ECOLOGY OF MYCORRHIZAE: A Conceptual Framework for Complex Interactions Among Plants and Fungi

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■ **Abstract** Mycorrhizae regulate elemental and energy flows in terrestrial ecosystems. We understand much of how mycorrhizae work, but integrating all possible mechanisms into a whole has proven elusive. Multiple evolutionary events and the long evolutionary history mean that different plants and fungi bring independent characteristics to the symbiosis. This variety results in extensive physiological variation. How do we integrate functional responses with diversity to understand the role of mycorrhizae in ecosystems? We review ecophysiological mechanisms of mycorrhizae and organize these into functional groups. Species-area relationships are not curvilinear, but resemble the "broken stick" model. We coupled functional groups with a metacommunity analysis to show how complex behavior can be generated using a simple matrix model of resource exchange. This approach provides insights into how we might integrate diversity and function across landscapes.

INTRODUCTION

Mycorrhizal associations, a symbiosis between plants and fungi, are crucial for both agricultural and natural resource management. This symbiosis has been studied for over a century, and our understanding of the interaction in the mechanisms of plant-fungus physiology is remarkably good. However, a single plant can form mycorrhizae with many fungi, and a single fungus can connect many plants. Thus, the complexity of possible combinations from the symbiosis is enormous.

Hart and associates (63) proposed three models whereby increasing mycorrhizal fungal species richness could improve ecosystem functioning, the rivet hypothesis, the diversity-stability hypothesis, and the redundant species hypothesis. Others

(8, 102) also evaluated mycorrhizal responsiveness as a sequence of change through succession. These suggest that there are predictable patterns in the sequence of community development. However, in carefully evaluating our own experimental data collected over the past two decades, it becomes obvious that there are many alternative relationships and outcomes even among what should be similar experiments. We began to re-evaluate how mycorrhizae work within communities and how interactions between multiple species of mycorrhizal fungi, multiple species of mycorrhizal plants, and multiple species of nonmycorrhizal plants, would regulate community composition and ecosystem processes.

The field of biocomplexity has made remarkable conceptual advances during the past five years and mycorrhizal symbiosis provides a remarkable test case. Our goal is to examine the vast array of mycorrhizal data focusing on diverse wildland ecosystems. Using this background, we propose a framework for integrating the complex of soil, plant and mycorrhizal fungal data such that prediction and limits to prediction can begin to characterize our understanding of mycorrhizae in ecosystems.

THE EVOLUTION OF FUNCTIONAL DIVERSITY

Mycorrhizae have evolved many times since the invasion of terrestrial systems by plants (32). Arbuscular mycorrhizae (AM) are a monophyletic group of fungi, the Glomales (110), that evolved some 400 to 460 mya and radiated into the groups we know today as early as 350 to 400 mya (113). If the hypothesis of a single evolutionary event is correct, this may explain the low species diversity (c. 172 species). Even if we include the remaining unknown species, this number may only double or triple, which is still very low for such a widespread group of organisms. However, there may be immense diversity within a species. Indeed, some of these species (e.g., *Glomus intraradices*) are a phylogenetically unrelated species complex. All other mycorrhizal types, plus nonmycotrophy, are more recent and some have evolved independently many times. Ectomycorrhizal (EM) fungi are in three vast groups including Zygomycetes (Endogonales), Ascomycetes, and Basidiomycetes. Because there are so many independent evolutionary events, the distinctions between mycorrhizae, saprobic, and parasitic fungi are unavoidably blurred.

On a functional basis, however, there are distinct characteristics for fungi that can be defined as mycorrhizal. The fungus always extends into a root or rhizoid, and outwards into the surrounding substrate. As biotrophs, the fungi must acquire C from a host. In order to be mutualistic, the fungi must also provide soil resources to the plant. Research on mycorrhizae has generally focused on those nutrients that do not move by mass flow. Yet, as soil dries out or becomes highly organic, the ability of the external hyphae to utilize organic substrates and transport water and soluble nutrients can be very important. Linking the evolutionary history and the functional structure of mycorrhizae, poses an interesting challenge. AM have endured longer than either Angiosperms or Gymnosperms. EM and other mycorrhizal variants

have evolved many times independently. Thus, while we assign a distinct suite of functions to an individual mycorrhiza, the numerous genomic combinations signify that variation will occur in both form and function. Further, by combining high fungal genomic diversity with environmental heterogeneity and the extensive connectedness of plants and fungi, there emerges a complex suite of ways in which mycorrhizae can function. Mycorrhizae, as opposed to a mycorrhiza, become a highly complex network of plants and fungi interacting through a highly diverse environment. Although we recognize that there are many mycorrhizal types, for the remainder of this chapter we focus on AM and EM, the most common types in terrestrial ecosystems.

MYCORRHIZAL FUNCTIONING: STOICHIOMETRY, RESOURCES, AND DYNAMICS

When soil resources, such as P or N, limit photosynthesis, C is in excess. Mycorrhizal fungal hyphae explore the soil volume for P and N, and transport the nutrient (over distances of cm to m) in exchange for excess plant C. Mycorrhizal hyphae are more efficient at exploring the soil volume than even fine roots. As long as P or N are limiting, plants will support mycorrhizal fungi. Even as the availability of the limiting resource shifts through time, mycorrhizal fungi similarly shift resource provisioning (11, 14, 17, 91, 92). Linking space and time is important because as resources are depleted in one patch, the mycorrhizal fungi have the capacity to explore a neighboring patch (4, 37, 73). Since a complex network of fungal mycelia and plant roots are distributed horizontally across a landscape and extend vertically into the soil and rock substrate (45, 124), resource extraction becomes dynamic.

Energy, in the form of C compounds, is the currency for exchange of soil resources. These connections occur at the (fungus) membrane: interspace: (plant) membrane interface in the form of simple sugars or amino acids. Photosynthetic rates depend on the concentrations of N (as RuBP carboxylase and other enzymes), P (for ATP, ADP), Fe and Mg (for chlorophyll), internal CO_2, and water (to keep stomates open to fix CO_2). These interactions create several important and well-known linear and curvilinear relationships (3) that form the basis of stoichiometric ratios between elements. Mycorrhizae, by increasing P and N uptake, create a C sink and enhance the photosynthetic machinery. Mycorrhizae also increase water throughput, opening the stomates. Together, these increase the rates of total carbon gain by 10% to 40% (21). In the field, this increased CO_2 fixation is associated with environmental change, such as drought (7), or as a function of particular fungal-plant species combinations (20).

By the same token, with elevated atmospheric CO_2, the demands for N and P increase creating a greater need for mycorrhizae. On the other hand, as fertilizers (directly or in the form of N deposition) are added, leaf nutrient status increases and fixed C becomes limiting. In turn, the plant allocates a smaller amount of C to roots and subsequently, the mycorrhizal fungi. In this fashion, the relative
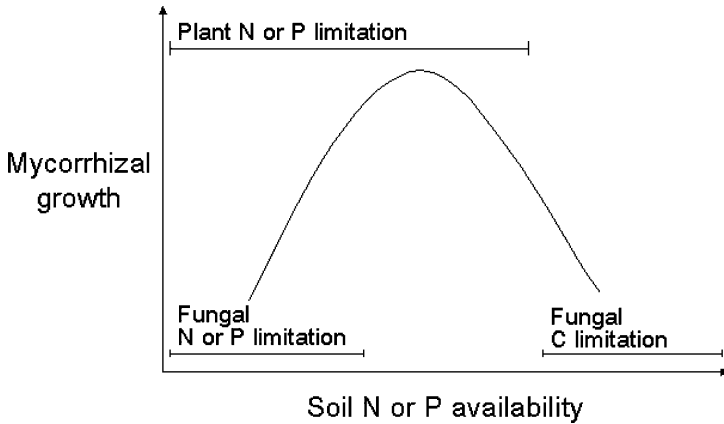
Figure 1   Interaction of nutrient versus carbon limitation on production of mycorrhizal fungi (120).

contributions of soil resources and mycorrhizae to host plant nutrition depend on the availability and uptake of resources. Additionally, if the plant is to acquire N or P from the fungus, the fungus must have an excess of both resources at the same time the plant has an excess of fixed C.

Such patterns can be described graphically (Figure 1) and reconstructed as stoichiometric ratios in the form of C:N, C:P, C:micronutrient, and so on. These ratios have been used previously to model ecosystem responses. The optimal C:N ratio for plant leaf tissue is $\sim$33:1 and $\sim$250:1 for C:P (68). For fungal hyphae, the nutrient requirements are much higher. Fungal hyphae are about 10:1 for C:N and about 20:1 for C:P (54). This differential requirement has major implications for mycorrhizal functioning and allocation of resources between plant and fungus.

