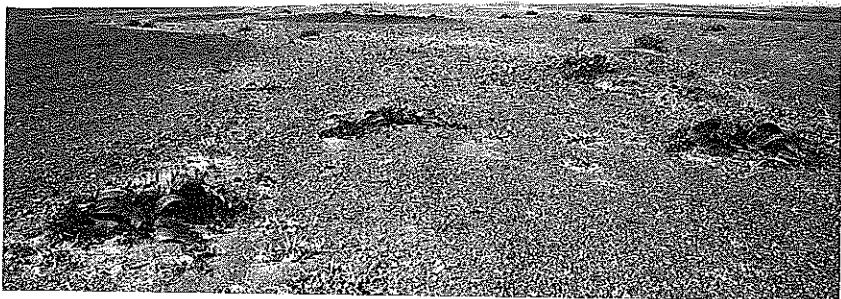


Fig. 4: The extensive gravel plains of the Namib Desert are home to the endemic gymnosperm, *Welwitschia mirabilis*.

plant communities adapted to the variable rainfall which typifies the region (Jacobson *et al.*, 1995).

Prevailing thoughts on fungal ecology in the Namib Desert

Researchers have characterized much of the flora and fauna found in the dunes, gravel plains, rocky deserts and ephemeral rivers of the region. In fact, much of our understanding of how various organisms are adapted to arid environments originated in the Namib Desert (Louw & Seely, 1982). But what of the fungi in this arid landscape? The general consensus among even the most seasoned Namib ecologists when I began my research on desert fungal ecology was that I was embarking on a futile study! A random soil survey conducted in the dune field in the late 1960's had shown that fungal spore densities were extremely low (le Roux, 1970). Few people could recall having seen macrofungi in the Namib Desert, and were thus convinced that the aridity of the region ensured that their presence was sporadic, rare, and definitely "atypical". Studies of termites and beetles in the driest regions of the Namib had also suggested that these organisms were the primary consumers of plant detritus (Seely, 1991; Crawford & Seely, 1994). At most it was thought that fungi could perhaps survive in the guts of these detritivores, aiding in the digestion of ingested plant material (Crawford & Taylor, 1984). As with most deserts of the world, fungi were thought to be unimportant, if not downright irrelevant, to ecosystems functioning within the Namib (Seely & Louw 1980).



Fig. 5: The ephemeral Kuiseb River, a linear oasis traversing the Namib Desert (seen here at Gobabeb, home of the Desert Research Foundation of Namibia).

Knowing where and when to look for fungi in deserts

Amidst all this skepticism, one might ask why I felt mycological studies in the Namib Desert would be a



Fig. 6: *Battarrea* cf. *phalloides* decomposes silt-bound organic material for 6 - 12 months following flooding in Namibia's ephemeral river beds.

fruitful research area. My initial interest in the Namib Desert resulted from a search for a suitable location to examine questions regarding the effects of extreme environmental factors, such as aridity and substrate stability, on arbuscular mycorrhizal fungi (Jacobson, In press:a). While conducting fieldwork for this study in the central dune field of the Namib Desert (Fig. 3), it became obvious that arbuscular mycorrhizal fungi were not the only fungi present. With minimal searching, my first field trip through the hot and dry dune field produced four different species of desert-adapted agarics and gasteromycetes. Further, a walk in the dry and dusty Kuiseb River bed (Fig. 5) adjacent to the Namib Desert Research Station, where I was based, revealed abundant fresh (i.e. culturable) *Battarrea* cf. *phalloides* (Dicks.) Pers. (Fig. 6), even though the most recent flooding of the river channel had been 6 months earlier. The dunes and ephemeral rivers of the Namib Desert were clearly suitable macrofungal habitat.

