Fungal ecology in the Etosha National Park

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ABSTRACT

A survey of the diversity and ecology of Namibian fungi was initiated in 1991 and is presently ongoing. This paper is a discussion of fungal ecology, utilizing the fungi collected to date in the Etosha National Park as examples. The majority of macrofungi collected in a single sampling of the Okaukuejo region following rains, were decomposers of various substrates: fallen *Colophospermum mopane* twigs, leaves and branches; buried grass detritus; zebra, horse and elephant dung. Initial investigations of the ecology of the mutualistic association between *Macrotermes michealseni* and *Termitomyces shimperi* are discussed. Mycorrhizal associations of an annual and a perennial grass species, subjected to different grazing pressures were also examined. The annual, an initial colonizer of disturbed regions, had lower root colonization levels than the perennial grass, which is less tolerant of overgrazing. These data corroborated studies conducted in the Namib Desert which attributed low colonization levels of annual grasses in overgrazed regions to a lack of spore inoculum. These results are discussed in reference to ongoing investigations of the effects of desertification on the below ground biota. The need for a long-term survey of fungal biodiversity and ecology is addressed, given the patchiness of rainfall as well as the diversity of habitats in Namibia.

INTRODUCTION

A survey of the diversity and ecology of fungi in Namibia was initiated in 1991 and is presently ongoing. While not limited to the proclaimed conservation areas of Namibia, such sites are of primary interest given the wealth of information available regarding their biotic and abiotic features. Fungi are heterotrophs and are thus dependent on other organisms for their nutrition. Previous studies of the other biota, particularly the flora, of the Namib-Naukluft, Waterberg Plateau and Etosha National Parks (Boyer 1989; Le Roux *et al.* 1988; Seely 1990; Seely & Louw 1980; Yeaton 1988) thus provide an essential ecological context in which to incorporate studies of the fungal flora. A large body of work has demonstrated the importance of fungi in ecosystem dynamics, including nutrient cycling (Christensen 1989; Harley 1971; St.John & Coleman 1983).

As this paper is being written at the outset of the survey, my goal is to discuss the ecological roles of fungi in semi-arid grasslands and woodlands, using material collected in the Etosha National Park as examples. To date, studies have been confined to two primary objectives in the Park:

I. An assessment of the diversity and ecological roles of macrofungi in the sweet grassveld and mopane treeveld.

II. A first approximation of the mycorrhizal status of dominant grasses of the sweet grassveld on lime, subjected to moderate and excessive grazing pressures.

ECOLOGICAL ROLES OF MACRO-FUNGI

Terrestrial fungi typically have a filamentous form consisting of hyphal cells delineated by septa. The hyphal network, collectively known as the mycelium, is the vegetative form of the fungal individual. Nutrients necessary for growth and reproduction are derived from the action of extra-cellular enzymes, which convert complex macromolecules into smaller component molecules that are subsequently taken in across the cell wall and cell membrane (Burnett 1976). Reproduction is by means of sexual or asexual microscopic spores typically produced in sporocarps (eg. mushrooms or bracket fungi). Spores are agents of dispersal and a means for enduring periods of climatic or nutrient stress (Moore-Landecker 1982). When conditions become favorable, the spores germinate to once again produce the vegetative mycelial growth form.

In terrestrial environments, fungi have developed a range of specializations for obtaining their nutrition. They exist as decomposers of dead plant or animal material, parasites of living plants or animals, or mutualists or commensalists with plants or animals. Decomposers of plant material have lignases and cellulases that allow them to degrade the complex macromolecules of plant cell walls (Moore-Landecker 1982). Decomposers of herbivore dung frequently have spores that require passage through the herbivore gut in order to germinate, ensuring inoculation and germination on the appropriate substrate. Fungi that decompose leaf litter are fast-growing and short-lived, making use of short periods of moisture availability. Most plant substrates, particularly wood and herbivore dung, are highly complex and require a battery of fungi, bacteria and detritivores for total decomposition (Christensen 1989). Thus one observes a succession of different organisms utilizing the substrate through time; each preferentially decomposing various components of the substrate.

