H5.3.

Windows of opportunity in desert ecosystems: their implications to fungal community development

John C. Zak, Robert Sinsabaugh, and William P. MacKay

Abstract: At the ecosystem level, all fungal activity in arid and semiarid systems is water regulated. However, as the observation scale is changed to allow for finer resolution of moisture effects, one finds that fungal community development in deserts may be influenced by either the temporal patterning of moisture pulses, or biotic factors that extend the benefits of moisture windows. When selected biocides were applied to the root region of a desert bunchgrass, *Erioneuron pulchellum*, to reduce microarthropod and nematode densities, fungal species numbers associated with the root surface were not altered. The temporal pattern in species numbers apparently reflect large scale seasonal responses of the fungi, microfauna, and plants to yearly differences in the occurrences of moisture windows. For wood on the soil surface, moisture windows of short duration coupled with high temperatures restrict fungal species composition in this habitat resulting in a lack of turnover in the dominant fungal species on surface wood. However, when wood was placed in the more amenable environment of a woodrat midden, patterns of fungal community development differed significantly from that observed for wood on the soil surface. These studies indicate that our understanding of the roles of fungi in the functioning of desert ecosystems is biased because the scale at which we usually make observations is too large to account for abiotic and biotic influences on fungal activity and community development. Moreover, we have to realize that the occurrence of favorable habitats for fungi in arid systems varies considerably in space and time. One consequence of the high spatial and temporal heterogeneity in favorable habitats is that functional diversity among fungi may be greater than would be predicted based solely on abiotic considerations.

Key words: deserts, environmental heterogeneity, functional diversity, scale, wood.

Résumé : Au niveau de l'écosystème, toutes les activités fongiques dans les systèmes arides et semi-arides sont règlées par l'eau. Cependant, lorsqu'on change l'échelle d'observation pour obtenir une plus fine résolution des effets de l'humidité, on constate que le développement de la communauté fongique dans les déserts peut être influencé soit par des zonages temporels des fluctuations de l'humidité, ou soit par des facteurs biotiques qui étendent les bénéfices des périodes humides. Lorsqu'on applique des biocides sélectionnés à la région racinaire d'une herbe désertique en touffe, l'*Erioncuron pulchellum* pour réduire les densités de microarthropodes et de nématodes, les nombres de champignons associés aux racines ne sont pas affectés. Le patron temporel des nombres d'espèces reflète apparemment les réactions saisonnières à grande échelle de ces champignons, de la microfaune, et des plantes ainsi que les différences annuelles des incidences de périodes humides. Sur le bois et à la surface du sol, les périodes humides de courte durée couplées avec des températures élevées restreignent la composition des espèces fongiques dans cet habitat conduisant à l'absence de cyclage des espèces fongiques dominantes sur la surface du bois. Cependant, lorsque le bois est placé dans un milieu plus propice tel que les latrines de rats, le développement des patrons de communautés fongiques différent significativement de ceux observés sur le bois placé en surface du sol. Ces études indiquent que notre compréhension des rôles des champignons dans le fonctionnement des écosystèmes désertiques est biaisée parce que l'échelle à laquelle les observations sont généralement conduites est trop grande pour faire ressortir les influences des facteurs biotiques et abiotiques sur les activités fongiques et sur le développement des communautés. De plus, il faut réaliser que l'existence d'habitats favorables pour les champignons en milieux arides varie considérablement dans l'espace et dans le temps. Une conséquence de la forte hétérogénéité spatiale et temporelle des habitats favorables est que la diversité fonctionnelle chez les champignons pourrait être plus grande qu'on ne saurait le prédire sur la seule base des considérations abiotiques.

Mots clés : déserts, hétérogénéité du milieu, diversité fonctionnelle, échelle, bois.
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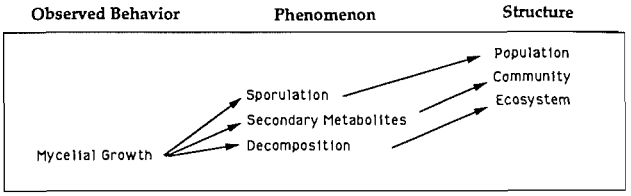
Introduction