During my initial 11-month study (September 1990 - July 1991) it rained only once, in April, at the end of the rainy season. This "event" was the key to understanding fungal ecology in the Namib Desert. As in all other ecosystems where fungi are active, moisture is an essential prerequisite for macrofungal fruiting, providing the most obvious sign that fungi are present. Knowing when and where to collect following rains and river-bed flooding was essential for effective sampling of fungal diversity in these habitats, as well as for studying their role in desert ecosystems. Understanding how fungi respond to these moisture inputs became the focus of my subsequent longer-term ecological studies in the Namib Desert.

"Dry season" collecting in the dune field

Searching the dune sea for dried, wind-blown specimens of desert-adapted gasteromycetes and agarics provided important information about substrate preferences, and clues for where to search for fresh specimens when and if it rained. *Podaxis pistillaris* (Pers.) Fr., a tall and stately woody likeness of *Coprinus comatus* (Mull. ex Fr.) S.F. Gray ("Shaggy Mane") was commonly found at the base of large perennial grass plants (Fig. 3). It thus seemed likely that this fungus was decomposing the woody roots and buried stem and leaf detritus of these plants. This species was also commonly found at the base of *Acacia erioloba* E. Meyer trees (Fig. 3), which survive the rigors of the desert climate by means of both shallow roots,

which access rain water that seeps into the dune sand, and deep roots which reach down towards the groundwater table.

Gyrophragmium delilei Montagne, a woody relative of the genus *Agaricus* (Miller & Miller, 1988), was also found beneath *A. erioloba*. An obvious assumption was that these two species might be decomposing the roots of *Acacia*, but another possible substrate existed. As the only shade-providing structures in a vast sand sea, each tree serves as a shady resting place for oryx, an elk-size ungulate which wanders the desert, often as a singular nomad. With game-trails converging from all directions at the trees, they also serve as communication outposts. The bases of the trees are littered with oryx dung, which is frequently turned and mixed in the sand by visiting oryx who deposit their own "message", and scrape and dig through the existing pile. The large accumulations of dung were also a possible substrate for the decomposing activities of *G. delilei* and *P. pistillaris*.

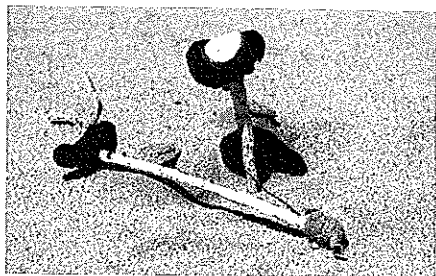


Fig. 7: *Montagnea arenaria* fruiting on the surface of the sand from depths of 6 - 10 cm.

In addition to these tree-associated dung middens, oryx also have frequent outposts all along the myriad trails traversing the dunes and intervening plains (Fig. 3). Where these game trails intersect, one commonly finds a midden. These isolated oryx middens are important habitats for desert-adapted fungi. *Schizostoma laceratum* Ehrenb., a stalked puffball whose peridium splits completely open revealing a red-brown spore mass, was found exclusively in association with oryx dung.¹ Interestingly, *P. pistillaris* and *G. delilei* were never found in middens that were not associated with *Acacia* trees. While *S. laceratum* clearly had a preference for dung middens, *P. pistillaris* and *G. delilei* were apparently associated with woody tree and grass substrates. A fourth species, *Montagnea* cf. *arenaria* (DC.) Zeller (Fig. 7) appeared to have a cosmopolitan distribution (Jacobson, 1996). This fungus was abundant in middens, on dune slopes among annual and perennial grasses, and under *A. erioloba* trees.

Rain in the desert: collecting during the "wet season"

In 1990, the summer months of January, February and March slipped by without a drop of rain and I steadily lost hope of observing macrofungal fruiting in the desert. The dune field was dotted with empty rain gauges, placed at locations where fungi had been found during the dry season. I had hoped to record a rain at one or more of these sites, but my efforts

¹ This species has been found in other deserts, but without any clear association with ungulate dung (Miller & Miller, 1988). As with so many of these desert-associated fungi that are rarely collected in fresh condition, accurate species descriptions and determinations are difficult. Taxonomic affinities are not well clarified, type specimens are often of poor quality and quantity (for example, see Morse, 1933) and much interesting systematic work remains to determine the evolutionary associations of these fungi (Miller & Miller, 1988).

seemed to no avail. Towards the end of April, however, the massive storm clouds began to build in the east again, and this time the west wind didn't blow them into oblivion. One afternoon, they built to a great height, and from the research station it appeared that the eastern reaches of the dune field were receiving a heavy, lightning-charged deluge.

