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## **Mycorrhizal Fungi in Successional Environments: A Community Assembly Model Incorporating Host Plant, Environmental, and Biotic Filters**

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### **7.1 INTRODUCTION**

Succession in plant communities, and associated mycorrhizal fungi, can be defined as a “directional change in the composition, relative abundance, and spatial pattern of species comprising communities” (Frankland, 1992, 1998). In other words, component species replace one another as the dynamic communities change in space and time, and each species is adapted to the occupation of particular niches within the successional seres. A number of model systems have sought to follow the succession of mycorrhizal fungi. We will briefly review examples of those for background and, in turn, introduce our proposed conceptual model.

Observations of the plant colonization in successional seral environments have indicated that nonmycorrhizal or facultatively mycorrhizal plants are often first to establish in severely disturbed sites (Allen et al., 1987; Allen, 1988, 1991). There appears to be a continuum of mycorrhizal dependency along successional gradients. Nonmycorrhizal and facultatively mycorrhizal plants tend to occur and dominate in highly disturbed ecosystems. In turn, these are replaced by obligately arbuscular mycorrhizal (AM) plants, followed by ectomycorrhizal (EM) plants and ultimately ericoid mycorrhizal plant species (Read, 1989,

1992). Plant establishment thus follows a predictable pattern toward communities with a greater dependence on mycorrhizal fungi with different characteristics in their resource use, especially nitrogen (N) and phosphorus (P).

Using coastal sand dunes as a model system, Read (1989) related plant and mycorrhizal community succession to changes in soil conditions. The proportion of obligately mycorrhizal plants was found to increase with decreasing soil base status and pH. However, the periodically disturbed and nutritionally enriched high-tide line was colonized by ruderal species with minimal mycorrhizal associations. In turn, the plant communities were defined by distinctive nutrient limitations and their dominant mycorrhizal types. Plant species that were facultatively dependent on AM mycorrhizal colonization tended to occur in dune areas with limited P availability (see also Smith and Read, 1997). The extramatrical mycelium of AM fungi also stabilized the dune systems by aggregating sand and soil particles (Miller and Jastrow, 1992). The availability of AM inoculum also determines the plant community dynamics by changing the competitive balance among the early nonmycorrhizal and facultatively mycorrhizal plant species (Allen and Allen, 1984, 1988, 1990). Over time, the accumulation of soil organic matter reduces pH and inhibits nitrification. As ammonium becomes the major source of N, N replaces P as a main growth-limiting element. As a result, EM plants tend to predominate, organic matter accumulates, and base depletion proceeds. In this environment, plants with ericoid mycorrhizal associations become more important because of their ability to utilize nutrients bound in acidic organic complexes (Read, 1996). Read's (1989) model system elegantly relates the shifts in mycorrhizal community and plant mycorrhizal dependency to the modification of ecosystem properties during succession. However, this model does not provide a mechanistic basis to explain why certain species of mycorrhizal fungi are selected at various stages of plant community succession.

The early- and late-stage model attempts to explain the successional occurrence of EM fungi by correlation with stand or tree age (Dighton et al., 1986; Mason et al., 1983). Deacon and Fleming (1992) thoroughly reviewed this successional concept, and we will only briefly introduce it here. The early-stage fungi approximate ruderal strategies (*r*-selected sensu; Grime, 1979), whereas the late-stage fungi appear more stress tolerant or combative (*S*-selected or *C*-selected) (Deacon and Fleming, 1992). Early-stage fungi readily colonize available host roots when their spores or mycelia are added (Fox, 1983; Mason et al., 1983) and are likely to be among the pioneering colonizers of young plants in deforested environments. As the host tree ages, early-stage fungi nearer the tree trunk are replaced by late-stage fungi. Late-stage fungi often fail to establish mycorrhizae by spores or mycelial inoculum (Deacon et al., 1983; Fox, 1983). However, they are able to dominate the root systems once established on a large tree. Furthermore, the late-stage fungi readily colonize seedlings planted adjacent to these larger trees (Fleming, 1983), but not when inoculated onto seedlings in the absence of such parent trees (Fleming, 1985; Mason et al., 1983). In this fashion, establishment only occurs from an existing food (carbon) base (Fleming, 1983; Fleming et al., 1984).

Apart from tree age, fungal succession has been attributed to differences in photosynthate availability in proximal and distal parts of the root systems (Gibson and Deacon, 1988, 1990), or the size of the food (carbon) base (Deacon and Fleming, 1992). Bruns (1995) uses a "leaky hose" analogy to explain: short roots closest to the stem receive the greatest amount of photosynthates, and the more distal roots only receive what is left after the preceding leaks. Accordingly, late-stage fungi are those requiring more host photosynthate, whereas early-stage fungi colonize roots when photosynthate availability is limited (Gibson and Deacon, 1988). Pure culture studies have confirmed that the late-stage fungi, indeed, require more sugars to grow (Gibson and Deacon, 1990). Although this model is