To elucidate fungal dynamics in desert environments and the mechanisms that control fungal activity, one first has to understand how the large-scaled levels (e.g., abiotic environment) constrain the activities (e.g., growth rates, colonization patterns, species interactions) of the lower levels (individual, population, community). A system is considered hierarchical if the upper levels constrain lower level functioning (Allen and Starr 1982). However, to understand the functioning of the lower levels we should be responsive to the scale necessary to determine the interactions among the various levels. The scale of any ecological level is determined by the resolving power of the data and the extent of the observations that are required (Allen and Hoekstra 1992). When we are unable to elucidate the mechanisms that may account for observed spatial or temporal patterns in fungal community dynamics or ecosystem level processes in which fungi are involved, we indicate that the system is complex. What we usually do not acknowledge is that we may not have given critical attention to the spatial and temporal scales necessary to link the interactions among ecological levels and the abiotic environment. Furthermore, we must be careful to realize that ecological complexity may have little to do with the number of variables (e.g., species) we are measuring (Allen and Starr 1982). Rather, complexity may be related to the number of interactions between levels of organization within the system. As Allen and Starr (1982) have indicated, biological systems are complex because they involve the interactions of differently scaled processes. Nowhere is this more apparent than in attempting to link fungal community dynamics with ecosystem processes or in trying to understand the relationships between spatial and temporal patterns of plant biodiversity and fungal biodiversity.

The difficulty in attempting to link levels in natural systems is that the criteria for organization and dynamics of one level are inappropriate for either aggregating the lower levels to explain higher level processes (e.g., biodiversity), or for deciding how to subdivide higher level processes into component lower level units (e.g., population dynamics and community composition) (Allen et al. 1987). Often times we change levels in making observations, or we change criteria when moving between levels, without realizing the distinction. As a result, we collect data at various scales of resolution that are inappropriate to the hierarchical levels we are trying to link. Allen et al. (1987) emphasize that there are no absolute levels of observation that are independent of the observer. For example, if the level we choose to observe is the fungal mycelium, and the observed behavior is mycelial growth, then depending upon our criteria, we could observe three different phenomena: sporulation, secondary metabolite production, or decomposition dynamics (Fig. 1). Each of these phenomena would link the lower level structure, fungal mycelium, with three different upper level structures (i.e., population, community, and ecosystem). Important and critical to the discussion here is the notion that as one moves up and down through levels of ecological organization, the other levels are not fixed by what other observers have chosen as their starting points (Allen et al. 1987). Therefore, it is critical that attention be given to the scale of the observation (i.e., the scale at which data is to be collected relative to the question asked).

Fig. 1. The relationship between observation scale and observed phenomena. Different phenomena derived from the same observed behavior are linked to differently scaled structures. (Modified from Allen et al. 1987.)



Spatial and temporal heterogeneity

Although heterogeneity occurs in all ecosystems, deserts have the greatest variability for a large number of parameters, as compared with other systems, affecting the composition and richness of communities occurring in these systems (Polis 1991). The spatial and temporal patterns of resource distribution, at various scales, have been shown to influence a number of ecological processes in deserts and contribute to the high spatial heterogeneity of arid ecosystems (Whitford et al. 1987). Climate and topography, however, are the main driving variables that create the spatial and temporal patterns of plant community dynamics that are characteristic of arid ecosystems (Allen 1991).

The soils and vegetation patterns of arid regions are closely integrated, with soil characteristics affecting plant species composition, and plants influencing nutrient cycling, soil development (Crawford and Gosz 1982), and subsequent fungal species occurrences and activity. The productivity of arid and semiarid ecosystems, however, is limited by the abundance and variability of precipitation more so than in any other ecosystem (Evans and Thames 1981). Ludwig (1986) reported that the net annual productivity of various ecosystems in the Chihuahuan Desert varied by more than an order of magnitude, even between sequential years, if precipitation was substantially different.

Wicklow (1981) indicated that deserts have a greater number of fungal species than would be predicted based on abiotic conditions. While low moisture and high temperature certainly limit species activity, it is the high temporal and spatial heterogeneity in abiotic conditions and resource availability that may account for the unexpectedly high fungal species diversity observed for arid environments.