What looked like a massive storm from afar was in fact a typical, patchy desert rain. Much of the desert was still dry, but two of my rain gauges recorded significant rains from this single storm: 12 mm at the Far East Dune and 25 mm at Bushmen's Circle Dune. Visiting these sites was an all-day trip requiring tricky driving over the dunes. Time, expense and logistical constraints allowed me to visit these sites only at 5-6 day intervals following the rain. But, even with these large gaps in time, much was learned about the fruiting patterns of these fungi and how they respond to different amounts of rain.

Abundant fungal fruiting following the rain permitted closer examination of the habitat preferences previously observed during the dry period. Easy digging in the dune sand confirmed that *S. laceratum* decomposes oryx dung, whereas *P. pistillaris* and *G. delilei* specialize in woody stems and roots of Acacia trees and perennial grasses. What had previously been identified as a single *Montagnea* species was clearly two different species, characterized by a different attachment of the gussets (woody gill structures bearing spores) to the pileus, as well as different substrate preferences. *Montagnea arenaria* (DC.) Zeller specializes in decomposing buried grass stems and was found everywhere over the dunes, whereas *Montagnea haussknechtii* Rab. was only found decomposing oryx dung in middens and along well-established game trails.

The sporocarps initially revealed their presence during the day as 1 - 2 cm cracks in the sand surface. During the cool evening hours, they pushed through the surface, greeting the morning with fully developed sporocarps ready for the dry, desiccating winds which immediately began to disseminate their dark, thick-walled spores. *Schizostoma laceratum*, *G. delilei* and both *Montagnea* species completed the development of their spores prior to stipe extension and breaking the sand surface. In contrast, *P. pistillaris* with multiple peridial layers amounting to a thickness of 0.5 to 1.0 cm, developed its spores above ground. Despite these differences in spore development, one obvious similarity among all gasteromycete and agaric species found in the dunes was their comparatively long stipes. This feature permits them to complete much of their growth and development from 6 - 20 cm beneath the surface of the sand. There they are not subject to the high temperatures and drying winds of the Namib Desert.

Macrofungal phenology in response to rain

In addition to these observations of fungal fruiting, interesting information about fungal response to differing rain amounts was gathered. At the Far East Dune, which received only 12 mm, *S. laceratum* and both *Montagnea* species formed fruiting bodies four days after the rain. In contrast, the larger fruiting bodies of *P. pistillaris* and *G. delilei* did not appear until 18 - 22 days following the rains. At the Bushmen's Circles Dune,

which received twice as much rain, *Montagnea* and *S. laceratum* fruiting began at four days but fresh sporocarps could still be found seven days later. The fruiting of *P. pistillaris* at Bushmen's Circles Dune did not begin until 28 days after the rain and was similarly protracted over a much longer period (5 weeks). Clearly the greater amount of rain resulted in longer periods of fruiting of *Montagnea*, *S. laceratum* and *P. pistillaris*, as well as considerable delays in fruiting for *P. pistillaris*. By digging numerous pits in the sand, we soon discovered a plausible explanation for these patterns. If one dug a hole large enough to see the soil in profile, it was possible to monitor how the rain percolated into the sand over time. These observations revealed that the moisture gradually evaporated from the surface while being retained at deeper levels. The cohesive moist sand (>3 % water by weight) formed a band which was easily distinguished from loose dry sand (<1 % water by weight), and observing how these bands progressed deeper through the sand layers provided important clues to why fungal fruiting was delayed by the greater rainfall.