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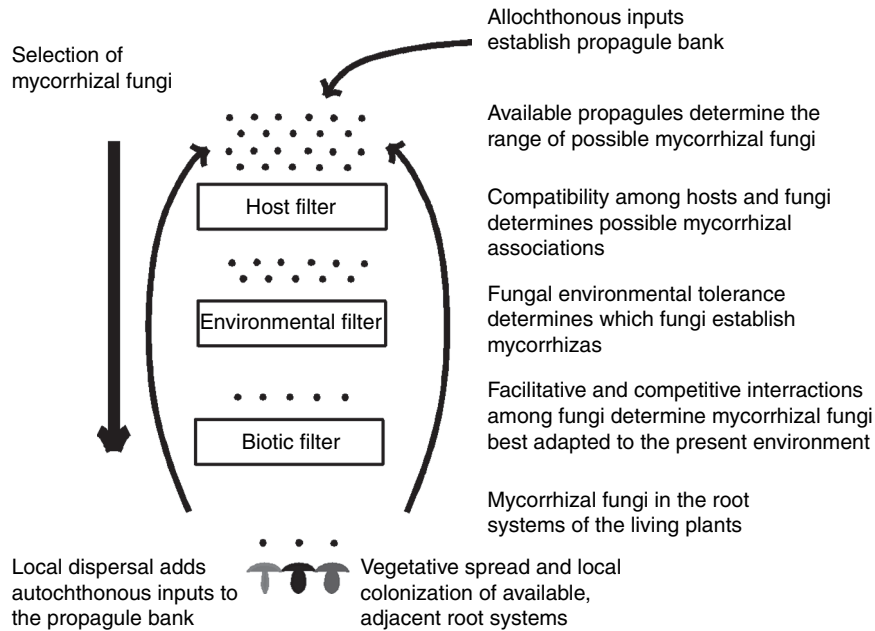
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an elegant effort to integrate physiology of the hosts as well as their mycorrhizal fungi, it has been criticized for not acknowledging the stand-level environmental parameters that change with the age of the stand (Jumpponen et al., 1999a; Keizer and Arnolds, 1994). Furthermore, the early- and late-stage model does not incorporate the complex competitive and facilitative interactions among the soil-inhabiting microorganisms.

The concepts of fungal adaptation and the resulting environmental tolerances have often been ignored in contemporary models of fungal succession that seek to explain the occurrence of fungi based on their physiology. Deacon and Fleming (1992) also emphasized the need to resolve the more fundamental issues of fungal occurrence: To what degree is the behavior of mycorrhizae determined by soil and environmental factors? We emphasize that a comprehensive model for succession of mycorrhizal fungi must account for various aspects of fungal life strategies and their environmental tolerances. Earlier models such as *r*- and *K*-selection models focus on the reproductive output that facilitated rapid fungal invasion and establishment, the ability of fungi to tolerate stress and intensifying competition as ecosystem properties stabilized, or the increased niche overlap among component species. Instead, we aim to focus on mechanisms that explain how fungi can successfully establish and proliferate in the successional environments. Our goal is to propose a successional model that is applicable on an ecosystem scale by integrating fungal propagule availability and dispersal, host preferences and physiology, fungal environmental tolerances, and biotic interactions among mycorrhizal fungi and soil-inhabiting microorganisms (Figure 7.1). We acknowledge that such a model is a simplification of the natural successional phenomena, as we focus only on arrival of propagules and selection of mycorrhizal fungi through host, environmental, and biotic filters. Clearly, plant community dynamics and competitive and facilitative interactions, even those that are not mediated by mycorrhizal fungi, are important (Connell et al., 1987; Connell and Slatyer, 1977; Pickett et al., 1987). For example, the interactions among establishing plants and the resultant distribution of resources, including photosynthates, are likely to alter environmental conditions that influence the fungal community composition.

We also seek a mycocentric view and aim to identify the factors or processes that select the fungi that colonize hosts in successional environments. Our ultimate goal is to develop a predictive model for extant communities when data on the species pool and prevailing environmental conditions are available. We have adopted and modified concepts of assembly rules used in plant community ecology as a general ecological framework to identify processes of community assembly (Cole, 1983; Diamond, 1975; Hunt, 1991). These rules outline the constraints on the selection of community assemblages from larger local or regional species pools (Weiher and Keddy, 2001), and mechanisms and ecological processes that function to produce organismal communities (Drake et al., 1993). In other words, we seek the factors that control the community composition reflecting “both the applicant pool and the community’s admission policies” (Roughgarden, 1989, p. 218). Thus, we follow Keddy (1992) and apply these rules to emphasize the different environmental tolerances among the component fungal species.

The environmental controls are expressed as filters in our model following examples presented elsewhere (see Keddy, 1992; Weiher and Keddy, 1995, 2001). We define a filter as the biotic and abiotic environments, or their combined characteristics, that remove species otherwise available in the local and regional species pools, but lacking the ability to persist in the community under prevailing conditions (see also Grubb, 1977; Southwood, 1988; van der Valk, 1981). The use of the filter concept is particularly useful in our approach to successional ecology of mycorrhizal fungi, as it serves our overall goal to discuss the determinants of fungal persistence in successional ecosystems. To incorporate fungal dispersal and a dormant propagule bank, as proposed in Jumpponen (2003), we



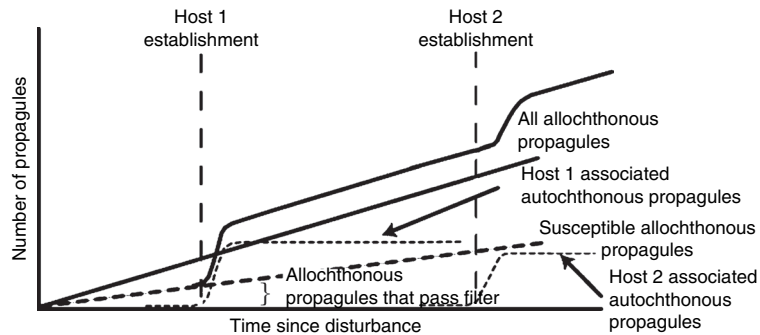
**Figure 7.1** Conceptual community assembly model for mycorrhizal fungal communities during succession. Initially, out-of-site, allochthonous propagules establish available species pool (propagule bank). Successful component species are selected by filtering out those species that are incompatible with available hosts in their present physiological state (HOST filter), those species whose environmental tolerances do not include the prevailing conditions in the successional environment (ENVIRONMENTAL filter), and those species that are outcompeted by others in the prevailing environment (BIOTIC filter). Species with adequate fitness to reproduce contribute to the autochthonous propagule bank via production of vegetative mycelium or via production of sexual and asexual propagules.