Moisture windows

The intermittent periods of favorable temperature–moisture, that are characteristic of desert ecosystems, provide "windows of opportunity" that are crucial for the activities of fungi. Not only is total moisture important, but the temporal and spatial patterning of moisture inputs may determine the extent of fungal activity (Zak 1993) and possibly the fungal species composition associated with either surface or buried litter in desert environments. It may indeed be the temporal and spatial heterogeneity in the windows of opportunity that regulate interactions among the desert biota, and that may contribute to the apparently high fungal diversity associated with arid ecosystems.

Scale again becomes an issue when discussing the effects of moisture windows on fungal activity and community com-

Fig. 2. A midden of the white throated woodrat *Neotoma albigula* located under mesquite in the northern Chihuahuan Desert.

position, since the effects of the windows are dependent upon the spatial and temporal scales at which observations are made (Zak 1993). For example, litter that occurs on the soil surface is subjected to extremes in temperature and moisture that limit fungal activity, while litter that occurs under shrubs can be buffered from these extremes. Root systems are also important centers of fungal activity in desert environments with moisture affecting fungal growth directly. Indirect effects of moisture may include regulation of microfaunal grazing of fungal hyphae (Zak 1993). Additionally, windows of opportunity can be modified and extended by the activity of animals concentrating litter in nests or middens, thus directly uncoupling fungal activity from abiotic constraints.

The remainder of this chapter will explore the roles of windows of opportunity and scale as they determine fungal community dynamics associated with root regions, surface wood, and wood in woodrat middens from the Chihuahuan and Sonoran deserts of the southwestern United States.

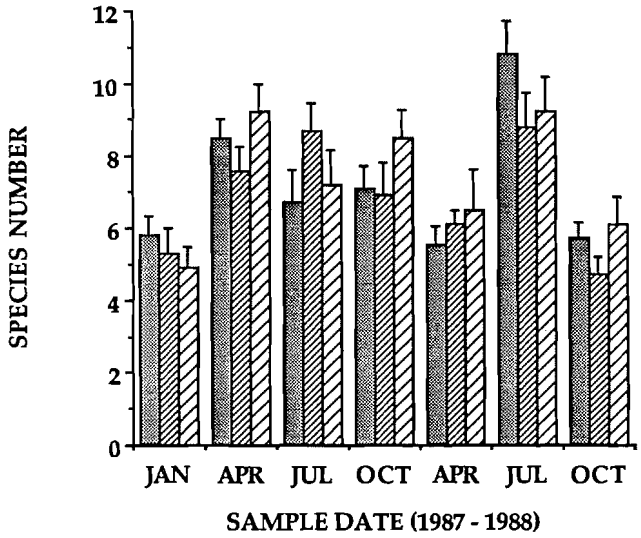
Root region dynamics

The root region of plants is a dynamic center of microbial activity and interactions between the microflora and the microfauna. Microfaunal grazing of fungi in the rhizosphere and along the root surface has been shown to regulate nutrient availability and nutrient uptake (e.g., Coleman et al. 1988). Moreover, grazing of fungal hyphae has been shown to stimulate fungal growth and activity (e.g., Moore 1988). In the Chihuahuan Desert, the largest hot desert in North America, the productivity of this system is regulated by moisture but limited by nitrogen availability (Zak and Freckman 1991). The temporal and spatial heterogeneity in moisture windows may, therefore, affect directly root region fungal activity and subsequent plant growth.

Woodrat middens

Woodrats (*Neotoma* spp.) are common inhabitants of arid ecosystems in the southwestern United States, where they collect woody litter to construct middens (Fig. 2) that are usually associated with shrubs and cacti. Middens can be numerous in a given location and quite large (20–70 cm in height and 1–2 m in diameter) (Vorhies and Taylor 1940).

Fig. 3. Fungal species richness associated with the root surfaces of fluff grass growing at the Jornada Long Term Ecological Research site in the northern Chihuahuan Desert on control plots (▩) and those receiving Nemacur to reduce nematodes (▨) and Chlordane to reduce microarthropods (▧). Values are means ± SE. Six plots were established per treatment with two plants sampled per plot.



Woodrats build middens by depositing dead wood and cacti on top of their burrows, with the midden structure dependent upon the type and quantity of woody litter available (Brown et al. 1972). Based on laboratory observations, a single individual can gather as much as 359 items of woody litter per night (Bonaccorso and Brown 1972). In the Sonoran Desert, a midden on average can contain greater than 1500 pieces of woody litter of various sizes. Preliminary studies by Rainey (1956) and J.C. Zak (unpublished data) indicates that the microclimate and nutrient characteristics of woodrat middens are more favorable for fungal growth than occurs for wood on the soil surface.