The day after the rain fell, the top 1 cm of sand was already dry at both sites. Thereafter, the rate of evaporation from the surface was similar at both sites for about two weeks. By four days, when the *Montagnea* species and *S. laceratum* were fruiting, the upper 5 - 7 cm were dry. Digging out *Montagnea* species, it was clear that these sporocarps were fruiting at the interface of visibly wet and dry sand. Below the fruiting bodies, the sand was still moist and above it was dry. At the Far East Dune, 18 days following the rains, *P. pistillaris* was similarly observed fruiting from the wet-dry sand interface which had now progressed to 15 - 20 cm below the sand surface. Because of the greater amount of rain which fell at the Bushmen's Circle Dune, the moisture was retained there at depths below 12 - 15 cm for a much longer period of time. When *P. pistillaris* finally did appear, 4 - 8 weeks after the rains, they too were fruiting from the wet-dry interface at 15 - 20 cm. These observed delays in fruiting in response to greater rainfall suggest that the fungi were fruiting as a result of the drop in soil moisture. A corollary is that the greater the rainfall, the longer the period for decomposition by these fungi prior to fruiting. The fact that the small fruiting bodies of *Montagnea* and *S. laceratum* were fruiting much earlier, and from a shallower depth, than those of the bulky *P. pistillaris* and *Gyrophragmium*, certainly supported this idea.

Decomposition in the Namib Desert: a wet or dry season process?

The ubiquitous presence of macrofungi in the dunes of the Namib Desert revealed that the role of fungi in ecosystem processes had been greatly underestimated. In fact, it seemed clear that the importance of rain events to nutrient processing in general might well have been neglected. It is well known that rains in the desert are infrequent and unpredictable and that plants and animals have developed effective adaptations to take advantage of these brief inputs of moisture. Somehow though, the fact that below-ground organisms driving nutrient processing (detritivores and decomposers) might have adaptations allowing effective use of rare moisture inputs, had been overlooked (Seely & Louw, 1980). Because rains are spo-

radic and unpredictable, experiments to examine nutrient processing emphasized dry-season processing (Crawford & Seely, 1994). While termites and beetles were found to be important processors of material during the dry season, the total quantities of material decomposed during dry and wet seasons had not been compared. My preliminary observations suggested that, depending on amount, moisture from a single rainfall could be present in sandy substrates for 3 - 6 weeks or more after a rain, providing a window of opportunity for the accelerated activity of termites, beetles, nematodes, fungi and other detritivores and decomposers. It appeared that a considerable amount of decomposition was occurring during wet cycles, as a result of the synergistic burst of activity of all these organisms.

Opportunistic experiments confirm importance of "wet season" decomposition

In order to fully understand the importance of these rain events to nutrient processing in the Namib Desert, I designed an experiment to compare the amount of decomposition occurring during dry and wet periods. Researchers have examined belowground decomposition rates in different ecosystems using a standard Oxford-cloth substrate (Fig. 8) (Harrison *et*

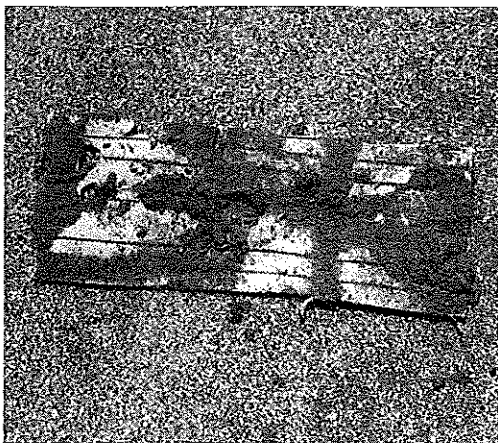


Fig. 8: Cotton strips used in the decomposition experiment, removed from desert sands 7 days following rain. Note the termites which were active on the substrate at the time of removal, and are responsible for the holes in the cloth. Sand adhered to the cloth because of the fungal hyphal network. When the cloth dried, the sand was easily removed, revealing fungal staining and hyphae adhering to cloth.

al., 1988). The cloth is composed entirely of cellulose, the same material which comprises the bulk of the grass detritus. Grass also contains lignin and hemicelluloses, however, so the cloth is organically a simpler material than that which organisms are decomposing under natural conditions in the dunes. Nonetheless, the value of using this standard cloth was that, when strips of uniform size were used, comparisons between different sites could be made without having to account for differences among various natural substrates. The material also provided an effective means for observing whether fungi were colonizing and decomposing the material.