Using this approach, nutrients needed by the plant that can be supplied by mycorrhizae are calculated using the feedback equations (3, 79). For example, at ambient CO_2, a plant's dry mass is 100 g and the dry mass changes to 130 g when CO_2 increases from 350 to 550 ppm [using the model of Loladze (79)]. At the same time, C increases from 50 to 65 g and foliar N concentration decreases from 3 to 2.3%. To regain N, 0.9 g N must be acquired. A similar pattern for P can also be determined. As P declines from 2 to 1.54%, requiring an additional 0.6 g P to make up the difference, we can set the stage for using C:nutrient ratios in quantifying the roles of mycorrhizae where

$$N_{plant} = \left(NO_3^-\right)_{plant} + \left(NO_3^- + NH_4^+\right)_{fungus}. \qquad 1.$$

Since C fixation is linearly related to N concentration ($C = 33*N$), we can rewrite the equation as

$$C_{plant} = [N_{plant}*33] + 33*\left[\left(NO_3^-\right)_{plant} + \left(NO_3^- + NH_4^+\right)_{excess\ fungus}\right]. \qquad 2.$$

The same equations can be constructed based on C:P, C:H$_2$O, or any limiting resource. Subsequently, a model of comparative nutrient limitations can be constructed for N:P or similarly meaningful ratios. In other examples, mycorrhizae acquire K and P to balance the high levels of Na in saline soil (12), improved Ca:Mg availability in bedrock (46), or increased Mg to increase Mg:Mn in alleviating Mn toxicity (83).

The same ratios become relevant at the ecosystem scale. N-limited versus P-limited ecosystems can delineate dominant mycorrhizal types (100). In our studies in the Yucatan Peninsula, wetland plants were more N limited and EM fungi were abundant whereas upland trees were more P limited and consistently had AM (unpublished data). Just as important, we can calculate the growth response curves for different combinations of plants and fungi. Depending on whether N, P, micronutrients, water, or another resource is limiting, maximal productivity, allocation of C from plants to fungus (i.e., fungal biomass), allocation of N and P to plants (relative growth rates, photosynthesis), and interactions between many plants and fungi can be constructed.

In the remainder of this chapter, we outline a novel approach to understanding the linkages between mycorrhizal fungal diversity, the structure of mycorrhizal communities, and resource stoichiometry to set the stage for integrating the complexity of mycorrhizal relationships in wildland ecosystems.

MECHANISMS OF RESOURCE ACQUISITION

The crucial role of mycorrhizal fungi in improving the mineral nutrition of their host plants is well established. Mycorrhizal roots take up P, N, Zn, Cu, Ni, S, Mn, B, Fe, Ca, and K from soil more efficiently than nonmycorrhizal roots, especially at low fertility levels (34, 78, 85, 116). The external hyphae of AM fungi contribute up to 80% of the P, 10% of the K, 25% of the Zn and 60% of the Cu absorbed by plants (76, 85) and 25% of plant N (85). The extraradical hyphae effectively increase the volume of soil explored for nutrients, by growing beyond the areas of nutrient depletion around the roots. The small diameter of fungal hyphae also allows them to penetrate small soil pores and access microsites that roots cannot reach (45). Hyphae can proliferate rapidly and profusely in enriched nutrient patches. EM hyphae extend away from the EM mantle and increase the total absorbing surface by several orders of magnitude, and are responsible for much of the nutrient uptake. Moreover, the kinetics of P uptake into hyphae are often characterized by high affinity at low P concentrations in the soil solution and by high maximal uptake rates (36, 69). Because of all these attributes, mycorrhizal hyphae can effectively compete with other soil microorganisms for nutrients during periodical flushes.

EM fungi often predominate in forest ecosystems where organic N predominates and amino acids and amides can be readily absorbed in intact form (1, 116). Likewise, a large part of the P in forest soils is present in organic forms such as phytates, nucleic acids and phospholipids, and EM fungi produce an array of

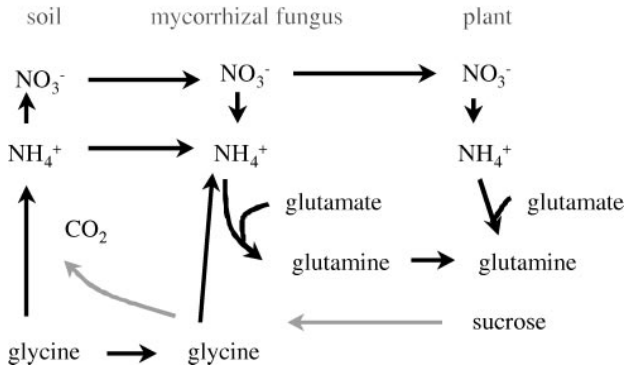# N transport and transformation

Figure 2 Forms of N transformed within and transported between soil, mycorrhizal fungi, and host plants.

phosphatases to degrade and use these compounds. Mycorrhizal fungi can also mobilize essential plant nutrients directly from minerals through excretion of organic acids such as oxalate, citrate and malate (19, 71, 74).

Nutrients are taken up by the fungus but rarely transported and transferred to the host in exactly the same form. N is an example (Figure 2). NO_3^- can be transported directly (48) but also is moved via mass flow so that direct transport is generally less important in many ecosystems. On the other hand, NH_4^+ is an important resource provided by mycorrhizal fungi but cannot be transported as NH_4^+ within the fungal tissue because it is toxic. For that reason, NH_4^+ must be converted to glutamine (NH_4^+ plus glutamate) to be translocated through the fungal tissue and transferred to the plant. This issue demonstrates the difficulty of comprehending the diverse array of responses. For example, Hobbie and associates (67) suggest that offset $\delta^{15}N$ values in sporocarps reflect fractionation. Others (55) argue that the values reflect different sources of N. In our work on oak savannah, we found an extreme range in $\delta^{15}N$ values for sporocarps with no differences between high and low N deposition areas (Table 1). We even found the same range in sporocarps associated with a single individual oak (A. Lindahl & M.F. Allen, unpublished observations). We infer that, simultaneously, fractionation and different sources are reflected in both of these numbers.

Mycorrhizal fungi can improve host plant water relations in a number of different ways (22). These include increased stomatal conductance and transpiration rates, especially under drought conditions (7), acceleration of recovery from stress, and other aspects of host drought physiology, particularly hormonal relations involving abscisic acid and cytokinins. Extraradical AM hyphae directly increase soil water uptake and transport to the host (13, 49, 60, 106). Likewise, extraradical mycelia of EM fungi play an important role in soil water absorption and transfer

TABLE 1 $\delta^{15}N$ and N concentration of sporocarps associated with different fungi from two *Q. agrifolia* forest patches (Sky Oaks Ecological Research Station and San Dimas Experimental Forest). The Sky Oaks is an undisturbed site whereas San Dimas has 30 kg/ha N deposition. The deposition increases the soil NO_3^- availability (Cario & M.F. Allen, unpublished data), but not the leaf N concentration

Species	N (mg/g)	$\delta^{15}N$
Sky Oaks Ecological Reserve		
Lactarius alnicola	41	6
Amanita rubescens	37	3
Pisolithus tinctorius	28	11
Hebeloma crustuliniforme	54	9
Amanita magniverrucata	57	7
Boletus dryophilus	45	6
Amanita calyptera	45	2
Lactarius fragilis	23	8
San Dimas Experimental Forest		
Russula macula	35	3
Cortinarius sp.	39	12
Boletus flaviporus	30	5

to their host plants (30, 75, 116). EM fungi, capable of producing extensive thick rhizomorphs such as *Rhizopogon* and *Cortinarius*, are usually the most effective at ameliorating the water status of their hosts, as these specialized fungal structures provide effective conduits for the transport of water from soil to roots over long distances.

Recent studies have shown that directional flows can also reverse. The integrity and functionality of the EM and AM external mycorrhizal mycelium in extremely dry surface soil can be sustained by direct nocturnal water transfer from their deep rooted host plants (99).

Mycorrhizal fungi acquire most or all of their C from their host plant. On average, plants allocate 10% to 20% of their net photosynthetic yield to their fungal mutualists, although this value can range from 5% to 85% (111, 119). Depending on the rates of turnover, mycorrhizae can provide up to 15% of the total organic matter biomass in forest soils (125). Between 36% to 73% more C is assimilated in mycorrhizal than non-mycorrhizal plants owing to increased photosynthetic rate in mycorrhizal plants (94). As mycorrhizal fungal tissue grows, much of that C is transferred from the host plant and allocated to the pool of live fungal tissue (20% to 29% net biomass C). A substantial amount of fungal C is allocated to the synthesis of recalcitrant compounds such as chitin (60% of the cell wall). The remaining C is respired (43% to 64% C), accumulated as fungal-specific storage carbohydrates (mannitol, trehalose) or lipids, or deposited within the rhizosphere (111).

In wildland ecosystems, a large proportion of C is deposited as either labile compounds (sugars, amino acids) that support rhizobacteria or highly recalcitrant fungal C compounds (chitin, glomalin, 30% C by weight) that persist in the soil for years to decades (103). Such recalcitrant C substrates contribute to increased soil aggregation, stability, and C storage (121), which, in turn, facilitate water-holding capacity.