Fungal community development

Root region

Microarthropods and nematodes associated with the root region of *Erioneuron pulchellum* (H.B.&K.) Tateaka, fluffgrass, in the Chihuahuan Desert were manipulated over 2 years using Nemacur and chlordane (see Zak 1993 for details). Fungi were isolated from root surfaces of fluffgrass using a washing procedure described by Zak and Parkinson (1984). Briefly, a 4-cm region of root nearest the root–hypocotyl axis was removed from plants in the laboratory and subjected to fifteen 2-min washes. Twelve replicate root samples were obtained from each treatment including control plots. After washing, fifty 1-mm root segments were plated per replicate onto malt extract agar with 50 mg chlortetracycline and 100 mg of streptomycin added per litter to control bacterial growth. Plates were incubated at 22°C for 2 weeks before subculturing representative isolates onto potato dextrose agar (PDA) for species identification. Sterile forms were grouped into morphological taxa according to hyphal and cultural characteristics on potato dextrose agar and potato carrot agar (Stevens 1974).

Table 1. Dominant fungi (frequency of occurrence equal to or greater than 4%) associated with creosote bush wood placed on the soil surface under creosote bush shrubs in the Chihuahuan and Sonoran deserts, U.S.A.

Taxa	Time since field placement (mean ± SE) 1 Year	2 Year	9 Year
Chihuahuan Desert			
Alternaria alternata (Fr.) Keissler	10.2±3.1	5.5±1.7	9.1±2.8
Coleophoma sp.	92±2.2	95.5±1.7	84.5±3.7
Fusarium acuminatum Ellis & Everhart	24±4.0	26.7±3.9	13.7±3.4
Phialophora richardsiae (Nannf.) Conant	7.5±2.4	3.3±1.4	0
Mean no. of species per wood unit	7.2±0.5	7.8±0.9	7.9±0.5
Sonoran Desert			
Alternaria alternata	11.8±2.5	12.3±1.8	
Coleophoma sp.	97±0.9	98±0.9	
Fusarium acuminatum	7.8±3.3	5.8±2.6	
Libertella sp.	0	5.8±3.1	
Phoma sp. 400	8.7±4.1	27±6.9	
Sistotrema brinkmannii (Bres.) Eriksson	4.7±2.4	1.2±1.1	
Basidiomycete 109	0	6.8±5.1	
Sterile dark 121	0	6.3±3.3	
Mean no. of species per wood unit	5.3±0.4	7.3±0.6	NA

NOTE: Freqencies of occurrence were based on the number of 1-mm wood particles out of the 50 particles plated per replicate from which an isolate was obtained. There were 12 wood units sampled per site.

Although the biocides drastically reduced the densities of microarthropods and nematodes in the root region, there were no substantial differences in the average number of fungal species associated with fluff grass root surfaces (Fig. 3). However, differences in species numbers were detected within and between years irrespective of treatment. The temporal pattern in species numbers apparently reflect large-scale seasonal responses of the fungi, microfauna, and plants to yearly differences in the occurrences of moisture windows. What the study was unable to evaluate effectively were the short-term responses of the root-surface fungi to changes in the root-region microfauna in response to the duration and size of moisture windows. The temporal scale was not at a fine enough grain (resolution) to determine if changes in microarthropod densities and trophic groups resulted in altered fungal species occurrences during moisture windows. Furthermore, the lack of differences in fungal species numbers among treatments suggests that linking fungal species numbers to patterns in root-region microfaunal activity may be inappropriate. The numbers of fungal species in this root-surface community may be controlled by higher level interactions that involve plant-root dynamics rather than microfaunal effects. Changes in grazing dynamics by the root-region microfauna might be expected to influence species composition of the root-surface community more directly than species numbers (richness).