The majority of macro-fungi collected in a single sampling of the Okaukuejo region of Etosha National Park 5-7 days following rains in March 1991, were decomposers of various substrates (Table 1). These fungi produced macroscopic fleshy sporocarps, many of which were mushrooms.

Decomposers of woody substrates

Leaf and twig decomposing Agaricales frequently produce small mushrooms (cap 4-10 mm broad) during or immediately after rains. Still evident at the time of sampling on fallen *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard twigs and leaves was a delicate brown mushroom, *Crinipellis calderi* Pegler (cap 3-5 mm, stalk 0.5-1.0 mm). This fungus was originally described from East Africa, as a general leaf and twig decomposer. Three additional species, which were abundant on dead *C. mopane* branches, have tough, woody shelf-like fruiting bodies which can be observed year-round on these substrates. However, active decomposition of the wood and subsequent fruiting only occur following rains. An *Oxyporous* sp. and a *Peniophora* sp. have yet to be positively identified, and thus the extent of their substrate specificity is presently unknown. *Schizophyllum commune* (Fr.) ex Fr. however, is a cosmopolitan wood decomposer found throughout temperate and tropical regions of the world. Further sampling will likely reveal a wide range of wood decomposers in the park, given the relatively high diversity of woody plants (Le Roux *et al.* 1988).

Decomposers of buried grass material

Four species were observed fruiting from the ground in the grassveld regions surrounding Okaukuejo (Table 1). Excavations at the base of the fruiting-bodies revealed fungal colonization of dead grass roots and detritus. Three of the species were Agaricales, producing mushrooms of different statures. *Lepiota polysarca* (Kalch. & MacOwen) Sacc. is a large white fleshy mushroom recorded in South Africa, without substrate information (Reid 1975). *Crinipellis stipitaria* (Fr.) Pak. is a wide-spread decomposer of stems and roots of Gramineae (Pegler 1971). A medium size, yellowish-white *Agaricus* species with pink gills becoming purple black, was abundantly present in the sweet grassveld, fruiting in large numbers. The fourth species collected, *Montagnea arenaria* (D.C. ex Fr.) Zeller, is a desert-adapted relative of the mushroom family Coprinaceae ("inky caps"). A small fungus, 15-20 mm wide and 5-10 cm tall, *M. arenaria* has a characteristic appearance (Fig. 1). A woody stalk bears upturned black woody gills called gussets that eventually break off in the wind, disseminating the spores. The spores are darkly pigmented and thick-walled, protecting them from intense solar radiation and desiccating winds. This fungus is wide-spread throughout arid and semi-arid regions of the world and has been collected throughout Namibia by the author. *M. arenaria* primarily decomposes buried grass roots, but has also been found decomposing gemsbok dung in the Namib Desert.

FIGURE 1: *Montagnea arenaria*: decomposer of buried dung and grass, found throughout Namibia.

Decomposers of dung

Herbivore dung represents a substrate that is high in partially degraded organic matter. A number of organisms utilize this substrate as their primary food source, most prominent of which in African savannas are the dung beetles. Numerous fungal genera are also dung specialists. Kingston (1977) observed that dung beetles only utilize elephant dung that is freshly deposited during the rainy season. Dung deposited during the dry season and re-wetted by summer rains however, is primarily decomposed by microbial activity. Four fungal species were observed decomposing herbivore dung in this preliminary study in the Etosha National Park: *Agrocybe broadwayi* (Murr.) Dennis on horse dung, *Conocybe pubescens* (Gill.) Kuhn on zebra dung, *Cyathus microporus* Tulasne on zebra and horse dung, and *Paneolus antillarum* (Fr.) Dennis on elephant dung. Other

TABLE 1: Macro-fungi collected to date in the Etosha National Park.