The obligate fungal requirement for C may also fuel more complex fungus-plant interactions. Coexistence among fungi may be explained by the differential partitioning of C resources among fungal species. A fungal partner may also maximize its C gain by utilizing multiple plant hosts either temporally, spatially, or over successional time. On the other hand, C-based substrates (e.g., amino acids) acquired by one fungal partner may move through the mycelium and be dispersed among neighboring plants linked by a common mycorrhizal network (116). Carbon transport through hyphal networks is directed and allocated toward those plant species with the highest mycorrhizal dependency. For example, a 6% net C gain by Douglas fir seedlings was derived from the neighboring tree via mycelial connections (112). Alternatively, C substrates may be leaked into the soil by hyphae of one plant and subsequently captured by hyphae linked to a different plant or microbial opportunist (25).

The potential for root colonization corresponds to the sum of the number of new root tips, hair roots or root segments available for colonization in concert with the differential infection strategies, competitive ability, and proliferation patterns among fungal species (51, 64). For instance, the first AM taxa to invade a root is frequently the most abundant colonizer within the root, i.e., possession is nine tenths of the law (61, 62). The fastest AM colonizers (e.g., family Glomaceae) produce the most extensive colonization and fungal biomass within the root whereas the slower colonizers produce more extensive extraradical biomass (e.g., Gigasporaceae). In this fashion, spatial segregation may occur between individual fungal taxa on a root at scales ranging from microns to millimeters.

Scaling potentially maintains neighborhoods of dominant fungal species, with the simplest level of association being between a host plant and mycorrhizal fungi. The next level of complexity is where either several host plants share a single fungal species, or more commonly, several fungal species are shared among a number of host plants [three to six fungal species per root (23)]. This opens up the possibility for root colonization mediated by interspecific fungal interactions, including competition, antagonism, and dominance.

When we incorporate time with root colonization patterns, there are three key points. The first is that mycorrhizal colonization is a reflection of previous, as well as current, infection levels since C can be stored within mycorrhizal structures and subsequently reallocated to the newer infection units. Second, active root infection declines with host ontogeny since older roots are highly suberized and less conducive to mycorrhizal occupation. Third, the dimensions of root space colonized and utilized by fungi are not directly correlated to cell volume (40). For example, active arbuscules and coils average 11% and 41%, respectively, of the cell volume in onion roots colonized by species of *Glomus* or *Scutellospora*. It follows

that any factors that alter root volume, such as root age and season, potentially influence mycorrhizal colonization in a nonlinear fashion. Consequently, particular factors may increase or diminish in importance, and may switch from exerting a positive to a negative effect (or vice versa).

As new root tips provide points for new internal infections, production of new mycorrhizae and the turnover of the old both regulate C and nutrient fluxes and the complexity of interactions between fungi and plants. These vary in time, and C allocation is comprised of both standing crop and turnover. Yet continuous observations of mycorrhizal production and turnover, either in vitro or in situ, are rare. Laboratory studies by Cox & Tinker (35) and Friese & Allen (53) and field observations by K.K. Treseder and M.F. Allen (unpublished observations) reported that an AM infection unit survived ~1 week. An infection unit developed behind each root tip at 1 mm intervals, and the external hyphal absorptive network (bifurcating hyphae up to 120 cm in length) radiated outward for 6–8 cm (53). Allen (16) used these observations to construct a model of AM infections. The rate whereby new roots are formed (N_t) from past roots (N_0),

$$N_t = N_0 e^{rt}. \qquad 3.$$

The new roots (N_t-N_0) are available for infecting depending on the inoculum, and the rate of formation of new mycorrhizal units (M_t) from old (M_0) where

$$M_t = M_0 e^{rt}. \qquad 4.$$

The new mycorrhizal roots (M_t-M_0) depend on the inoculum available for infecting the newly formed tip (N_t-N_0). Both equations further respond to the rate of new root growth, which can be very rapid.

The patterning of the external mycelium can, in some cases, also be calculated because hyphae dichotomously branch to a known number of branches with decreasing hyphal diameters (53). For example, the maximum number of branches per infection unit was 8, with a 0.5 cm length per branch unit. Thus, hyphal growth has a geometrically increasing number of segments times the length of the segment as follows:

$$\text{Hyphal length (h)} = a(1) + a(2) + a(4) \ldots,$$

where a = segment length = 0.5 cm.

This simple geometric equation can be rewritten as

$$h = \sum_{1}^{n} [a(r^n - 1)]/(r - 1), \qquad 5.$$

where a = segment length = 0.5 cm, r = branch ratio = 2, and n = # branches, 1–8.

For the *Glomus* spp. studied, h = 122 cm/entry point, a maximum value very close to reported observations (53). This means that for every mm of new root (and roots can expand several cm/day), 122 cm of hyphae are formed. If roots expand at 2 cm/cm^{-3}/day, then up to 20 m of hyphae can develop based on the root growth

in a single cm^3 of soil! Luckily, each external infection unit formed and died back within about a week, the same time response observed for the infection units in the growth chamber (53) and in the field (K.K. Treseder & M.F. Allen, unpublished data). These data demonstrate that AM dynamics can be very fast, and that any C allocation estimates must include turnover as well as standing crop.

Lifespan and turnover of EM are difficult to verify because EM root tips can last for months to years (82, 107). Orlov (95) described EM tips that lasted up to three years and a group of infected root tips lasted four years. Then again, Pregitzer et al. (98) suggested that most (mycorrhizal) root tips are short-lived, and Ruess et al. (105) found that individual mycorrhizal root tips in black spruce varied in longevity depending on the time of formation. Four years of monitoring a suite of mycorrhizal root tips in *Pinus edulis* illustrated that most root tips lived only a few months. However, certain individuals lived up to 3 years, depending on their "birth" period, and the local environmental conditions (Figure 3). ^{14}C analysis confirmed that these individual mycorrhizae were up to 3 years old, and age variation among tips was largely a function of the individual species identity (K.K. Treseder, C.A. Masiello, J.L. Lansing, M.F. Allen, unpublished data). The average life span of
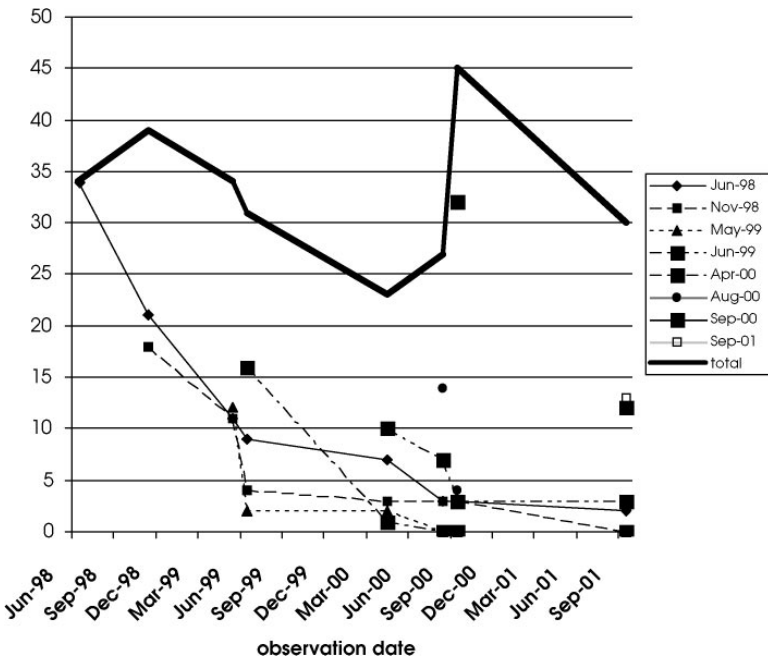

Figure 3 Relative survival of cohorts of individual mycorrhizal roots per m tube from June 1998 to September 2002 in *P. edulis* from the Sevilleta LTER site in New Mexico using mini-mycorrhitron imaging (M.F. Allen, unpublished data). Also shown are the total numbers of mycorrhizae observed.

individual rhizomorphs was 7 months (K.K. Treseder & M.F. Allen, unpublished observations). Conversely, sporocarps were always comprised of C fixed during the year of production. Since some rhizomorphs and EM root tips are relatively long-lived, the rate of root turnover in EM trees could provide an upper bound on the lifespan of these mycorrhizal structures (105).

SPECIES RICHNESS, COMPOSITION, AND DYNAMICS

The simplest measure of mycorrhizal diversity is species richness, or the number of fungal taxa present. The hierarchy of species richness per community (α-diversity), turnover (β-diversity), or landscape (γ-diversity) is used to provide linkages between the species and landscape level. Some 8 to 20 types of fungi often colonize an individual root system (α-diversity), β-diversity values typically demonstrate turnover of four to six species between communities, and landscape γ values plateau at 40 to 50 species (20). The species-area curve can be used to explore the patterns of species richness. Not surprisingly, fungal species richness increases with the area sampled owing to an increase in the spatial complexity of habitat structure. Much of the earlier influential work focused on comparative geographic studies and on patterns of nonrandom (deterministic) community assembly in a handful of fungal species that could be identified and communities. Any patterns were usually explained by simultaneous or sequential competition for resources, such as C or niche preemption.