consider the disturbed patch (successional environment) as an island that is surrounded by a nondisturbed mainland. Severity of the disturbance within the patch determines whether any resident organic legacies (e.g., propagules, surviving individuals, organic matter, nitrogen) remain within the island after disturbance. The size of an individual island determines the scale on which dispersal mechanisms occur, namely, autochthonous vegetative spread as mycelium or within patch spore dispersal vs. an exclusive reliance on aerial or vector-mediated propagules that originate outside of the patch. Our model (Figure 7.1) concentrates on primary successional ecosystems and briefly addresses its possible relevance in secondary successional systems. Further, we limit the scope of this proposed model to EM and AM fungi, as very little is known about the successional community dynamics of other mycorrhizal fungi. The sections below are arranged to address various components of the model individually.

## 7.2 DISPERSAL OF FUNGI AND AVAILABILITY OF PROPAGULES IN SUCCESSIONAL ENVIRONMENTS

We will first consider primary successional ecosystems that rely primarily on allochthonous sources for species establishment (Matthews, 1992). Examples of primary successional

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**Figure 7.2** Schematic of the accumulation of mycorrhizal propagules in the propagule bank. Propagules accumulate linearly from allochthonous sources. Autochthonous propagules are produced only after functional mycorrhizal symbioses have been established. Note the increasing relative importance of autochthonous propagules over time.

ecosystems include glacier forelands, mine tailings, and volcanic substrates and islands. We will relate fungal community dynamics in these ecosystems to our successional model, and consider the relevance of this conceptual model for secondary successional ecosystems. There is little doubt that mycorrhizae can have tremendous impacts on plant growth and performance in these environments. Early transplant experiments clearly demonstrated the pivotal importance of mycorrhizal colonization: without mycorrhizae, plants often did not survive or grew at extremely slow rates (see Hatch, 1936; Mikola, 1970; Trappe and Strand, 1969). Thus, primary successional ecosystems present a challenging environment for establishment and growth of mycotrophic plants, and the availability of mycorrhizal propagules will be critical for plant succession.

Successional ecosystems vary in their availability of mycorrhizal propagules. Jumpponen et al. (2002) concluded that EM propagules on the forefront of a receding glacier were few, but their availability increased with time since deglaciation. Similarly, AM propagule numbers increased with time in pioneering communities in maritime sand dune (Nicolson and Johnston, 1979) and in mine tailing (Zak and Parkinson, 1983) ecosystems. The limited supply of infective fungal propagules in these environments underlines the importance of allochthonous sources of propagules. In large landscape fragments, such as volcanic islands or the forefronts of receding glaciers, mycorrhizal colonization propagules may be solely provided by allochthonous sources until susceptible host plants have established and thus allow autochthonous propagation (Figure 7.2).

Mycorrhizal fungi colonize the roots of as many host plants as possible and transfer (Chilvers and Gust, 1982) by vegetative dispersal (Finlay and Read, 1986a, 1986b). However, plant individuals are sparsely dispersed in primary successional ecosystems and fungal vegetative expansion between new individuals is unlikely. Therefore, in early primary successional ecosystems, the vast majority of the propagules are likely to arrive aerially and establish a dormant spore bank as hypothesized by Jumpponen (2003). Since propagule availability restricts the establishment and growth of mycorrhizal plants (Janos, 1980), autochthonous propagule production may be reduced. Stochastic events such as landslides or fecal deposits by animals may create patches of increased propagule availability (Cázares, 1992; Jumpponen et al., 2002; Kjølner and Bruns, 2003). The stochastic landscape can also determine the distribution of fungal propagules and heterogeneity: microscale topographic variation, soil surface structure, or the proximity of rocks. Both plant and mycorrhizal establishment have been shown to vary among such microsites

(Jumpponen et al., 1999b; Titus and del Moral, 1998; Titus and Tsuyuzaki, 2002). These microsites can function as safe sites for both plant and mycorrhizal propagules since infective propagules can be cached or protected, or mycorrhizal colonization of the host plants can be facilitated (Titus and Tsuyuzaki, 2002). The co-occurrence of fungal propagules and susceptible hosts may be particularly important for the successful establishment of obligately mycotrophic plants in primary successional environments (Trappe and Luoma, 1992).

Not all propagules in the propagule banks, however, are equally likely to colonize the roots of susceptible hosts. Some (early-stage) fungi can readily colonize roots of susceptible hosts when their spores are introduced into soil, whereas others (late-stage) have great difficulty establishing by spores (Deacon et al., 1983; Fox, 1983; Mason et al., 1983). The ability to colonize host roots may be controlled by host physiology (Gibson and Deacon, 1990) as well as the carbohydrate or environmental requirements of an individual fungus. In addition, some fungi are unable to form mycorrhizas as monokaryons and require dikaryotization (an anastomosis event) prior to successful mycorrhiza formation. For example, *Laccaria bicolor* (Kropp et al., 1987) and *Hebeloma cylindrosporum* (Debaud et al., 1988) were able to colonize host roots as monokaryons, whereas *Tuber melanosporum* (Rougenol and Payre, 1974) or *Suillus granulatus* (Ducamp et al., 1986) were not. Consequently, both host physiology and fungal life history govern the fungal taxa that are able to colonize the susceptible host roots in primary successional ecosystems, be it from aerial inocula or deposited by animals.