Fungus	Order	Substrate	Ecological role
Agaricus sp.	Agaricales	Ground	Grass root decomposer?
Agrocybe broadwayi	Agaricales	Horse dung	Herbivore dung decomposer
Conocybe pubescens	Agaricales	Zebra dung	Herbivore dung decomposer
Crinipellis cf. *calderi*	Agaricales	Dead mopane leaves and twigs	Leaf litter decomposer
Crinipellis cf. *stipitaria*	Agaricales	Grass detritus	Decomposer of grass
Leucoagaricus polysarca	Agaricales	Ground	Grass root decomposer?
Paneolus antillarum	Agaricales	Elephant dung	Herbivore dung decomposer
Schizophyllum commune	Agaricales	Dead mopane branches	White rot decomposer of wood
Termitomyces schimperi	Agaricales	Termite mounds	Wood decomposer
Oxyporous sp.	Aphyllophorales	Dead mopane branch	Wood decomposer
Peniophora sp.	Aphyllophorales	Dead mopane branch	Wood decomposer
Montagnea arenaria	Hymenogastrales	Ground	Grass root and herbivore dung decomposer
Cyathus microporus	Nidulariales	Zebra and elephant dung	Herbivore dung decomposer
Broomeia congregata	Sclerodermatales	Base of *Terminalia prunioides*	?

workers suggest that these species are generalist herbivore dung decomposers (Bottomley 1948; Pegler 1971).

Fungi with unknown substrate preferences

The ecological role of *Broomeia congregata* Berk., collected at the base of *Terminalia prunioides* Lawson by W. du Plessis, is unknown, as is its taxonomic status (Miller & Miller 1988). Endemic to southern Africa, and predominantly found in arid to semi-arid regions, developmental stages of the fruiting structures have not been observed, nor the physical association of the fungus with nearby trees (Bottomley 1948). It is possible that the fungus forms a mutualistic ectomycorrhizal association with the tree, obtaining carbohydrates from the tree in exchange for increased nutrient and moisture uptake (see Section II). Alternatively, the fungus may either be parasitic on the associated tree or simply decomposing its dead roots. Bottomley (1948) maintains that *B. congregata* is usually associated with trees, particularly *Acacia* species, that are exuding gum from the trunks. Whether and how the fungus might be causing this secretion by the tree is unknown. Like many arid adapted fungi, *B. congregata* still requires extensive study to determine its ecological role and taxonomic affinity.

The fungus-termite mutualism

Numerous classes of fungi have developed unique mutualisms involving nutrient acquisition. A fascinating mutualism prevalent in the Park and in other Namibian savanna regions is that between the termite, *Macrotermes michealseni* (Sjostedt), and an Agaricales species, *Termitomyces shimperi* (Pat.) Heim ("omajowa")(Van der Westhuizen & Eicker 1991). The termites cultivate the fungus in chambers below the large termite mounds. The fungus produces large conspicuous white mushrooms around the base of the mound following the first heavy summer rains (Fig. 2) These fungi are choice edibles throughout their range in Namibia, an utilized by numerous animal species including warthog, gemsbok, steenbok, porcupine, black-backed jackal, as well as people (U. Kaiser, pers. comm.).

FIGURE 2: *Termitomyces schimperi* fruiting from the base of a *Macrotermes michealseni* mound in the Otjiwarango district of Namibia.

Not all mounds produce fungi each year and the reasons for this are unknown. As part of a preliminary investigation into the ecology of *T. schimperi* in Namibia, two *M. michealseni* mounds were excavated on a farm in the Otjiwarango district. The excavations were done after seven days of consecutive rainfall totalling approximately 100 mm. One excavated mound (3 m tall and approximately 4 m wide) had 20 mushrooms fruiting around the circumference of the base. The other mound was active, exhibiting freshly deposited mud on the outer wall of the mound, but no fungi were fruiting.

The excavation at the first mound showed that the mushroom stalk grows from a 'pseudorhiza' (long narrow stalk) which extends deep beneath the mound (1-2 m). These pseudorhizae grow from their point of origin under the mound to the surface via air channels that ventilate the mound. The mushroom itself develops from the pseudorhiza, just below the surface of the ground, rather than forming deep within the mound and being pushed to the surface fully formed. Each mushroom forms from a separate pseudorhiza and the pseudorhizae may come from many discrete chambers in the mound. The chambers are composed of a labyrinth of mud shelves (Fig.3), on which the termites construct the fungus comb (Fig.4). The latter is the site at which the fungus-termite interaction is physically occurring.