How do cohorts of species within a species pool assemble or coalesce to form a community? Generally, mycorrhizal communities are dominated by genets of two or three species (29, 89, 109). Fungal diversity undoubtedly depends upon local disturbance and recolonization of many species, including the little known taxa. Fungal diversity patterns are also inherently complex because complexity arises from the shifting peaks of taxonomic diversity that, in turn, depend on the ecological requirements of an individual fungal species, their life-history strategies, and host associated factors. What could a different view of mycorrhizal diversity look like?

Emergent properties of a complex mycorrhizal system, such as predicting the composition of ecosystems and identifying "rules" that operate over different spatial and temporal scales, may be useful tools in identifying patterns of fungal diversity. Many coniferous forests are dominated by a single species whose roots occur within a mosaic of n mycorrhizal species. To model the diversity dynamics in this mosaic, we assume that there is a simple replacement among the n species on root tips across space and through time. Upon growth or death, fungal species 1 is replaced by fungal species 2, and so on up to species n. The rate of change in species is then

$$dX_i/d_t = -M_i X_i + M_{(i-1)} X_{(i-1)} + \ldots M_{(I-n)} X_{(I-n)}, \qquad 6.$$

where X_i is the fraction of patches occupied by species i, $X_{(i-1)}$ is the fraction of patches occupied by the preceding species in the successional sequence, and $M_{(i-1)}$ is the mortality rate for the preceding species in the successional sequence. This
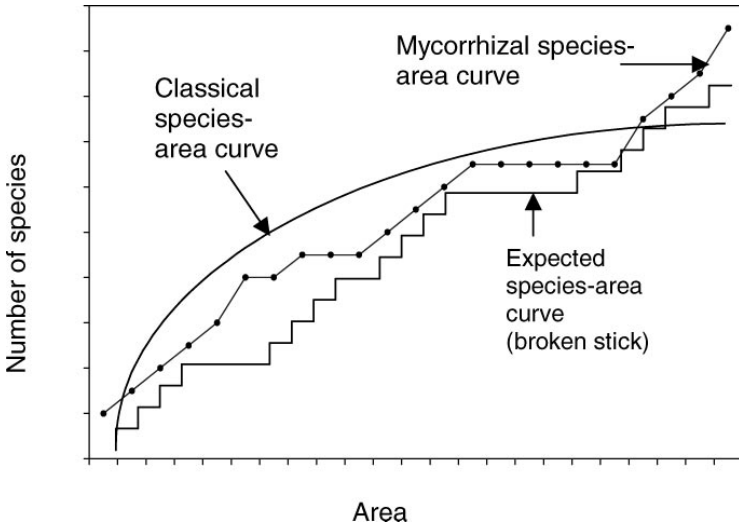
Figure 4   Species-area curves illustrating the expected (classic) model of mycorrhizal species richness approaching an asymptote versus actual species turnover (z-values) and broken-stick model (progressive inclusion or deletion of species with increasing area) of mycorrhizal species in oak woodland in California and Illinois (L. Egerton-Warbuton, unpublished data; 77).

equation can then be solved to obtain the pattern of abundance of fungal species, expressed in terms of species turnover [Figure 4 from Egerton (46); see also (77, 114)].

Fitting data to the conventional species-area relationship illustrates that the cumulative number of fungal species encountered progressively increases and then asymptotes with the area surveyed. However, reanalyzing these patterns with Equation 6 shows that the trend is in fact one towards increasing diversity with no asymptote, a phenomenon encompassed within the "broken stick" model (123). This broken stick model explains the distribution of species (as species turnover events) over time and across space. The name comes from a hypothetical stick that can be randomly broken into many pieces. The resulting pieces are of all sizes, with the majority being small and only a few being large. Small-scale changes (turnover) in fungal species composition are a common occurrence and occur on individual roots or root tips. Large-scale turnover events, on the other hand, are rare and are likely connected to major biotic or abiotic disturbances.

Clearly, if these data and results are taken as a guide, the current estimates of fungal diversity in the landscape are inherently low, the methods for describing the patterns of fungal species distribution are insufficient, and empirical evidence and theoretical argument of this relationship will be pivotal to understanding fungal community structure and functioning.

FUNCTIONAL DIVERSITY

There is a growing consensus that functional diversity, rather than species richness per se, is the major determinant of ecosystem functioning (39, 117). Functional diversity is defined as the value and range of the functional traits (characteristics relevant to ecosystem processes) of the species present in a given ecosystem. Recent studies of plant diversity and ecosystem functioning have shown that the rates and magnitudes of ecological processes are more strongly correlated with functional composition (presence of certain functional types or traits) and functional richness (number of different functional types or traits) than with the total number of plant species. This mechanistic approach might also prove fruitful if the role of mycorrhizal fungal diversity in ecosystem functioning were better understood.

The recognition of six distinct major types of mycorrhizae (e.g., arbutoid, EM, orchid, ericoid, and AM) represents the best-established structural/functional classification to date (90). However, there is a pressing need to further differentiate functional groups at a finer-grained level. Improving our understanding of mycorrhizal diversity-function relationships across ecosystems will require linking phylogeny with function (126). Mycorrhizal functional types can be defined as sets of fungal taxa showing similar effects on ecosystem processes or similar responses to environmental variables. In this respect, several attempts have been made in the past to classify mycorrhizal fungal taxa into broad guilds such as "late-stage," "early-stage," and "multistage" (38, 86), "protein," "nonprotein," and "intermediate" (1), "r" and "K" strategies (128), or based on structure (2). However, these are partial classifications that arbitrarily select only one or a just a few of the multiple functionally relevant criteria possible. The limited or nonexistent information available on the ecophysiology or even the life-history characteristics of a vast majority of mycorrhizal fungi represents a major obstacle for this analysis. Moreover, the high intraspecific variability of important physiological features observed for many fungi (31) makes generalizations difficult and further complicates a mechanistic approach. Nevertheless, we believe that the functional trait approach offers the potential to significantly further our insight into the relationships between mycorrhizal fungal community composition and the ecophysiological processes mediated by them. Outlining a tentative framework of criteria for a fine-grained functional classification of mycorrhizal taxa will, it is hoped, stimulate much needed research on the ecophysiological diversity of these fungi (Table 2).

High species richness of mycorrhizae in many ecosystems suggests a high level of functional heterogeneity even at the local scale (e.g., Table 1). According to the local niche complementarity model (118), each species possesses certain traits that allow it to utilize available resources differently and as diversity increases, each species utilizes a different component of the resource pool. Each, then, positively contributes to ecosystem function (122). However, the probability that taxa will overlap in their resource use also increases with diversity, thus creating a decelerating relationship between taxonomic diversity and ecosystem function (28).

TABLE 2   Mycorrhizal traits relevant for a functional effect classification of mycorrhizal fungi

a. Specificity of association with host plant (according to plant species and plant age/developmental stage) 1,2,3,4,5,6,7,8,9

b. Biomass and morphological/structural traits:

Size and spatial distribution of individual fungal genets 1,2,3,4,8

Total biomass per soil volume 1,2,3,4,8

Intensity of root colonization (% infection) 1,2,3,5,6,7

Characteristics of the radical phase of fungus: structure and thickness of EM fungal mantle (1,5,9), presence and abundance of AM arbuscules and vesicles (1)

Characteristics of the extraradical phase of fungus: mycelium architecture and hyphal branching and density (1,2,3,4); distance mycelium extends away from roots (1,2,3,4); relative growth rate (1,2,8); presence of cords, rhizomorphs, fans or mats (1,2,3,4); ability to proliferate in resource rich spots (1,2); hydrophilic or hydrophobic properties of mycelium (3,4)

Production/abundance of sporocarps (EM), spores or other propagules (AM and EM) (1,8)

c. Other life history traits:

Lifespan of individual fungal genets, longevity and turnover rates of mycorrhizal roots and external mycelium 1,2,4,8

Primary strategy of root colonization: spores vs. mycelial inoculum 1,2

d. Physiological/biochemical characteristics:

Enzymatic capabilities, ability to utilize organic sources of nutrients, ability to mobilize nutrients from minerals (rocks) 1,2

Ability to excrete organic acids, modify soil pH and mobilize nutrients from minerals (rocks) 1,2,4

Membrane transporters present in hyphae, differential capability and efficiency to absorb various nutrients or nutrients in different form 2

Stable isotope values of fungal tissues as measured in sporocarps (EM) or spores (AM): δ^{13}C, δ^{14}C, δ^{15}N 1,2

Metabolic rate and nutrient uptake efficiency (carbon invested in fungus per nutrient gain for host plant) 1,2

Nutrient immobilization in fungal tissues: nutrient requirements of fungus, nutrient concentration of fungal tissue, proportion of labile/recalcitrant components in hyphae (C:N ratios, etc.) 1,2,4,8

Saprotrophic capabilities (ability to obtain carbon from sources different from host plant) 1

Production of antibiotics, phenolics or other secondary metabolism compounds 1,6,7,8

Production of phytohormones 1

Production of heavy metal chelating compounds 9

Enzymatic capability to degrade toxic organic compounds (biotic or xenobiotic) 1,9

Exudation of organic materials to the hyphosphere 1,4,8

Some relevant traits for a functional response type classification of mycorrhizal fungi

a-Optima and tolerance range for seasonally fluctuating or spatially heterogeneous abiotic factors: soil temperature, moisture, pH, depth, organic matter content, nutrient concentration, soil texture, etc.

b-Competitive ability against other mycorrhizal fungi (competition for roots or for soil resources)

c-Competitive ability against saprotrophic fungi or soil bacteria (competition for soil resources)

d-Vulnerability/adaptability to natural or anthropogenic disturbance: grazing by fungivores, animal burrowing, tillage, fire, logging, mining, increasing levels of elevated CO_2, nitrogen deposition, heavy metal contamination, etc.