Additional factors may play important roles in the ability of propagules in the soil propagule bank to germinate and colonize susceptible roots. Soil fungistasis may inhibit propagule germination and hyphal extension in soil (Lockwood, 1977, 1992). Sensitivity to fungistasis among the fungal taxa may vary substantially (de Boer et al., 1998; Lockwood, 1977), so that not all fungal propagules will have an equal chance to establish colonization on the available host roots. We will return to fungistasis later in the section on biotic interactions. A variety of factors — including host physiology, fungal life history strategies, and soil fungistasis — can also select fungi from the soil propagule bank that are able to colonize susceptible hosts. We stress that an essential component of our model is that a variety of fungi may be present in the propagule bank, but only a limited selection of those will successfully colonize available hosts.

Propagule availability in secondary successional systems differs dramatically from that in primary successional ecosystems. Secondary successional processes may also take place in a wider variety of scales, ranging from a single windthrow to vast wildfires that (temporarily) eliminate all live vegetation over hundreds or thousands of hectares. There are various possibilities for mycorrhizal establishment after such disturbance events. Mycorrhizal colonization can establish from active mycelia that survive the disturbance event, resistant propagules other than mycelium (dormant structures, including spores and sclerotia), or, similarly to primary successional systems, aerially dispersed propagules from adjacent undisturbed areas (Bruns et al., 2002). Surprisingly, Taylor and Bruns (1999) observed minimal overlap between EM community structures in mature *Pinus muricata* forest and resistant propagule banks in air-dried soil samples from the same site. Such observations suggest that any disturbance of the mycelial network may inhibit colonization by the active mycelia in secondary successional stands, and result in the patchy distribution of a great diversity of fungi with differing life history strategies (Taylor and Bruns, 1999). Nonetheless, whether the mycorrhizae establish from active mycelium or a resistant propagule bank in soil, we argue that the allochthonous inoculum sources are of lesser importance than autochthonous inoculum sources in secondary successional ecosystems (see Figure 7.2). The relative importance of inoculum sources obviously depends on the



severity of the disturbance. Fast canopy fires allow the survival of surface and litter-bound mycelium, whereas the hotter surface fires typically eliminate the active mycelium that is close to the soil surface and mycelia tends to survive only at greater soil depths (Baar et al., 1999).

Fungal life history strategies, including life span and turnover, are also likely to play an important role. Recent evidence suggests that some fungi may require frequent recolonization from newly dispersed propagules (Redecker et al., 2001). Guidot and coworkers (2002) found that *Hebeloma cylindrosporium* genets rarely, if ever, could be detected in the same locations in two consecutive samplings in coastal *Pinus pinaster* stands. These findings suggest that some fungi may establish as annual mycelia and rely nearly exclusively on reestablishment annually, whether or not the site is disturbed.

### 7.3 HOST FILTER

Both aspects of host physiology and susceptibility to mycorrhizal colonization vary among host species and hosts of different ages. Following Molina and coworkers (1992), we will focus on host receptivity and host range of the mycorrhizal fungi here. Clearly, these two factors will limit fungal colonization from the limited propagule banks in primary successional systems. We acknowledge that these factors are also likely to be controlled by various environmental factors that impact host physiology and performance, as well as molecular interactions between the fungus and host plant. Furthermore, the plant community structure will also influence the identity of fungal taxa residing in the propagule bank (Figure 7.2) and those fungi that establish and sustain colonization in a root system of a host (Vandenkoornhuyse et al., 2003).

#### 7.3.1 Host Ranges of Mycorrhizal Fungi

There are very few examples of hosts that form mycorrhizae with only one species of fungi. Some dipterocarps may be an exception to this rule (Smits, 1983). Another possible exception may be members of Monotropeae, as these plants appear to form associations with a single fungal genus or closely related group of fungi (Bidartondo and Bruns, 2001, 2002). The AM fungi were, until recently, thought to form functional associations with a wide variety of potential host species (Smith and Read, 1997), including species that are not normally considered AM hosts (see Cázares and Trappe, 1993; Chen et al., 2000; Lodge and Wentworth, 1990; Moyersoen and Fitter, 1999). However, AM fungi have been shown to be diverse and select different primary hosts even when the plants grow in mixed communities (Bever et al., 1996; Eom et al., 2000; Helgason et al., 2002; Husband et al., 2002; Lovelock et al., 2003; Vandenkoornhuyse et al., 2001). Further, different host–fungus combinations may yield symbiotic associations that are less compatible when measured in terms of benefits to each of the symbiotic partners (Bever, 2002; Molina et al., 1992; van der Heijden and Kuyper, 2001; van der Heijden et al., 1998).