Macrotermes species feed on above and below ground cellulosic substrates which they obtain while foraging through tunnels that extend outward from the mound (Coaton & Sheasby 1972). They are unable to completely digest these wood and grass substrates however, lacking a critical group of enzymes required for cellulose digestion, the C_1-cellulases (Martin & Martin 1978). They therefore regurgitate masticated woody material (Martin & Martin 1978) as small balls, which are cemented together to make the fungal comb (Fig. 5). The termites then inoculate the surface with cells of *Termitomyces schimperi*. The fungus has the necessary enzymes for decomposition of the masticated woody material and rapidly colonizes the surface of the comb with a fluffy hyphal network (Fig. 6). Specialized microscopic cells (cystidia) are formed on the hyphae which cover the comb surface. The termites subsequently graze these cells and the decomposed comb, but concentrate on macroscopic nodules also formed on the mycelial surface, composed

FIGURE 3: The fungal chambers of *Macrotermes michealseni* are composed of a labyrinth of mud shelves bearing the fungus comb

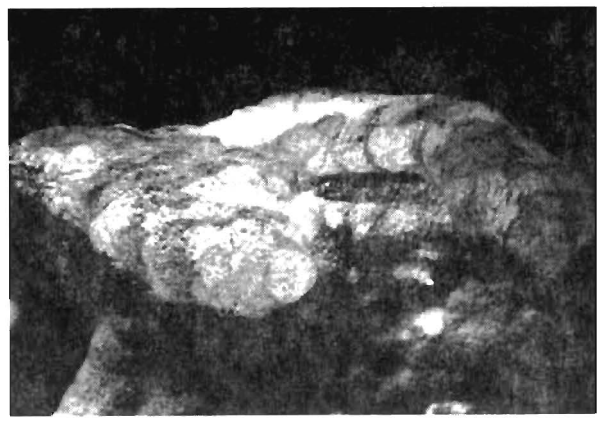

FIGURE 5 Small balls of masticated woody material are regurgitated by the termite and cemented together to form the fungal comb.

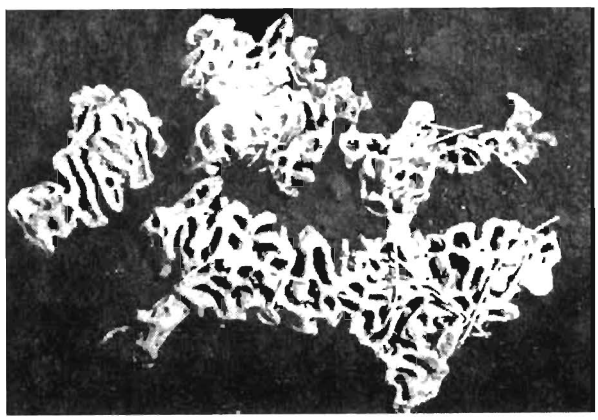

FIGURE 4 The fungus comb built by *Macrotermes michealseni* and inoculated with *Termitomyces schimperi*.

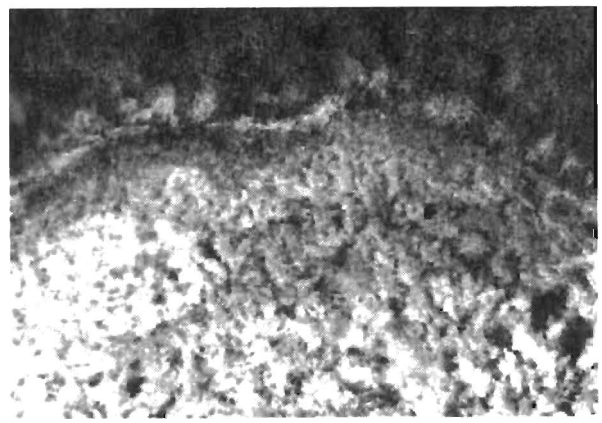

FIGURE 6: The fluffy mycelium of *Termitomyces schimperi* colonizing fungal comb constructed by *Macrotermes michealseni*.

almost entirely of these cystidia. These nodules, varying in size from 2-5 mm in diameter, are the termite's source of the C_1-cellulases required for complete digestion of cellulosic materials in the mid-gut (Martin & Martin 1978).