Surface wood

Wood pieces (10–12 cm length and 0.5–1 cm diameter) of creosote bush, *Larrea tridentata* (D.C.) Cov., were placed on the soil surface under the canopy of creosote bush at the Jornada Long Term Ecological Research (LTER) site in the Chihuahuan Desert, near Las Cruces, N. Mex., and at the former International Biological Program site in the Sonoran Desert near Tucson, Ariz., to compare fungal community development and mass loss dynamics in these two desert ecosystems. Wood was placed at the two desert locations in August 1984 and subsequently collected at 1, 2, and 9 years after placement. Twelve replicate samples of wood were collected at each sampling time from each location. The wood pieces were subjected to ten 2-min washes (Zak and Parkinson 1984) before five, 1 × 0.5 cm strips were cut from the surface of each wood piece. These strips were subsequently cut into approximately 1-mm^2 particles and 50 particles were plated onto malt extract agar (50 mg chlortetracycline and 100 mg of streptomycin added per litter to control bacterial growth) per replicate for fungal isolations. Plates were incubated at 22°C for 2 weeks and representative isolates were subcultured onto PDA for species identification. Treatment of sterile isolates was as described for the root-region fungi in the previous section.

Neither the mean number of species nor the dominant fungi (i.e., frequency of occurrence equal to or greater than 4%) associated with creosote bush wood on the soil surface in the Chihuahuan Desert changed substantially over the 9-year period (Table 1). Three species, *Alternaria alternata*, *Coleophoma* sp., and *Fusarium acuminatum* had high frequencies of occurrence on creosote bush wood at all sampling times in the Chihuahuan Desert. A fourth species, *Phialophora richardsiae*, was a dominant member of the community only at the 1-year sampling time. Other fungi were isolated from creosote bush wood in the Chihuahuan

Table 2. Densities (mean ± SE) of dominant fungi (those species with a density of three isolates or greater) isolated from mesquite wood placed in woodrat middens at three locations in the northern Chihuahuan Desert, U.S.A.

		Time from placement (months)		
Taxa	Initial	3	6	12
Alternaria alternata	8.4±2.7			
Coleophoma sp.	46.4±3.6			
Fusarium sp.	8.8±3.4			
Sterile hyaline 1	22.6±6.0			
Sterile hyaline 2	7.4±2.7			
Mean no. of species per wood unit	10.4±0.6			
Jornada site				
Colephoma sp.		36±4.4	39.2±2.3	40.4±3.0
Trichoderma harzianum Rifai		13.4±2.9	23.4±6.7	23.2±5.4
Sterile orange		15±6.6	0	0
Mean no. of species per wood unit		9.8±0.5	6.6±1.1	3.4±0.3
Rio Salada site				
Coleophoma sp.		39.4±4.4	41.8±4	42±2.9
Trichoderma harzianum		23.4±4.1	18±4.6	21.2±6.7
Sterile dark		12.8±6.4	0	0
Mean no. of species per wood unit		4.6±0.6	3.8±0.5	3.0±0.2
222 site				
Coleophoma sp.		39.6±6.0	28.6±7.1	40.2±4.8
Penicillium sp.		0	0	3.2±1.4
Trichoderma harzianum		5.0±1.0	1.6±0.9	3.2±1.1
Sterile orange		28.2±5.6	0	0
Mean no. of species per wood unit		7.6±0.6	8.2±0.7	8.4±1.0

NOTE: Densities based on fifty 1-mm particles plated per replicate. Five wood pieces were sampled per midden with wood collected from five middens per site.

Desert. However, these taxa were never isolated with a frequency of occurrence greater than 4%, and were highly variable in their occurrences.