Numbers indicate functions that can be most directly influenced by each trait (there are all sorts of possible feedbacks determining indirect influence too). Some functions of mycorrhizae in ecosystems. 1: plant carbon sink; 2: soil nutrient uptake and transfer to plants; 3: soil water uptake and transfer to plants; 4: effects on soil physical-chemical properties and carbon sequestration; 5: plant protection against pathogens; 6: plant protection against herbivores; 7: production of phytohormones; 8: food source for other organisms; 9: plant protection against toxic compounds. Functions are scale dependent: other ecological functions, such as influence on plant growth (individual level) and primary productivity (ecosystem level) are "hierarchically higher" and integrate some of the above.

A degree of functional redundancy may exist in mycorrhizal fungal communities, with many species likely performing roughly similar ecological functions (10). A few morphotypes usually make up the bulk of the EM root tips present in a given tree stand, while there is a long tail of relatively infrequent morphotypes (20, 68). It is reasonable to assume that the dominant fungal species are the most functionally relevant and account for most of the fungal biomass, nutrient uptake, and C cost to the plant. Walker and colleagues (126) argued that the small number of dominant species in any given ecosystem tend to differ functionally, resulting in niche separation. Alternatively, the numerous minor species [subordinates or transients (59)] are largely functional equivalents of the dominant ones, but with different environmental requirements and tolerances. Minor species contribute to ecosystem resilience in the face of changing environmental conditions, since they are functional analogues of the dominants that are capable of replacing them should they decline ["insurance effect" (80)]. The validity of this hypothesis remains to be specifically tested for mycorrhizal fungal communities, but it seems plausible.

The criteria selected for developing a functional categorization of mycorrhizal fungi may vary depending on the particular focus and scale of interest. Therefore, no single classification of functional types can pretend to be universally valid across scales and ecosystems but we suggest that many approaches are appropriate depending on the particular environment of interest.

INTEGRATING DIVERSITY AND FUNCTIONING: GENERATING COMPLEXITY

Two issues underlie the integration of diversity and function. First, soil resources tend to limit plant growth. No additional C can be fixed if water, N, or P cannot be acquired in sufficient quantities. Even in rich soils, as plant numbers increase per unit soil, resources per plant decline (5). Second, mycorrhizae alter the competitive outcomes between mycorrhizal plants (50, 65, 84, 93, 115), and between mycotrophic and nonmycotrophic plants (6, 8). A variety of mechanisms contribute to these outcomes. These can be competition for nutrients or, in some cases, direct parasitism of one of the competitors (18). High soil N or P fertility also exerts a net negative C balance that can reduce plant growth (47, 70). The proposal of redirected resources via an interconnected mycelium remains controversial (89, 101). Clearly, C, N, and P can be added to one plant and detected in another. However, the quantities transferred are usually very small (<1%), or occur in specialized ecological [N from N-fixers to nonfixers (26, 48)] or edaphic circumstances [C between sun and shade plants (112)]. Both Bever et al. (27) and Golubski (58) demonstrated theoretically the conditions under which negative feedbacks between plant and fungi can persist. Relative scaling differences between plant and fungi can also allow for persistence of less effective mycorrhizal fungi, or "cheaters" (15).

Are there other mechanisms that can change these outcomes as well? Maurer (87) used a linear matrix approach based on linear equations to evaluate community-level interactions between populations of predators and prey, or among

competitors. This approach can be readily adopted when resources provided by different entities are additive. Based on functional groupings of fungi (Table 2), let us return to Equation 1, where NO_3^- and NH_4^+ are provided by the plant and one mycorrhizal fungus, respectively. One fungus may be adept at acquiring NH_4^+ by scavenging a large spatial area (e.g., *Thelephora terrestris* or *Pisolithus tinctorius*). If organic N is also predominant, a second may be adept at acquiring organic N (e.g., *Hebeloma crustuliniforme*, *Lactarius subdulcis*, *Amanita rubescens*, *Suillus bovinus*) (Table 2) (33). In this case, the equation expands to

$$\text{Plant N} = \left(\left[NO_3^-\right]_{plant}\right) + \left(\left[NO_3^-\right]_{fungus} + \left[NH_4^+\right]_{fungus} + \left[N_{org}\right]_{fungus}\right). \qquad 7.$$

If we add different resources, such as P in its organic and inorganic forms, we express them in additive form. We can combine the values of the nutrient availability functions into an overall matrix that represents plant productivity as a sum of the nutrient contributions of the fungi to plant growth and exchange of C from plant to fungus. Defining a matrix, P, as a function of nutrients available to the plant, the contribution of each organism (plant $+ n$ fungi) can be summed in an overall matrix, P:

$$\text{plant growth}, P = \begin{bmatrix} NO_{3_{pl}} & P_{i_{pl}} \\ NO_{3_{f1}} + NH_{4_{f1}} & P_{i_{f1}} + P_{o_{f1}} \\ NO_{3_{f2}} + NH_{4_{f2}} + N_{org_{f2}} & P_{i_{f2}} \end{bmatrix} = \begin{bmatrix} N_{pl} & P_{pl} \\ N_{f1} & P_{f1} \\ N_{f2} & P_{f2} \end{bmatrix}, \qquad 8.$$

where plant $= pl$, fungal species 1 $= f1$, fungal species 2 $= f2$.

To observe the effect of adding each species of mycorrhizal fungi to a plant, we can express the additive effects of each species as a vector:

$$\text{productivity}_{plant} = f(p) = \begin{bmatrix} \sum_{j=1}^{2} P_{1,j} \\ \sum_{j=1}^{2} P_{2,j} \\ \sum_{j=1}^{2} P_{3,j} \end{bmatrix} = \begin{bmatrix} Tot_{pl} \\ Tot_{f1} \\ Tot_{f2} \end{bmatrix}, \qquad 9.$$

where *Tot* represents the total contribution of each organism to plant productivity.

The nutrient contribution matrix can be expanded indefinitely, depending upon the number (n) of fungi connected and the number (j) of limiting nutrients—including water and C—that we choose to include.

$$P = \begin{bmatrix} N_{pl} & P_{pl} & C_{pl} & \cdots & nutrient\ j_{pl} \\ N_{f1} & P_{f1} & C_{f1} & \cdots & nutrient\ j_{f1} \\ N_{f2} & P_{f2} & C_{f2} & \cdots & nutrient\ j_{f2} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ N_{fi} & P_{fi} & C_{fi} & \cdots & nutrient\ j_{fi} \end{bmatrix}. \qquad 10.$$

Utilizing this framework, we can construct a model based on a few of the known mechanisms to describe the effects of increasing the complexity of a mycorrhizal community and the consequent effects on plant productivity. To constrain the complexity of the model, rather than describing the contributions of individual fungi, we can employ a physiological functional-effect framework and construct the model based on three functional groups of fungi: (*a*) AM fungi; (*b*) EM fungi capable of utilizing inorganic compounds (EMi) fungi; and (*c*) EM fungi capable of utilizing organic material, (EMo) fungi. We can also summarize micronutrients into a generalized category, Mic, and restrict the model to a set of nutrient substances that are of particular relevance to mycorrhizal exchange: nitrogen ("N"–total of NO_3^-, NH_4^+, and organic N); phosphorus ("P"–total of Pi and Po); micronutrients ("Mic"–K, Mg, Fe, etc.); water ("W"); and carbon ("C").