Termitomyces schimperi mushroom formation is always associated with the first summer rains in Namibia, but whether the increased moisture availability has a direct or indirect effect on mushroom development is not known. Fruiting in Basidiomycetes is a complicated phenomenon that can be associated with decreasing nutrient availability, temperature, moisture availability and/or light intensity or wavelength, depending on the fungus (see Moore-Landecker 1985 for a general discussion). I observed that the mound that did not exhibit fruiting had a comb that was firmer and had younger mycelial growth than that of the mound with mushrooms. The nodules and pseudorhizae were equally abundant in both mounds however, and are thus not structures formed only in response to fruiting. The observations that mushroom formation occurs from apparently older regions of mounds, suggests that the decreasing quality of the comb as a nutrient substrate may result in fruiting.

A FIRST APPROXIMATION OF THE MYCORRHIZAL STATUS OF SWEET GRASSVELD GRASSES.

Mycorrhizae are modified roots that are comprised of fungus and plant tissues, and are another example of a mutualistic relationship in which both organisms benefit nutritionally from the association. The sole source of carbon for the fungus is plant photosynthate, while the plant obtains increased moisture and nutrient uptake, particularly phosphorus (see Harley and Smith 1983 for a review of mycorrhizal physiology). Mycorrhizal associations occur in 90% of all land plant families surveyed (Harley and Smith 1983) and are found in virtually every type of terrestrial ecosystem (Allen 1991). Two types of mycorrhizal associations predominate. Ectomycorrhizae are characterized by an external root sheath composed of hyphae and a lack of plant root cortical cell wall penetration by the fungus. Nutrient exchange thus occurs across the plant and fungal cell walls. Ectomycorrhizae are of particular importance in temperate forest regions of the world where they form associations with the dominant trees species. Many ectomycorrhizal fungi produce macroscopic fruiting bodies such as mushrooms.

Vesicular arbuscular mycorrhizae (VAM) are the second dominant mycorrhizal type. These mycorrhizae are characterized by extensive hyphal proliferation within the root cortical cells (Fig. 7), and specialized highly branched structures called arbuscules, where nutrient exchange occurs between the fungus and the plant. Vesicles are fungal storage structures that also form within the plant cortical cells, hence the derivation of the name of this type of mycorrhizal association. VAM mycorrhizae predominate in tropical regions and grasslands.