Duddridge (1986) used EM host specificity as a measure of selectivity. We contend that selectivity may be most appropriate for the purposes of this contribution. Selectivity indicates the combination of processes that determine whether a fungal–host combination will yield functioning mycorrhizae (Molina et al., 1992). Different host species may select different fungi from the same soils. Newton (1991) used seedlings of *Betula* and *Quercus* to bait EM fungi from a variety of soil samples and found that different fungi colonized the seedlings, even when seedlings were planted in the same soil. Interestingly, the EM fungi also differed when hosts were planted in mixtures or monocultures (Newton, 1991). Thus, different fungi are able to establish mycorrhizae from different sources of inoculum:

a fungus that may be unable to colonize one host from propagules other than active mycelia may be able to do so when a more susceptible host is present and provides a supply of photosynthates. Similar resource limitations have also been applied to host colonization by AM fungi (Bever, 2002).

Plants within the same genus or family may be capable of hosting similar suites of EM fungi (Malajczuk et al., 1982; Molina et al., 1992). During primary succession and when propagules arrive mainly from allochthonous sources, broad-host-range fungi may be most successful. There are two main arguments why EM generalists should have a higher abundance than specialists. First, a generalist may colonize many plants and therefore be able to occupy a wider geographic area. Thus, the total resources potentially available for uptake and transfer to the plant are greater. Second, fungal generalists can promote the geographical expansion of a plant species because the fungal taxa tend to tolerate a broad range of environmental conditions. In secondary successional ecosystems, the case may be the opposite. Host-specific fungi may provide plants with access to exclusive pools of nutrients. For example, in the case of a stand-replacing wildfire, forests of *Pinus muricata* or *Pinus contorta* are often replaced by conspecific seedlings whose establishment depends on fire. In these ecosystems, fungi with narrower host ranges may benefit from being able to establish from the roots of fire-damaged mature trees. For instance, there may be lesser competitive potential of the nonconspecific hosts or competition from fungal taxa with broad host ranges.

Field evidence for mycorrhizal host preferences is limited. In mixed stands of EM, *Pseudotsuga menziesii*–*Pinus muricata* and *Pinus contorta*–*Picea engelmannii* illustrate that nonspecific fungi account for more than 80% of the mycorrhizal biomass in both plant taxa (Cullings et al., 2000; Horton and Bruns, 1998). Many of the same fungi also occurred on roots of the arbutoid mycorrhizal plant, *Arctostaphylos glandulosa* (Horton et al., 1999). In contrast, fungi with narrow host ranges, e.g., species of *Suillus* or *Fuscoboletinus* that are thought to be exclusively associated with *Larix* species, are unlikely to colonize a nonpreferred host under the harsh environmental conditions of severely disturbed ecosystems.

### 7.3.2 Host Receptivity

The receptivity of the host for mycorrhizal colonization varies greatly among host species and individuals, and might be related to host age (Tonkin et al., 1989). It is also possible that receptivity is related to the early- and late-stage model discussed above. If so, receptivity would correlate with differences in photosynthate availability among mycorrhizal hosts of different ages or between proximal and distal parts of the root system (Deacon and Fleming, 1992; Gibson and Deacon, 1988, 1990). Early-stage fungi are likely to colonize younger trees or younger regions of the root systems (Gibson and Deacon, 1988, 1990), and therefore be pioneering colonizers of young plants in deforested environments. In contrast, late-stage fungi are unable to establish mycorrhizae by spores or mycelial inoculum (Deacon et al., 1983; Fox, 1983) and instead depend on an existing carbohydrate reservoir for successful establishment and colonization (Fleming, 1983; Fleming et al., 1984; Gibson and Deacon, 1988).

In this manner, the species distribution of hosts and coinciding mycorrhizal inoculum may govern the range of possible compatible host mycorrhizal fungus combinations. In a study of the responses of six early and late successional tree species to early or late successional AM inocula, all tree species had the greatest growth response to early seral fungi. However, the response to late seral inoculum varied: two tree species (*Ceiba pentandra*, *Guazuma ulmifolia*) were smallest with late seral inoculum, even smaller than the uninoculated plants, whereas the other species (*Brosimum alicastrum*, *Havardia albi-*



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*cans*, *Acacia pennatula*, *Leucaena leucocephala*) had intermediate growth with late seral inoculum. Of these, *Brosimum*, *Havardia*, and *Ceiba* occur in late successional forest, and the others are early seral (Allen et al., 2004). The host trees, through preference for fungal symbionts or changes in physiology and carbohydrate availability, selected the mycorrhizal fungi that are able to colonize and establish in their root systems. The inocula and their sources present a further challenge. In primary successional ecosystems where no live mycelial inocula possibly exist, the fungal abilities to colonize via spores and airborne propagules become critical.