To quantify the stoichiometry in terms of a common currency, we can make the simplifying assumption that there is a common unit (e.g., ATP) for the relationships between the values for each resource contribution. We can then define the inputs to the model as relative contributions to plant productivity. In other words, the plant alone is able to take up 1 unit of each of the nutrients and lose 0 units of C, summing to a productivity value of 4 in the absence of fungal symbionts:

$$\text{Plant} = [1 \quad 1 \quad 1 \quad 1 \quad 0]$$
$$f(plant) = 4. \tag{11.}$$

The array of contributions of a given fungal functional group, such as the "EMo" fungi, is constructed from the contributions/drains of each fungal species in the group. For example, if we have *n* species of AM fungi, we can express the contributions of the AM functional group:

$$AM_{tot} = \begin{bmatrix} N_{AM1} & P_{AM1} & Mic_{AM1} & W_{AM1} & C_{AM1} \\ N_{AM2} & P_{AM2} & Mic_{AM2} & W_{AM2} & C_{AM2} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ N_{AMn} & P_{AMn} & Mic_{AMn} & W_{AMn} & C_{AMn} \end{bmatrix}, \tag{12.}$$

which can be expressed as averaged contributions to productivity:

$$AM_{tot} = \begin{bmatrix} \dfrac{\sum_1^n N_{AM}}{n} & \dfrac{\sum_1^n P_{AM}}{n} & \dfrac{\sum_1^n Mic_{AM}}{n} & \dfrac{\sum_1^n W_{AM}}{n} & \dfrac{\sum_1^n C_{AM}}{n} \end{bmatrix}. \tag{13.}$$

The row vector consisting of the average of the elements in each column of the functional group matrix can then be incorporated into the overall plant productivity matrix, *M*, whose successive rows represent first the plant without fungi and then the contributions of additional fungal functional groups:

$$M = \begin{bmatrix} N_{pl} & P_{pl} & Mic_{pl} & W_{pl} & C_{pl} \\ N_{AM} & P_{AM} & Mic_{AM} & W_{AM} & C_{AM} \\ N_{EMi} & P_{EMi} & Mic_{EMi} & W_{EMi} & C_{EMi} \\ N_{EMo} & P_{EMo} & Mic_{EMo} & W_{EMo} & C_{EMo} \end{bmatrix}. \qquad 14.$$

Summing each row produces a 4-row × 1 column vector representing the total contributions to plant productivity supplied by each category of organism:

$$Q = \begin{bmatrix} \sum_{j=1}^{5} M_{1,j} \\ \sum_{j=1}^{5} M_{2,j} \\ \sum_{j=1}^{5} M_{3,j} \\ \sum_{j=1}^{5} M_{4,j} \end{bmatrix} = \begin{bmatrix} Pl_{tot} \\ AM_{tot} \\ EMi_{tot} \\ EMo_{tot} \end{bmatrix}. \qquad 15.$$

We can then define a function, $R = f(Q, a, b, c)$, where the arguments a, b, and c represent the row subscripts of the fungal functional groups (Table 2). Note that fungal groups begin with row 2, therefore the values for a, b, and c will be chosen from the set [2, 3, 4]. This function produces the successive sums of row 1 (plant alone) with rows a, b, and c in a cumulative matrix:

$$R = \begin{bmatrix} Q_1 \\ Q_1 + Q_a \\ Q_1 + Q_a + Q_b \\ Q_1 + Q_a + Q_b + Q_c \end{bmatrix}. \qquad 16.$$

The row number arguments to this function allow us to compare the contributions of differing combinations of mycorrhizal functional groups added in different sequences to the overall productivity of their associated plant(s). Row 1 of R represents the productivity of the plant alone; row 2 represents the productivity of the plant plus one fungal functional group, a; row 3 represents the plant plus two functional groups, a and b; and row 4 represents the plant plus all three functional groups. By specifying the sequence of row numbers specified by a, b, and c in $f(X, a, b, c)$, we can calculate all combinations of the plant and one, two, or three functional groups of mycorrhizal fungi (Table 3).

This phytocentric model represents availability to the plant. The C column of the matrix represents a drain from plant to fungus and will therefore be zero for the plant alone and a negative value for addition of any mycorrhizal group. This is also an additive model—an assumption that requires closer examination. As presented here, this model does not describe the stoichiometric coupling between resource availability and capacity of mycorrhizae to make nutrients available to the plant.

TABLE 3   Stoichiometric model of mycorrhizal nutrient exchange

	a	b	c
	AM	EMi	EMo
	AM	EMo	EMi
A.	EMi	AM	EMo
	EMi	EMo	AM
	EMo	AM	EMi
	EMo	EMi	AM

B. * (a) $f(M_1, 2, 3, 4) = \begin{bmatrix} 4 \\ 5.8 \\ 6.3 \\ 8.3 \end{bmatrix}$ (b) $f(M_1, 2, 4, 3) = \begin{bmatrix} 4 \\ 5.8 \\ 7.8 \\ 8.3 \end{bmatrix}$ (c) $f(M_1, 3, 2, 4) = \begin{bmatrix} 4 \\ 4.5 \\ 6.3 \\ 8.3 \end{bmatrix}$

(d) $f(M_1, 3, 4, 2) = \begin{bmatrix} 4 \\ 4.5 \\ 6.5 \\ 8.3 \end{bmatrix}$ (e) $f(M_1, 4, 2, 3) = \begin{bmatrix} 4 \\ 6 \\ 7.8 \\ 8.3 \end{bmatrix}$ (f) $f(M_1, 4, 3, 2) = \begin{bmatrix} 4 \\ 6 \\ 6.5 \\ 8.3 \end{bmatrix}$

C.   (a) $f(M_2, 2, 3, 4) = \begin{bmatrix} 4 \\ 5.8 \\ 5.8 \\ 7.8 \end{bmatrix}$ (b) $f(M_2, 3, 2, 4) = \begin{bmatrix} 4 \\ 4 \\ 5.8 \\ 7.8 \end{bmatrix}$

D.   (a) $f(M_3, 2, 3, 4) = \begin{bmatrix} 4 \\ 5.8 \\ 5.3 \\ 7.3 \end{bmatrix}$ (b) $f(M_3, 4, 3, 2) = \begin{bmatrix} 4 \\ 6 \\ 5.5 \\ 7.3 \end{bmatrix}$

A: Sequential additions of three functional groups of mycorrhizal fungi: arbuscular mycorrhizal fungi, AM; endomycorrhizal fungi capable of making inorganic nutrients available to the host plant, EMi; and endomycorrhizal fungi capable of making organic nutrients available. *B*: All output vectors from $f(M_1, a, b, c)$ where M_1 is the input matrix of nutrient availability contributions (see text for full explanation of matrix). Values represent relative contributions to plant productivity. Each row of the output vectors represents successive combinations of plant alone (row 1); plant plus the first fungal group (row 2); plant plus first and second fungal groups (row 3); and plant plus all fungal groups (row 4). C: Selected output vectors from $f(M_2, a, b, c)$. In (a), $a =$ AM fungi, $b =$ EMi fungi, and $c =$ EMo fungi (see text for explanation of functional groups). In (b), $a =$ EMi fungi, $b =$ AM fungi, and $c =$ EMi fungi. Values and rows are as in B. D: In (a), $a =$ AM fungi, $b =$ EMi fungi, and $c =$ EMo fungi. In (b), $a =$ EMi fungi, $b =$ EMo fungi, and $c =$ AM fungi. Values and rows as above.

However, even such a simple model can begin to illustrate how the complexity of a mycorrhizal community can have unexpected results as a consequence of the interactions between the constituent organisms.

For example, assume that the summary matrix, *M*, were filled with the following values based on the flow of values from individual species × nutrient arrays:

$$M_1 = \begin{bmatrix} N_{pl} & P_{pl} & Mic_{pl} & W_{pl} & C_{pl} \\ N_{AM} & P_{AM} & Mic_{AM} & W_{AM} & C_{AM} \\ N_{EMi} & P_{EMi} & Mic_{EMi} & W_{EMi} & C_{EMi} \\ N_{EMo} & P_{EMo} & Mic_{EMo} & W_{EMo} & C_{EMo} \end{bmatrix} = \begin{bmatrix} 1 & 1 & 1 & 1 & 0 \\ 1 & 0 & 1 & 0.8 & -1 \\ 0 & 1 & 0 & 0.5 & -1 \\ 1 & 0 & 1 & 1 & -1 \end{bmatrix}. \quad 17.$$

This matrix represents a plant that is able to take up 1 unit each of the necessary nutrients for photosynthesis and growth. AM fungi can increase the N and micronutrient supply to the plant by 1 unit each, add 80% more water availability, and draw 1 unit of C in exchange. The EMi fungus increases P uptake by 1 unit, water uptake by 50%, and draw 1 unit of C. EMo fungi add similar benefits as the AM fungi. Although these values are hypothetical, they reflect some realism in terms of what each functional group can provide to the host.

For example, setting $Q = M_1$, $a = 2$ (AM), $b = 3$ (EMi), and $c = 4$ (EMo), into $f(Q, a, b, c)$ we get the output vector

$$M_1 = \begin{bmatrix} plant\ alone \\ plant + AM \\ plant + AM + EMi \\ plant + AM + EMi + EMo \end{bmatrix} = \begin{bmatrix} 4 \\ 5.8 \\ 6.3 \\ 8.3 \end{bmatrix}. \qquad 18.$$

By plugging all combinations of rows 2, 3, and 4 into $f(M_1, a, b, c)$, we can explore all combinations and sequences of addition of fungal functional groups based on M_1 (Equation 17) and the consequent effects on plant productivity (Table 3B). Examining the first three rows of each vector, it is clear that the addition of one or two functional groups (rows 2, 3, or 4) has very different consequences for plant productivity, depending on the combination or sequence of addition. This is a phenomenon related to the notion of "assembly rules" (24, 41–43) and is somewhat analogous to a successional sequence. In this case, all sequences of addition result in successive increases in plant growth, and as would be expected, the total effect of all three functional groups (row 4) is consistent across all ordered sequences of mycorrhizal addition. Differences in various combinations of functional groups and assembly order are illustrated graphically in Figure 5A. This type of output can be illustrated in the classic studies of van der Heijden et al. (122) and the variations described by Hart et al. (63).