Over two separate periods of dry-wet cycles, strips of cloth were buried at depths of 10-12 cm and subsequently dug up at routine intervals over 8-month periods (Jacobson, 1966b). These experiments were set up, along with rain gauges, at various locations throughout the dune field with the hope of being able to contrast as many different rainfall amounts as possi-

ble. Once again, the weather cooperated. Two dry periods of 3-6 months showed that material was indeed being processed by termites and beetle larvae under conditions which were much too dry for fungal activity. Cloth substrates excavated during the dry season were as clean as when they were put in, showing no staining from fungal activity. Holes in the cloth or missing cloths resulted from consumption by beetle larvae or termites. This confirmed the observations of other researchers that dry season processing by termites and beetle larvae was occurring.

While beetle larvae and termites found the cloth to be a palatable dry season meal, consumption during the dry period accounted for only 10-15% of the total processing in each experiment. The remainder of the material was processed following rains of 11 - 45 mm. Strips removed during the weeks following rains showed increasingly heavy termite and beetle larvae activity, as well as fungal colonization (Fig. 8). Remarkably, by the time the sand became dry at the level at which the strips had been placed, all strips were reduced to mere threads or had disappeared completely. This was true for even the minimal 11 mm of rain (Jacobson, 1966b).

In addition to the cloth experiments, I continued my observations of fungal fruiting in response to differing rainfall amounts. Longer periods of delayed fruiting again resulted from larger amounts of rainfall. A single rain of 44 mm resulted in moisture being held in the sand for three months at depths of 15 - 20 cm. By this time, the aboveground desert had desiccated (except for perennial grasses which could access this deep moisture), and yet *P. pistillaris* was still fruiting from the wet-dry interface. While all fungal activity cannot be attributed solely to Basidiomycetes, clamped hyphae were identified on many of the cotton strips placed in the oryx middens where *S. laceratum* and *M. haussknechtii* were abundant. Without question, the Basidiomycete flora is a common component of the rain-activated biological community within the Namib Desert.

The minimal rains to which macrofungi effectively respond, as measured by fruiting observations, was measured as 11 mm. It appears that 10 mm is simply inadequate to sustain sufficient activity to produce fruiting bodies, as none were observed in response to this amount. Similarly, rains of less than 11 mm resulted in some surface staining of the cotton strips, but no loss of integrity of the material. Interestingly, 11 mm is also the minimal amount of rain required for germination of plant seeds in the dunes (Jacobson, 1966b). Similarly, mycorrhizal spores associated with these grasses don't germinate at amounts less than 11 mm. This amount is clearly an important minimum to which many Namib organisms are adapted. It is not surprising that different organisms would exhibit similar response minima. The costs of untimely germination are severe in this harsh environment.

Fungal ecology and diversity in other Namib Desert habitats

Fungal decomposition in the Namib depends on soils with good infiltration and aeration. As a result, macrofungal collecting on the gravel plains and rocky mesas, where most rainfall runs from the surface with little infiltration, was limited to periods of relatively high rainfall. In contrast,

drainage lines dissecting the gravel plains were particularly productive, yielding many of the same species found in the dunes, as well as *Broomeia ellipsozona* Berk. (Fig. 9). This strange endemic gasteromycete is thought to be a member of the Sclerodermatales (Miller & Miller, 1988), although no one has yet collected immature or developing stages of the sporocarp. Without a stalk, specimens are found lying on the gravel with no evidence of how or when they develop. A thick peridium, which covers the peridioles and is eventually sloughed off in the desert wind (peridium absent in Fig. 9), suggests that the entire maturation process might proceed on the sand surface. If so, this strategy is contrary to that of all the other desert-adapted macrofungi collected in the Namib which develop belowground under relatively moist and cool conditions. Collecting sites were easily found and yielded abundant dry specimens, and yet observed rains of up to 25 mm never produced specimens. Despite my best efforts to learn more about this fungus, the development, physiology and ecology of *B. ellipsozona* remain a mystery.