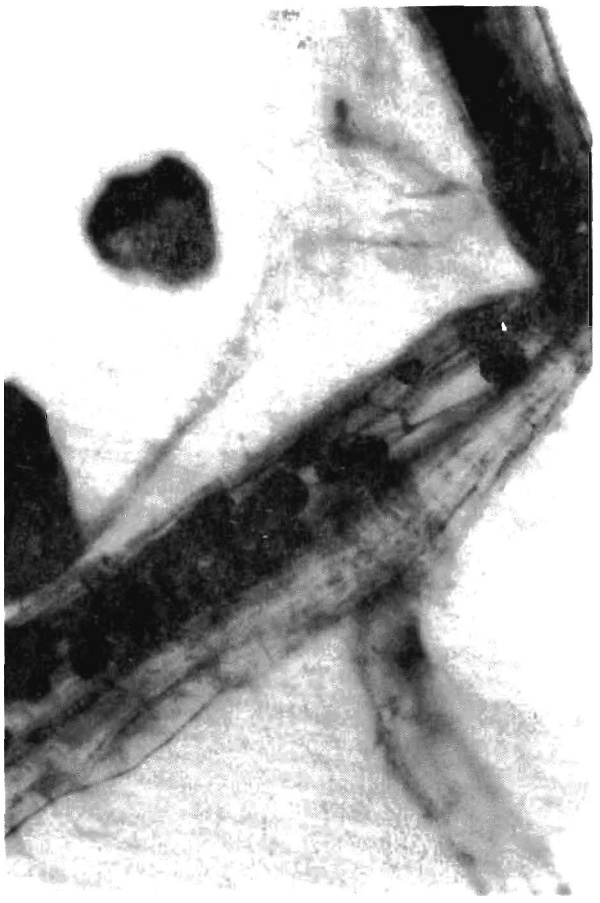

FIGURE 7: Colonization of grass root cortical cells by vesicular arbuscular mycorrhizal fungi, showing internal hyphae and spores.

These fungi (Glomales: Zygomycetes) apparently access only those forms of nutrients that are also available to the plant (Cooper 1984). The advantage the fungus provides the plant is increased surface area for water and nutrient absorption. Fungal hyphae are substantially finer than plant roots and grow much faster, colonizing regions around the root and increasing the surface area of the root structures by as much as 200% (Sieverding 1991). To date, approximately 250 species of mycorrhizal fungi have been identified based primarily on characteristics of the microscopic asexual spores that form below the soil surface in association with the roots (Schenk & Perez 1990). These fungi have broad host and geographic ranges, their distributions being limited primarily by climate, pH, nutrient availability and physical soil parameters (Brundrett 1991). For example, a cosmopolitan flora of at least five VAM fungal species was found with grasses throughout the arid regions of Namibia (Jacobson 1992; Jacobson *et al.* 1993).

Sweet grassveld on lime was identified by Le Roux (1988) as the most important grazing land in the Etosha National Park. The shallow soils underlain by calcrete result in the lowest levels of water availability in the Park. While this area normally experiences heavy grazing pressure throughout the rainy season, during the dry season the animals overgraze parts of this habitat adjacent to waterholes. Two grass species occurring in this region were chosen to examine the effects of grazing on their mycorrhizal status. *Enneapogon desvauxii* Beauv. is an example of an annual grass which is tolerant of different habitats and soil types (Gibbs Russell *et al.* 1991), including over-grazed regions. It is one of the first grasses to become established in overgrazed regions, reproducing itself primarily by seed. *Eragrostis nindensis* Fical. & Hiern is a perennial species which sprouts rapidly from previous year's growth following sufficient rains (Gibbs Russell *et al.* 1991). It is drought tolerant and provides important forage for herbivores. Like other climax perennial grasses however, it is sensitive to overgrazing. I was particularly interested in contrasting the mycorrhizal status of annual and perennial grass species, because annuals are frequently the initial colonizers of disturbed regions, whereas perennial grasses generally are less tolerant of over-grazing.

METHODS

Sampling was conducted at three sites within the sweet grassveld on lime community. Two sites experienced intense grazing, but were not overgrazed, and had good cover of both grass types. One site was located 40 km east of Okaukuejo, on the road to Namutoni; while the second site was located 3 km north of Okaukuejo, adjacent to the airport. The third site, located 3 km east of Okaukuejo, had been overgrazed and had only a light cover of *E. desvauxii*. Living roots were dug out from the base of the plants, at a depth of 10-15 cm. Roots from three plants of each species were sampled at each site and preserved in 50% ethanol. Roots were stained for mycorrhizal structures using the trypan blue method of Koske and Gemma (1989). Mycorrhizal colonization levels were assessed using the systematic slide method discussed by Giovanetti and Mosse (1980), at 100x magnification using a compound light microscope.

TABLE 2: Mean mycorrhizal colonization levels of *Enneapogon desvauxii* and *Eragrostis nindensis* at 3 sites in Etosha National Park. Mean values with the same letter are not significantly different (Duncan's Multiple Range Test; alpha = 0.05, n = 5).