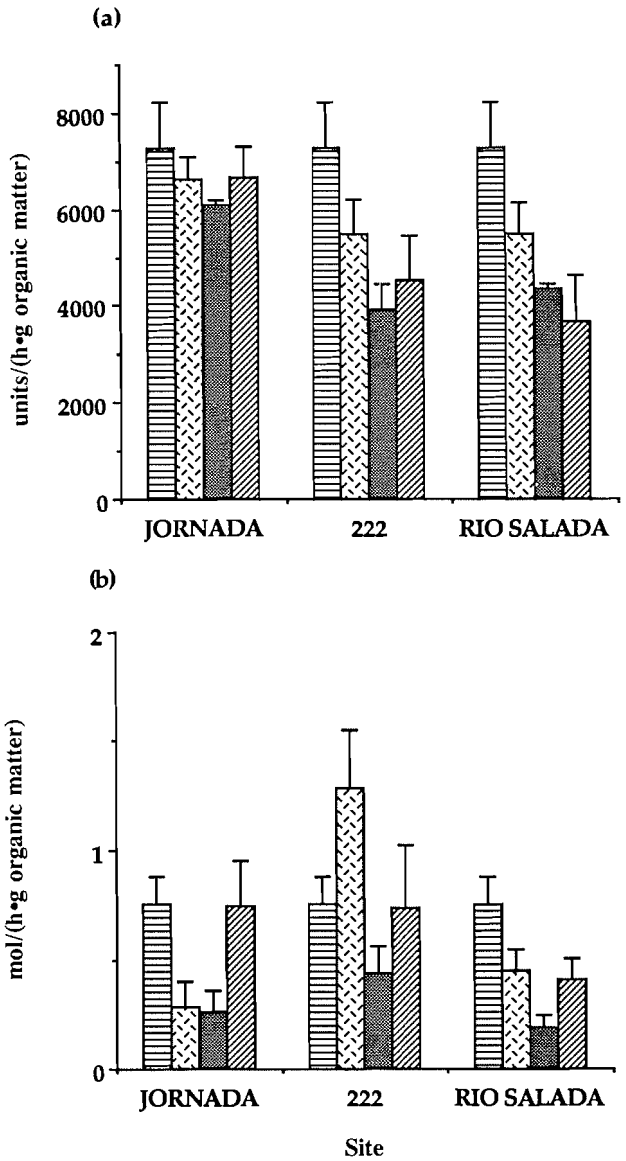
The mean number of species per wood unit and dominant members of the fungal community associated with the creosote bush wood placed in the Sonoran Desert increased after 2 years (Table 1). While *Alternaria alternata*, *Coleophoma* sp., and *Fusarium acuminatum* were also dominant members of the Sonoran fungal community during the first 2 years following field placement, three additional species, *Phoma* sp., a basidiomycete (109), and a sterile dark (121), became codominant during the 2nd year after placement. As with wood from the Chihuahuan Desert, the Sonoran creosote bush wood was also colonized by fungi with either low frequencies of occurrence or that had high densities, but very sporadic occurrence among replicates. Species identification of the isolates obtained from the 9-year sample have not been completed. However, preliminary identifications indicate that *Coleophoma* sp. was still a dominant member of the Sonoran fungal community associated with creosote bush wood on the soil surface.

Moisture windows of short duration coupled with high temperatures that are characteristic of surface wood in the Chihuahuan and Sonoran deserts (Crawford and Gosz 1986) would certainly restrict fungal species composition in this habitat. The lack of turnover in the dominant fungal species on surface wood over 9 years suggests that few taxa are able to persist in this extremely variable environment. Scattered pieces of wood in deserts of the southwestern United States, unless grazed by termites, decompose slowly (Zak and Whitford 1988), thus allowing fungal communities to persist undisturbed for long periods of time. When compared with other substrates in desert environments, such as buried wood or dead woody roots, turnover in the dominant members of a fungal community associated with surface wood would appear to occur over time scales in decades rather than years.

Woodrat middens

Standing dead mesquite wood, *Prosopis glandulosa* Torr., was cut into 10- to 15-cm length pieces (0.5–2 cm diameter), and placed into five middens located along a mesquite playa fringe on the Jornada LTER site and in five middens at each of two locations within the Sevilleta LTER site near Albuquerque in August 1992. One location, the Rio Salada site, was an area of arroyos that contained mesquite and creosote bush. The Rio Salada and Jornada sites are considered part of the northern Chihuahuan Desert. The second location, site 222, located in the foothills of the Magnelena Mountains is considered to be an extension of the Great Basin shrub steppe. Middens at the 222 site were located under either mesquite or Apache plume, *Fallugia paradoxa* (D. Don) Endl. Wood was retrieved from the middens at 3,