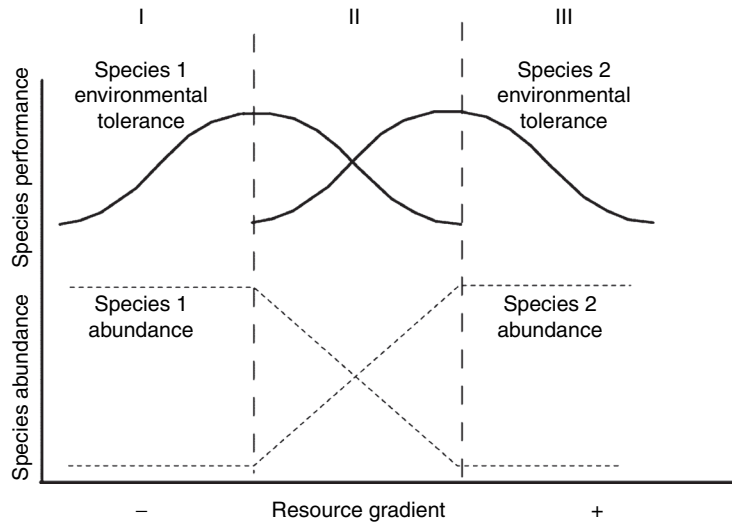
### 7.4 ENVIRONMENTAL FILTERS

Niche can be defined as the range of physical and biological conditions, including limiting resources, necessary for a species to maintain a stable or increasing population (Hutchinson, 1957). This definition can be visualized as a multidimensional space in which each of the dimensions corresponds to an independent physical or biological variable that affects the abundance of a target species (Morin, 1999). We emphasize that environmental tolerances and niches are not static in time or space, but are influenced by competitive and facilitative interactions among organisms, and interactions among different resource axes. For example, temperature has a substantial impact on the use of various carbon substrates by food and grain spoilage fungi (Lee and Magan, 1999). Here, we consider aspects of niche to include environmental tolerance (this section) as well as available resources for which mycorrhizal fungi may compete (see Section 7.5, specifically Section 7.5.3). Our environmental filters are based on the concepts of both realized and fundamental niches (Figure 7.3 to Figure 7.5).

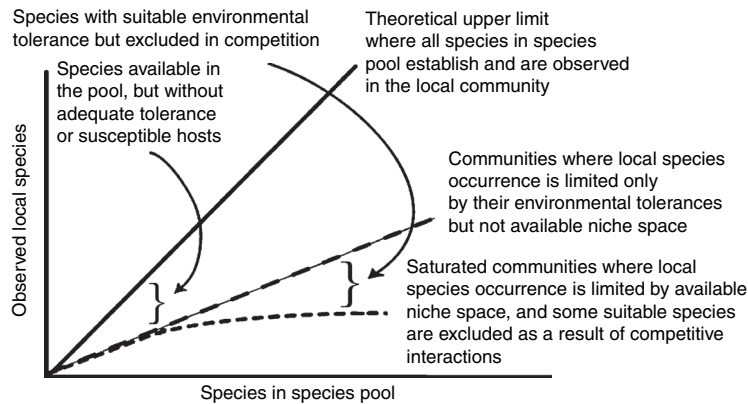
#### 7.4.1 Environmental Tolerances of Mycorrhizal Fungi

Every species has an optimal set of environmental conditions under which it will grow most efficiently and produce the most offspring. Different fungi, like plants, have different niches and thus physiological characteristics (Figure 7.3). While we cannot always differentiate between the absences of fungus and its inability to colonize a susceptible host, environmental factors can indeed control both fungal survivorship and the ability to colonize susceptible hosts (Bougher and Malajczuk, 1990; Marx et al., 1970; Thomson et al., 1994). Accordingly, we address the impacts of environmental heterogeneity on the occurrence of mycorrhizae or root colonization in successional environments.

Ecosystem-level disturbances often result in dramatic environmental heterogeneity. For example, the secondary successional environment of a terminal moraine in a receding glacier foreland can be adjacent to a primary successional ecosystem limited in organic resources. Similarly, areas affected by volcanic eruption or fires co-occur with undisturbed areas to create a mosaic of physically and chemically contrasting habitats across the landscape. Although the disturbance regime typically defines the character of a successional environment, there is also substantial variation in the environmental conditions within those disturbed environments. For instance, soil organic matter and nitrogen concentrations in glacier forefront systems tend to increase with time since deglaciation (Jumpponen et al., 1998; Matthews, 1992; Ohtonen et al., 1999). Likewise, the established vegetation patches in these environments also provide local, relatively enriched resource patches (Jumpponen et al., 1998; Ohtonen et al., 1999). Although extremes of resource availability such as these are largely absent in secondary successional systems, there are small-scale disturbances that alter the distribution of nutrients and inoculum. Postfire litter patches contain higher N, P, K, and water availability than the adjacent (bare) soil patches.

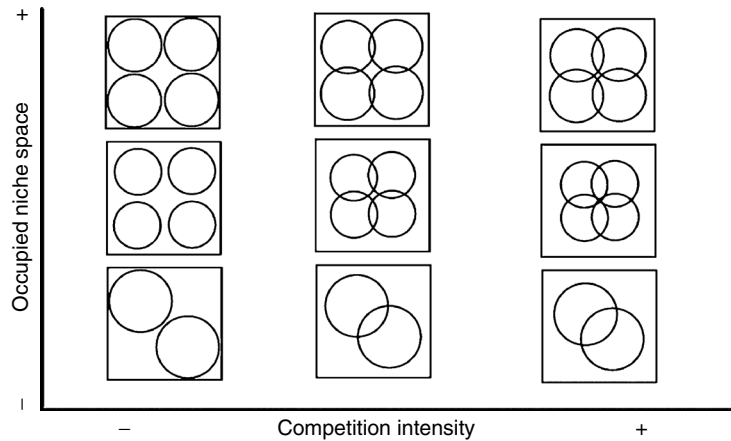


**Figure 7.3** Schematic of two mycorrhizal species' environmental tolerances and predicted outcome on their relative abundance. Species performance refers to yield along a resource gradient. The performance curves for the two species outline the use of one resource (fundamental niche), while other parameters are maintained optimal. In region I, species 1 occurs alone because available resources are outside the resource use ability for species 2. In region II, species 1 and 2 co-occur because their resource use abilities overlap in this region. In region III, species 2 occurs alone because available resources are outside the resource use ability for species 1.



**Figure 7.4** The relation between the observed number of species and the size of the available species pool. (Adapted from Connell and Lawton, *J. Anim. Ecol.*, 61, 1–12, 1992.) Note that at low levels of diversity (early succession), all species with adequate environmental tolerances can establish. Only after a large enough pool of species has established do competitive interactions remove species from this pool. AU: Is permission needed?