Fig. 9: Dry specimens of the elusive *Broomeia ellipsozona*, found in shallow drainages of coarse gravel on the Namib plains.

The habitats which yielded the greatest diversity of macrofungi in the Namib Desert were the ephemeral rivers, following annual flooding of their channels and floodplains (Fig. 5). Taxonomic work currently in progress suggests that the large variety of woody substrates and organic-rich soils in these shady linear oases support a diverse flora of more than 40 species. This includes agarics, gasteromycetes, ascomycetes (particularly cup fungi), and slime molds. Here again the quantity of moisture entering the ecosystem, in the form of muddy flood water from rains in the inland escarpment, is the key to fungal ecology. The great majority of fleshy fungal species are found in the river channel for a period of 4 weeks after the flood waters subside. Large floods which thoroughly soak the silty river banks and floodplain, in addition to the channel, result in a prolonged fruiting season of macrofungi which decompose buried wood, as well as the fine organic material incorporated into the freshly deposited silts.

Of particular interest are the giant, woody sporocarps of *Battarrea* cf. *phalloides* (Fig. 6) which fruit abundantly along the banks of the rivers, as much as 6-12 months after flooding. As in the dunes, fruiting is triggered by the drying trends of the soil. When digging out fresh specimens, the distinct wet layer lies right at the base of the sporocarp. Extensive digging in the silty banks where fresh sporocarps were fruiting yielded specimens at all stages of development, even the earliest stages of glebal development in buttons which heretofore had not been seen. Peridium and glebal development is completed at depths of 20-35 cm before the woody stipe elongates,

thrusting the spore load through the compacted silts to the surface.

Decomposition experiments in the Kuiseb riverbed, using the standard Oxford cloth, revealed that >90% of belowground decomposition occurs in response to moisture inputs from the floods. As *B. cf. phalloides* fruiting suggested, decomposition deep in the river banks continues for long periods after flooding, despite the dry and dusty appearance of the riverbed surface.

Redefining the ecological role of fungi in the Namib Desert

Researchers have long emphasized that, because of the lack of moisture in deserts, fungi play a less important role here than they do in more mesic ecosystems. Results from this study show, however, that infrequent rains and floods in the Namib Desert are important periods for nutrient processing. The uncommon "wet seasons" are the periods during which macrofungi are active, and when a large proportion of plant detritus and dung are rapidly decomposed. Belowground development of sporocarps is a key adaptation to a surface environment which is truly hostile to fungi. Beneath the hot, dry surface is a fungal world which is functioning like that in more mesic climates, except that the period during which germination, growth and reproduction must occur is much abbreviated.

The pulse-reserve paradigm (Noy-Meir, 1973) has been widely used to describe how fauna and flora cope with the desert environment. The "pulse" refers to the short period triggered by moisture inputs, during which organisms are actively growing, consuming foodstuffs necessary for growth, and ensuring continued existence of the species via reproduction. In contrast, the "reserve" refers to the long intervening periods during which organisms must survive extreme heat and aridity. Desert-adapted fungi are no exception. The rain "pulse" triggers germination of spores and consumption of plant detritus and herbivore dung, fueling rapid fungal growth. In response to the sand drying out, mycelial development culminates in woody sporocarps bearing dark, thick-walled spores - the "reserve" structures specialized to endure the lengthy dry times which characterize the deserts of the world.

Acknowledgments

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