When the initial input matrix is varied—even only slightly, this model produces interesting outcomes, suggesting that the addition of an additional fungal functional group is not always advantageous to the plant. For example, we can alter the micronutrient contribution of the EMi group from 1, as in M_1, to 0 in M_3, or alternatively change the carbon drain of the EMi group from -1 to -1.5:

$$M_2 = \begin{bmatrix} 1 & 1 & 1 & 1 & 0 \\ 1 & 0 & 1 & 0.8 & -1 \\ 0 & 1 & 0 & 0.5 & -1.5 \\ 1 & 0 & 1 & 1 & -1 \end{bmatrix} \qquad M_3 = \begin{bmatrix} 1 & 1 & 1 & 1 & 0 \\ 1 & 0 & 1 & 0.8 & -1 \\ 0 & 0 & 0 & 0.5 & -1 \\ 1 & 0 & 1 & 1 & -1 \end{bmatrix}. \qquad 19.$$

Such differences in input matrices would be expected if the species composition within the groups differed for a particular locale or "snapshot" moment in succession. Certain output vectors are worth noting (Table 3; Figure 5). In each of the output vectors of M_2 (Table 3C), addition of an additional fungal group at one
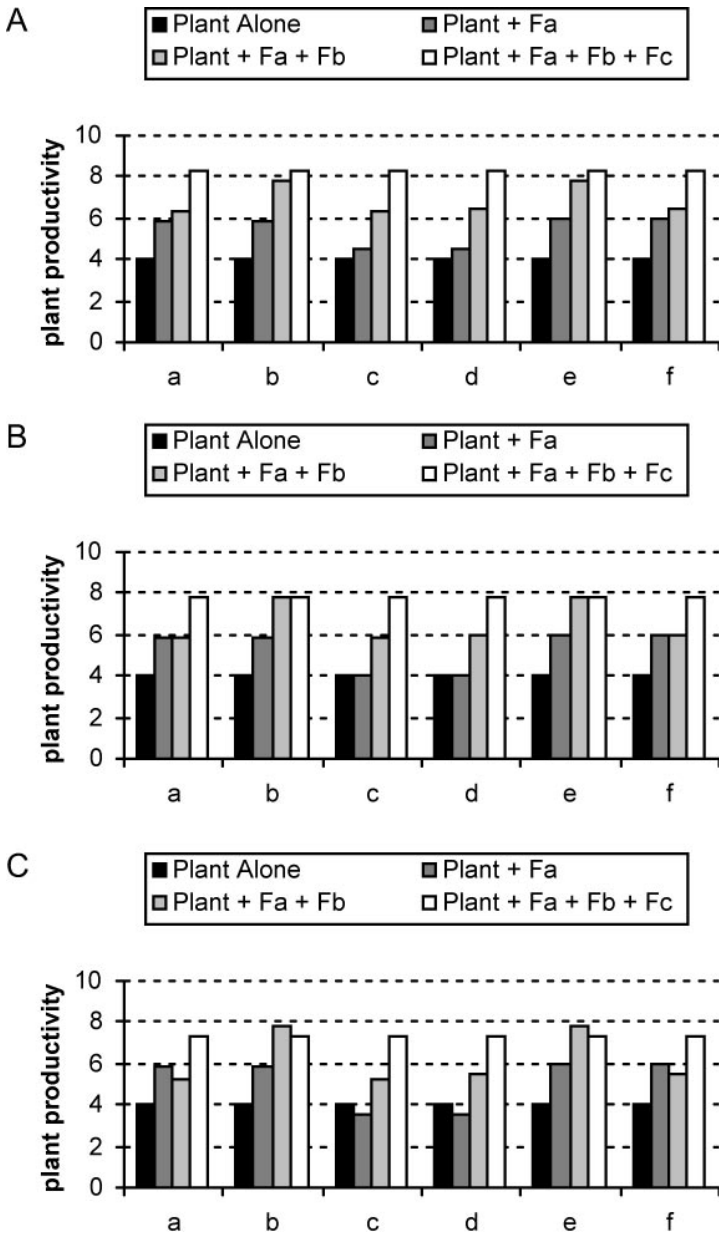
Figure 5   Matrix model results: output from $f(Q, a, b, c)$, where Q is the input matrix and a, b, and c are row numbers of Q (see text for full explanation of input matrix). Bars represent relative plant growth. (*A*) Q = M1; (*B*) Q = M2; (*C*) Q = M3. In each graph, the x-axis categories represent differing sequences of functional group additions: a—2, 3, 4; b—2, 4, 3; c—3, 2, 4; d—3, 4, 2; e—4, 2, 3; f—4, 3, 2.

point in the sequence does not increase plant productivity (Figure 5*B*). In each of the output vectors of M_3 (Table 3*D*) addition of a second fungal group to the plant plus a single fungal group actually decreases plant productivity (Figure 5*C*).

Is this result possible? Each of these variations (inputs M_1, M_2, and M_3) reflects differing stoichiometric relationships between fungal functional groups, plant physiology, and availability of soil nutrients. Not surprisingly, the outcomes of this simple model concur with experimental results and observations. One example, in a study in a Great Basin shrubland, M.F. Allen & E.B. Allen (Figure 6) (102) found that whole soil inocula (for two sites, two populations of plants) tended to have either intermediary or inhibitory growth effects on *Artemisia tridentata* compared with individual species inocula of *Acaulospora elegans*, *Scutellospora calospora*, or *Glomus deserticola*.

Further exploration of the inputs to this model will begin to illustrate the relationships between functional groups or of individual species of mycorrhizal fungi, and the dynamics of their interactions—in other words: "Who is doing what?" By filling these input matrices with values that are consistent with ecological stoichiometry, and employing a mass-balance approach [see section on Feedback Loops and Stoichiometry (79)], a more sophisticated implementation of this model should contribute to our understanding of the complex effects that mycorrhizal fungal community composition, assembly sequence (i.e., succession), and response to environmental change have on plant productivity. In particular, we should be
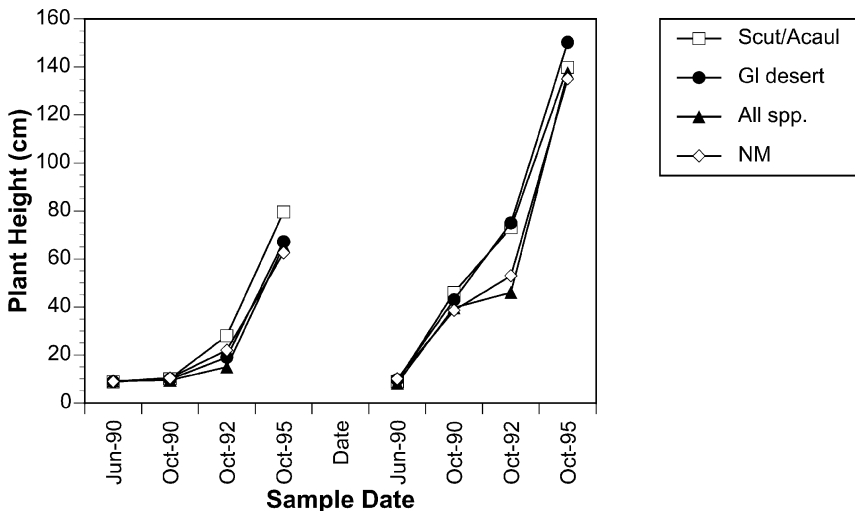
Figure 6   Sagebrush growth response to mycorrhizal fungal inocula after benomyl treatment of soil in a reciprocal transplant experiment (102). Note the comparative decrease in relative plant growth rate after three growing seasons (October 1992) in both nonmycorrhizal and all-species treatments. Data shown are for local plants and fungi only (i.e., San Diego plants with San Diego fungi, Reno plants with Reno fungi).

able to make predictions about mycorrhizal community response to local conditions on the continuum from nutrient-rich (CO_2-limited) to nutrient-poor (e.g., N-limited, CO_2-enriched) conditions. These simple models demonstrate that interactions among functional groups of mycorrhizal fungi can generate complex behavior. Numerous studies of AM on P uptake, or EM on N uptake, show a high degree of variation that can be readily and simply modeled.

METACOMMUNITY DYNAMICS

A growing body of literature examines the effects of the spatial dynamics of metacommunities on the growth and extinction of local populations or of species within local communities (52, 127). A metacommunity is a population of communities, each open to others through varying degrees of connectivity, from zero connection to complete connection.

Because local mycorrhizal communities contain a network of complex interactions among plant roots, mycorrhizal and fungi, and other organisms, their overall "behavior" (i.e., population growth or extinction and therefore community composition and function) can be expected to run the gamut from static to complex to chaotic. Given that nature is not static, nor could we expect life to survive if nature were completely unpredictable or chaotic, there is good reason to believe that mycorrhizal systems probably display many of the attributes of complex systems (72, 96, 97). Such systems are characterized by sensitivity to initial conditions, self-similarity in some form (e.g., fractal patterns of hyphal branching; "broken-stick" species-area relationship) or periodic patterns.