Site	Grass	Mean	SE
Airstrip	*E. nindenis*	93 a	2.5
Airstrip	*E. desvauxii*	56 b	4.5
3A	*E. nindensis*	90 a	0.8
3A	*E. desvauxii*	52 b	2.1
1A	*E. desvauxii*	22 c	1.0

RESULTS

All plants were mycorrhizal and had internal and external hyphae, vesicles, and arbuscules. An ANOVA test was conducted on the arcsine transformed data (Zar 1984) to determine whether significant difference in mycorrhizal colonization existed between the grasses sampled within a site and between sites (Table 2). Significant differences were observed (alpha = 0.001), and Duncan's Multiple Range Test subsequently showed that the differences were primarily between the two grass species at each site. *E. nindensis* had significantly greater mycorrhizal colonization than *E. desvauxii* at the two sites where they coexisted. *E. nindensis* species was highly mycorrhizal (70-100%) and *E. desvauxii* was moderately so (40-55%).

In addition, at the overgrazed site, *E. desvauxii* was mycorrhizal but colonization levels were significantly lower than those of *E. desvauxii* at the other two sites (26-35%).

DISCUSSION

These data corroborate studies conducted in the Namib Desert that showed that perennial grasses have significantly higher levels of colonization than annual grasses (Jacobson 1992). This was attributed to the fact that the mycorrhizal associations of the perennial grasses have already been established and thus when moisture conditions become favorable, fungus and plant experience synchronized growth. In contrast, annual grasses becoming established from seed each year must establish mycorrhizal associations from spores. The colonization levels achieved by annual grasses are thus largely dependent on the density of spore propagules in the soil.

Initial studies in the southern pro-Namib also showed that overgrazing was correlated with extremely low levels of mycorrhizal colonization of *Stipagrostis ciliata* (Desf.) De Winter, which normally exhibits high levels of colonization (unpublished data). These studies, as well as work done independently in Botswana (Veenendaal *et al.* 1992), suggest that mycorrhizal propagule density is one of the primary factors affected by overgrazing. The independent and synergistic effects of grazing and variations in annual rainfall on the mycorrhizal flora are currently being investigated, in order to determine why the mycorrhizal flora is thus impacted, and the implications of desertification processes on nutrient cycling by below-ground organisms. Ultimately, a means of evaluating the condition of the below-ground biota from correlated above-ground criteria will be developed. This will hopefully provide an effective means for incorporating below-ground communities into conservation and restoration efforts in the arid and semi-arid regions of southern Africa.

CONCLUDING STATEMENT

Due perhaps to the ephemeral nature of large fleshy mushrooms, and the microscopic size of most other fungi, the fungal kingdom has been largely neglected in biodiversity surveys (Stuart *et al.* 1990; Huntley 1989). This trend has changed recently however, with the recognition that the below-ground biota and indeed all organisms involved in nutrient cycling, require cataloging and further study for a better understanding of ecosystem functioning and subsequent conservation or restoration (Solbrig 1991). This is even true in regions of low moisture availability, where fungal floras have long been assumed to be unimportant in nutrient cycling processes (West 1991). It is clear from studies in the arid and semi-arid grasslands of Namibia that fungi do exist in moisture stressed environments, and that like most other organisms, they show pulsed activity in response to moisture inputs. As a result, decomposition and nutrient processing by fungi in arid and semiarid environments are much slower than in moister climates, but nevertheless do occur. Long-term studies are thus needed to effectively study the ecology of fungi in these regions.

The newly initiated fungal survey of Namibia provides an opportunity to examine the contribution of an entire kingdom to ecosystem functioning. The intended purpose of this paper was to introduce the roles of fungi in ecosystems, with specific reference to my investigations in the Etosha National Park. This report clearly indicates that the work of identifying and examining the ecological roles of fungi in the Etosha National Park, as well as all of Namibia, is in the preliminary stages. Given the patchiness of rainfall, as well as the diversity of habitats in Namibia, long-term surveys in different rainfall regions throughout the country are essential for an assessment of fungal biodiversity. Ecological studies, including investigation of substrate preferences and fruiting phenology in response to moisture input, are also needed in different habitats. In addition, many economically important fungi, such as plant and animal parasites and pathogens, have yet to be studied in Namibia.

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