Digging in and redistribution of soil by pocket gophers can either accumulate or reduce mycorrhizal inoculum (Allen, 1988). Ants also concentrate inoculum and nutrients by weaving colonized roots into their seed-caching areas of the mound. All of these examples underline the need to take environmental factors (and biotic interactions) into effect to correctly interpret mycorrhizal community structure, composition, and succession.



**Figure 7.5** Schematic of niche filling and competition intensity. Boxes aligning on a given level of competition intensity share similar levels of competition, while boxes aligning on the niche space axis share similar occupied niche space. Note that niche overlap, not number of species or total occupied niche space, determines competition intensity.

Differences in optima and tolerance ranges (Figure 7.3) for soil abiotic parameters such as temperature or moisture content may be at least partially responsible for filtering mycorrhizal species phenology, dominance, and community composition (Bruns, 1995; Pringle and Bever, 2002). Likewise, segregation of fungal taxa in different forest soil microhabitats has been explained in terms of their diverging preferences for soil organic matter content, moisture, pH, or fertility levels (Erland and Taylor, 2002; Goodman and Trofymow, 1998; Johnson and Wedin, 1997; Neville et al., 2002). Spatial, temporal, and chemical heterogeneity in soil resources can significantly influence mycorrhizal community composition (reviewed in Taylor, 2002). However, little effort and emphasis has been dedicated toward identifying which environmental variables are crucial to defining fungal communities.

Studies in Swedish beech forests identified base saturation and pH and organic matter content as the dominant parameters in determining macrofungal community compositions (Hansen, 1988, 1989; Hansen and Tyler, 1992). Similarly, a large-scale survey of sequestrate fungi (false truffles) in southeastern Australia identified climatic variables, such as moisture availability and temperature, to be important explanatory variables at a landscape scale (Claridge et al., 2000). At a local scale, topographic position, soil fertility, and time since last fire disturbance, as well as microhabitat structures, including leaf litter layer and amount of coarse woody debris, influenced the distribution of sequestrate fungi (Claridge et al., 2000). Studies such as those cited here allow preliminary assessment of the environmental ranges within which fungal species may occur. More importantly, they allow identification of those environmental parameters that may explain the presence of a given fungal species in one environment, but its absence in another. For example, Claridge et al. (2000) found that a commonly occurring taxon, *Cortinarius globuliformis*, occurred more frequently in environments with cold temperatures, high moisture availability, and extended periods between fire disturbances. Accordingly, *C. globuliformis* could be identified as a taxon with preference for stable, late successional environments in montane regions. In contrast, *Hymenogaster levisporus* occurred more frequently in environments with reasonably low moisture availability and thin litter layer. Accordingly, extrapolation from these data would identify *H. levisporus* as a taxon with preference for poorly

developed soils — possibly early successional — with little litter in environments that receive limited precipitation.

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Nitrogen is also an important editor of fungal community composition (Franklin and J.A., 2000), and often the most limiting resource for primary productivity in many terrestrial ecosystems (Vitousek et al., 1997). Primary successional environments, particularly during the early seral stages, have extremely low nitrogen levels, usually in the mineral form. Such conditions likely select for early colonizers such as *Laccaria laccata* (Carpenter et al., 1987) that appear to primarily use inorganic N (reviewed in Smith and Read, 1997). Both descriptive and experimental N enrichment studies also illustrate some of the differences in nitrogen tolerance, acquisition, and utilization among mycorrhizal fungi (Sawyer et al., 2003a, 2003b). For example, an increase in nitrogen availability leads to shifts in EM community composition in both coniferous (e.g., Kåren and Nylund, 1997; Peter et al., 2001) and deciduous forests (Avis et al., 2003; Baxter et al., 1999; Taylor et al., 2000). Lilleskov et al. (2002a) identified both nitrophilic and nitrophobic EM species from an anthropogenic nitrogen deposition gradient in Alaska. *Ampiphinema byssoides* and species of *Cortinarius* and *Piloderma* were nitrophobic, and thus abundant in sites with low nitrogen availability. Conversely, *Tomentella sublilacina* and *Thelephora terrestris* were considered nitrophilic and tended to dominate sites with higher overall nutrient availability. Observational studies such as these, however, are often unable to identify the causal factor(s) associated with such shifts in the fungal community. Nevertheless, Avis et al. (2003) showed that when limitations by nutrients other than N were largely controlled, the most substantial differences in EM communities tended to be imposed by N enrichment. Species of EM fungi that differed in their response to nitrogen enrichment also differed in their use of different nitrogen sources in axenic culture (Lilleskov et al., 2002b). Fungal taxa that were common in low-nutrient environments manifested a greater ability to utilize complex nitrogen sources than isolates from nitrogen-rich environments, indicating adaptation to prevailing conditions. Indeed, EM sporocarps associated with a single (unfertilized) oak stand had  $\delta^{15}\text{N}$  values ranging from +2 to +11 (A.E. Lindahl and M.F. Allen, unpublished data), because different species of fungi acquired N from different sources: certain EM taxa (*Hebeloma crustuliniforme*) acquire organic N from litter, whereas other taxa (*Pisolithus tinctorius*) acquire inorganic sources of N (Chalot and Brun, 1998).