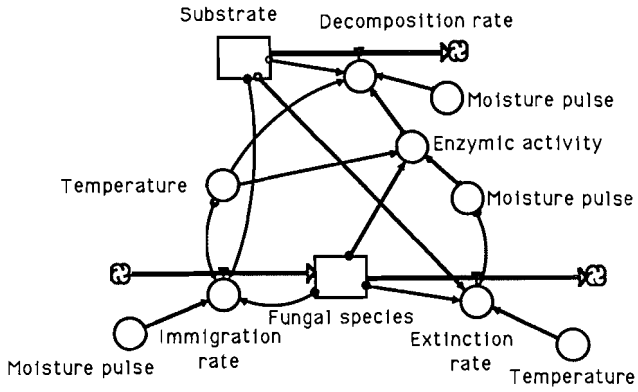
Fig. 4. Changes in (*a*) endocellulose and (*b*) phenol-oxidase activities associated with mesquite wood placed in woodrat middens located at three locations in the northern Chihuahuan Desert. Months from placement: ▤, initial; ▨, 3 months; ▩, 6 months; ▨, 12 months. The Jornada site is located at the Jornada Long Term Ecological Research Site near Las Cruces, N. Mex. The 222 and Rio Salada sites are located at the Sevilleta Long Term Ecological Research site near Albuquerque, N. Mex. Values are means of five middens ± SE.



6, and 12 months after placement. Fungi were isolated from the mesquite wood as described for creosote bush wood in the previous section.

As with the fungal communities from creosote bush wood placed on the soil surface in the Chihuahuan Desert, a *Coleophoma* species was the dominant member of the fungal community on mesquite wood prior to wood placement, and at all sampling times (Table 2). *Trichoderma harzianum* was the second dominant member of the fungal communities associated with wood in the Jornada and Rio Salada middens. While this species occurred at the 222 site, its density was low compared with the middens from the other locations.

Fig. 5. A model illustrating the influence of moisture pulses in controlling fungal colonization dynamics and enzymic activities during litter decomposition in arid ecosystems.



The low density of *T. harzianum* at the 222 site may be one reason for the higher species richness at this location compared with the other sites. Fungal species richness declined by 50% for wood placed in the Jornada and Rio Salada middens (Table 2) over 1 year, while species richness for the wood in middens at site 222 was not substantially different during this period.

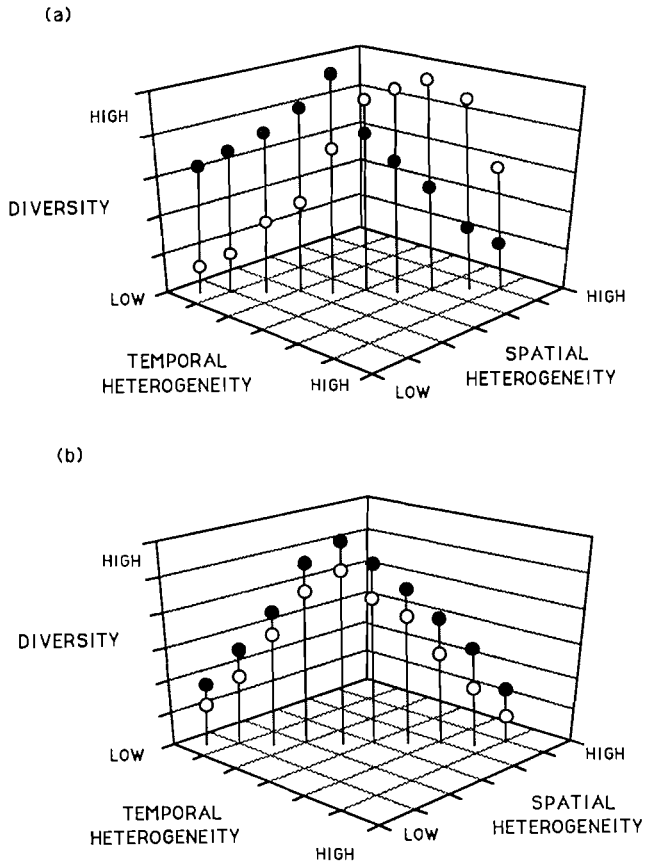
Endocellulose and phenol-oxidase activities were assayed (see Sinsabaugh et al. 1992 for methodological details) from the same wood used to isolate fungi to link fungal community composition with community level processes. The enzymic activities did not follow the patterns observed for species richness and species composition (Fig. 4). Endocellulose activities from the Jornada middens were consistently higher over the 1 year, while the Rio Salada site was similar in activity levels to site 222. Site 222 middens had the highest phenol-oxidase activities. Small differences in moisture patterns among the sites may account for the observed enzymic activity patterns and differences in fungal community composition. Substrate quality can be ruled out as a controlling factor since this parameter was kept constant by using the same wood at all locations.