Sensitivity to initial conditions may create the limits of mycorrhizal diversity. Restated, small differences in conditions at time 0 can lead to large differences at time t. This phenomenon is sometimes referred to as the "butterfly effect," based on an untested suggestion that the flap of a butterfly's wings in one part of the world may profoundly alter the severity of weather in another region some months later (57, 81). This sensitivity is deterministic in the sense that any identical set of conditions will always produce the same outcome. However, there is no way to determine the consequences of a set of conditions that lies between two such precisely described initial states (88). This means that tiny initial differences in species composition within local communities could produce large differences in community composition. These differences have important functional and evolutionary consequences, and determine α- and β-diversity.

For example, we would postulate that fungal species composition at the scale of individual trees varies. However, patches at this scale are largely repeatable communities across the landscape. The richness of EM communities associated with three species of *Quercus* spp. grown in a *Quercus agrifolia* (coast live oak) savanna demonstrate 64% to 75% similarity (Sorenson's index of morphotype, RFLP data), even under widely spaced trees. In addition, the richness of EM fungi associated with *P. edulis* increased with the number of trees sampled but did not reach an

asymptote. Instead, a few new species (turnover) were added (and lost) with each tree sampled (J. Lansing & M.F. Allen, unpublished observations; 56, 77).

Complex interactions within metacommunities can result in unexpected results at the larger community scale (127). Theoretically, any amplification of species divergence between patches in concert with a decrease in diversity within local communities may increase diversity at the metacommunity scale. Thus, the scale at which they are made drastically affects field measurements of diversity. For example, richness averaged 10 morphotypes per seedling in a *Quercus agrifolia* savanna in one growing season. In another site (Camp Pendleton, California), 58 species of EM fungi were collected in 900 m^2 plots over a four-year period. Because the scale and sampling techniques were dramatically different, the measures of richness cannot directly be compared. But z-values were calculated for each site because they are independent of sample size [z = species turnover, or β diversity, where s = ca^z (104)]. For oak seedlings, z = 0.57 (r^2, 0.96) compared favorably with z = 0.58 (r^2, 0.975) for sporocarp diversity. Such congruence suggests that richness of fungal metacommunities is relatively similar across a very large region. Thus, if there is a degree of connectivity between patches, measurements taken at a particular moment might not accurately reflect diversity. The numerical aspects of complexity in mycorrhizal fungal communities must be addressed in order to understand how the pieces fit together into viable, recognizable communities.

COMPLEXITY AND FUNCTIONING

We can define the spatial scale of a patch in terms of a single plant and its associated mycorrhizal fungi, or multiple plants connected by a single fungal species. In both cases, dispersal, hyphal exploration, and networking could then be modeled and tested to determine the degree to which they might significantly affect diversity and function within local communities and across the larger scale of a metacommunity.

Models in which spatially defined patches function as the independent agents can be constructed as direct analogs of metacommunities. Each patch within a grid of patches responds to its neighbors through a set of transition rules to determine its state in the next iteration of the simulation. Traditionally, these transition rules are kept simple, but even simple rules can result in complex or even chaotic behavior. However, it should also be possible to employ a more complex model such as we have described above as the set of transition rules. Specifically, variation in community composition among patches would result in varying degrees of plant productivity, as expressed through our matrix model. In turn, plant productivity and the stoichiometry of nutrient availability within individual patches would affect the state of adjacent patches through transition rules that model plant and fungal dispersal and the flow of nutrients between patches—either through abiotic leakiness or as a function of fungal facilitation of connectivity between patches. This effort would start to integrate a high diversity of mechanisms with a high richness of organisms.

Allen and colleagues (9) provide a good example of observed successional patterns that need to be modeled to describe the temporal effects of community complexity. In this study, a site in the Yucatan was cleared and burned in a manner simulating the fires that had swept through the region following escape from swidden agriculture. In this example, we set three initial conditions. First, no mycorrhizae were added. Second, trees were inoculated with early seral AM fungi (consisting of only small-spored *Glomus* spp.) from soils of the adjacent early plant seral stages (2 years following a fire). Finally, trees were started with late-seral fungi inoculum of AM fungi from the nearby late-seral forest. The late-seral inoculum contained a diverse array of fungi (up to 45 distinct taxa). These initial conditions had surprising effects on the subsequent plant growth. The plants inoculated with early seral AM fungi grew best, followed by either no inoculum (for early seral plants) or late-seral inoculum (for late seral plants). When fungi were taken out of their seral-state context, growth reductions occurred. But as the species composition began to converge following reinvasion from the nearby forest, the relative growth rates of the plants became similar.

Another example exists where succession is characterized by species invasions with each seral stage being dominated by different combinations of plant and fungal species. Helm et al. (66) studied the growth of transplants into different field seral stages at the Exit Glacier in Alaska. Richness of EM fungi varied for each of the different plant species depending on the seral stage of the patch into which they were planted. However, in no case did the growth, vigor, or % N relate to the richness of morphotypes of associated EM fungi (Figure 7).
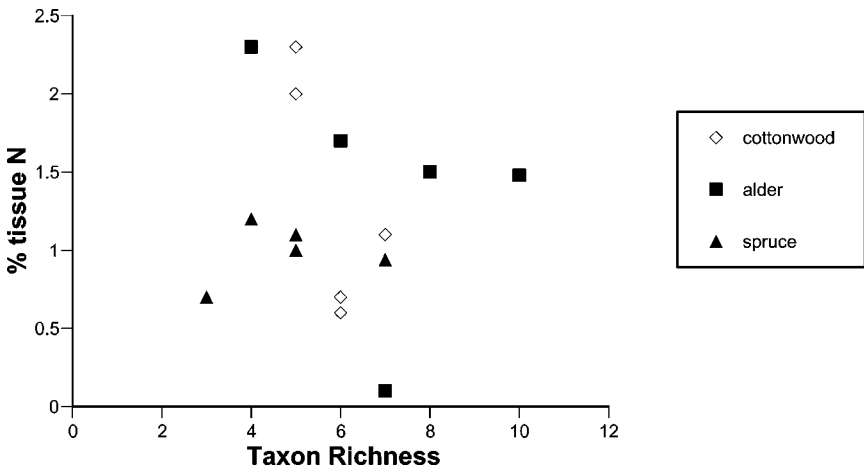
Figure 7   Absence of relationship between ectomycorrhizal species richness and leaf nitrogen content of associated plants at a field site near Exit Glacier, Alaska (66). N content (%) of leaf tissue in cottonwood (*Populus balsamifera*), alder (*Alnus sinuata*), and spruce (*Picea sitchensis*) as a function of EM morphotype richness.

CONCLUSION

In this chapter, we have presented a brief description of the array of mechanisms whereby mycorrhizae influence plant growth and fungal persistence, or substitute for fitness, in both partners. We have also presented an overview of the incredible number of taxon combinations that result in mycorrhizal symbioses and examined how that diversity might be structured. Not every taxon carries out each mechanism. To determine which combination of organisms and functions, we need a great deal more information on who the players are. Consequently, more physiological and molecular research will be required to expand upon the known mechanisms. With this, also comes a need to organize mycorrhizae into functional units. By creating simple matrix equations, we provide some examples of how diversity can interact with functional groups to change the growth of plants. Finally, we provide some examples from our own research ranging from molecular interactions to field community/ecosystem experiments that result in outcomes that are unpredictable based on a simple "mycorrhizal" response.

The equations described in this overview represent our initial foray into understanding the incredible diversity of responses that our experiments have created. These equations alone can generate considerable complexity in the response at the community level. The combination of numerous mechanisms of interaction and multiple partners creates a situation in which the responding fitness of plant and fungus depends on both the initial conditions and the subsequent invasions into occupied space by either fungus or plant. However, at this stage, our hypotheses of response complexity remain based on linear models. The problem with this approach is the assumption that all mycorrhizal interactions are additive or subtractive but the outcome always changes linearly with the composition and resource availability. The next step is to determine if these interactions are always linear, or if nonlinear interactions, such as thresholds, may also play an important role. In other words, is there predictability beyond the number and direct physiology of the players? Are there limits to mycorrhizal costs and benefits such that both diversity and functionality approach a definable limit? In fact, responses of plant communities to mycorrhizae show surprising convergence and divergence that cannot readily be explained by linear responses alone.

Some examples exist. Comparative growth response studies of oak seedlings in the greenhouse showed AM increased the growth of oak seedlings compared with no mycorrhizae (44). EM increased the growth even more than AM. However, when AM and EM were simultaneously added, seedling growth was lower than the nonmycorrhizal controls. Something in the interaction triggered a strong negative interaction that we did not predict. We are finding challenges in sustaining and restoring natural vegetation in the face of unique environmental change. The natural world has not experienced simultaneous global N deposition (reducing mycorrhizae) and elevated atmospheric CO_2 (enhancing mycorrhizae). In this context, we suggest that the linking of diversity and function is essential to exploration

into overall mycorrhizal functioning. The simple linear matrix modeling is only an initial step in this direction, and we hope that future mycorrhizal researchers will be able to integrate both a mathematical and experimental framework to explain how this complex symbiosis works in the world of agriculture and natural resource management.

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