The patterning of moisture windows directly influences not only fungal community development, but the activity of the fungal community through the production and activities of exoenzymes during fungal growth (Fig. 5). The influence of the size and duration of moisture windows on fungal dynamics would appear to operate at two temporal and spatial scales. At one scale of resolution, moisture patterns and any activity, such as midden building by wood rats, that can ameliorate abiotic constraints will influence fungal colonization and community development. At a level of resolution below the fungal mycelium, available moisture will control enzymic activities and subsequent decomposition rates, possibly, irrespective of the growth of the fungal mycelium (Sinsabaugh et al. 1991). Thus, attempts to link fungal community development and decomposition to patterns in moisture windows in arid systems should take into account that moisture may be controlling the decomposition process at several levels of resolution.

Biodiversity considerations

The spatially and temporally heterogeneous environment in arid ecosystems may select for greater functional diversity

Fig. 6. The theoretical influences of environmental heterogeneity on fungal species (●) and functional diversity (○) associated with (*a*) readily assimilable substrates and (*b*) recalcitrant substrates in an arid ecosystem.



among fungi than would be predicted based solely on abiotic considerations. Operationally, we define functional diversity as the numbers, types, and rates at which a suite of substrates can be utilized by the species comprising a fungal community in a given habitat. Therefore, functional diversity of fungal communities, we propose, is dependent in part upon the degree to which the component species exhibit versatility in enzyme and secondary metabolite production. Gochenaur (1975) had previously predicted that fungi in arid environments should have a greater nutritional versatility (i.e., functional diversity) as compared with species from more mesic regions. Furthermore, Flanagan (1981) reported that the enzymic versatility of arctic fungal isolates compared with the same species from temperate regions were greater. The Arctic can be classified as a cold desert and, like the hot desert environments, can exhibit high heterogeneity in moisture windows in space and time.

Theoretically, the pattern in species and functional diversity of fungal species in arid regions should be different between readily assimilable substrates and more recalcitrant material, such as wood (Fig. 6). For readily assimilable substrates, such as herbaceous plant roots, species diversity should peak at intermediate levels of temporal and spatial heterogeneity in moisture availability and nutrients. Functional diversity, however, should be lowest at low levels of spatial and temporal heterogeneity, and increase with greater system heterogeneity as abiotic rather than biotic interactions determines species occurrences. At high levels of heterogeneity, functional diversity associated with readily assimilable substrates should be greater than what one would predict from species diversity alone. For recalcitrant material, substrate quality and substrate longevity should be major regulators of species and functional diversity, in conjunction with environmental heterogeneity.

The pattern described above is similar to that predicted by the intermediate disturbance hypothesis (Connell 1978) for coral reefs and tropical rain forests. This hypothesis predicts that species diversity will be greatest at moderate levels of abiotic and biotic disturbances. In arid and semiarid regions, it is the level of temporal and spatial heterogeneity in moisture windows at several scales of resolution that determines the potential fungal species and functional diversity.

Conclusions

The dynamics of fungal communities in arid systems and attendant ecosystem functions are strongly dependent upon the size and frequency of moisture windows. These windows in turn may be modified by animal activity, which in the case of woodrat middens can extend the duration of the window. Our understanding of fungal dynamics in arid ecosystems is biased, however, because of the scale at which we perceive the interactions between the fungal mycelium and the abiotic environment. We tend to view arid systems as being mostly inhospitable to fungal activity owing to abiotic constraints. At the scale of the mycelium, fungi are colonizing spatially and temporally heterogeneous mesic habitats, which are embedded within a xeric matrix that we perceive. Therefore, the activity and dynamics of fungi in deserts should be comparable to those observed for mesic ecosystems if the observations are made at the appropriate scale and within an active window of opportunity.

If the degree of resource heterogeneity is indeed a major factor in determining fungal community dynamics in arid ecosystems, we could predict where the functional diversity of fungi within these systems should be the highest. While desert grasslands may be homogeneous at the scale of the plant (Whitford et al. 1987), they should be very heterogeneous at the fungal level owing to the high temporal and spatial variability in root growth, exudation patterns, and litter inputs. Shrub-dominated systems, which tend to develop following desertification, are heterogeneous at the level of the plant with regard to nutrients. Shrub-dominated systems should be homogenous at the level of the fungus resulting from the input of primarily recalcitrant substrates that are homogeneous in space and time.

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