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Similarly, AM communities have been shown to be responsive to environmental parameters, although studies focusing on the environmental control of their community composition are few. As with EM, differences among AM communities may reflect variations in soil moisture, temperature, and pH, which are known to influence AM sporulation (Cuenca and Meneses, 1996; Porter et al., 1987). Root colonization by *Glomus intraradices* (Augé, 2001) and *Glomus mosseae* can be influenced by soil temperature or available moisture (Stahl and Christensen, 1991). Further, Husband et al. (2002) found that non-random associations between AM fungi and their hosts were site dependent. Changes in the abiotic environment over time also corresponded with changes in AM species dominance and community composition. Such responses in concert with host phenology have also been used to explain temporal variation in AM communities (Daniell et al., 2001; Eom et al., 2000; Lee and Koske, 1994) and the successional recruitment of seedlings (Helgason et al., 2002).

Specific edaphic parameters also influence the incidence, growth, and turnover of AM fungi (Mosse et al., 1981). Johnson (1993) showed that experimental fertilization treatments altered both mycorrhizal community composition and functioning in a Minnesota grassland ecosystem. Similarly, Egerton-Warburton and Allen (2000) found that members of the Gigasporaceae and larger-spored *Glomus* spp. were largely eliminated

with N fertilization or prolonged nitrogen deposition in California shrub lands (largely from NO<sub>x</sub>, >30 years; Egerton-Warburton et al., 2001). Observational studies have attempted identification of AM fungal environmental preferences. Rathore and Singh (1995) reported a positive correlation between AM spore abundance and soil phosphorus availability, plus a negative correlation between spore abundance and soil clay content. They and others (Jasper et al., 1979; Schultz et al., 2001) also found that intensive P fertilization limited host dependence on mycorrhizal fungi in prairie soils and agricultural plots. This phenomenon may be due to community shifts among AM fungi; both Koske (1981) and Klironomos et al. (1993) were able to correlate the occurrence of individual AM fungal species to soil P content.

Spatial heterogeneity or stratification of resource availability also results in a patchwork of different environments at local scales. These microsites allow mycorrhizal fungi with different environmental tolerances or requirements to occur in close proximity. Both EM and AM community composition can be correlated with soil depth or horizon (An et al., 1990; Dickie et al., 2002; Malajczuk and Hingston, 1981; Rosling et al., 2003). This is because a number of variables (including O<sub>2</sub> and CO<sub>2</sub> content, pH, temperature, moisture, and competing soil organisms) covary with soil depth (Taylor and Bruns, 1999).

Changes in soil mineralogical properties also create different habitats for fungi. Intensive sampling of EM root tips in seven distinct soil horizons in a boreal forest podzol illustrated that two thirds of EM root tips occurred within the mineral soils, and that half of the EM taxa were restricted to mineral soils (Rosling et al., 2003). Fransson et al. (2000) recovered *Cenococcum geophilum* from organic layers, whereas *Tylospora fibrillosa* occurred in mineral soils. In addition, correlations were detected between the occurrence of mycorrhizal fungi and substrate physical (negative — bulk density) and chemical (positive — moisture content, N, N:P, Ca:Mg) properties in a soil-weathered bedrock (to depth of 2 m, Egerton-Warburton et al., 2003). Furthermore, metalliferous soils constitute strong environmental filters for mycorrhizas. Mycorrhizal types, taxa, and isolates can be selected for tolerance to potentially phytotoxic metals, such as Pb, Al, Ni, Cu, and Zn. Isolates of EM (e.g., *Pisolithus*) and AM (e.g., *Glomus*) fungi tolerant of high soil concentrations of heavy metals demonstrated the capacity to grow on media containing high concentrations of metals, in comparison with isolates from noncontaminated sites (Egerton-Warburton and Griffin, 1995; Jones and Hutchinson, 1986). Metal-tolerant fungal isolates also increased the host plant's tolerance to metals within the soil solution (see Hall, 2002; Meharg and Cairney, 2000a).

#### 7.4.2 Environmental Tolerances as Drivers of Successional Community Change

Clearly, various environmental parameters influence occurrence of mycorrhizal fungi in ecosystems at various scales. How is this relevant to the presence of mycorrhizas in successional ecosystems? As we noted previously, primary successional environments provide an elegant study system wherein drastic environmental differences exist between vegetated patches and adjacent interspaces. Levels of nutrients, especially nitrogen, soil organic matter, and moisture, are higher within these vegetated patches than interspaces, whereas soil temperatures are significantly higher in interspaces than vegetated areas. It follows that when mycorrhizal roots of mycorrhizal plants extend beyond the canopy or patch, they experience a very different set of environmental pressures. Furthermore, many environmental parameters change along the successional gradient, such as the chronosequence of a glacier forefront. Accordingly, we propose that these environmental pressures select a different suite of fungi from the propagule bank (Figure 7.4) that, in turn, colonize available and compatible hosts. These selected fungal communities are different at different



stages of a successional gradient as well as on a local scale within and beyond established vegetation (see Trowbridge and Jumpponen, 2003).

Are such environmental effects also likely in secondary successional ecosystems? We use examples of prescribed fire as a disturbance and its effects on the communities of mycorrhizal fungi. Fire is a frequent disturbance event in many shrub and forest ecosystems. However, not all fires are standing replacing. In fact, prescribed burning has been used extensively as a tool to reduce fuel loads. It is difficult to estimate the effects of fire on fungal communities because of the extreme spatial heterogeneity in root-inhabiting fungal communities. Nonetheless, Stendell and coworkers (1999) were able to show that responses of ectomycorrhizal species to fire differed. The abundance and spatial patterning of fungi in the postfire environment provided clues to their survival. First, the most abundant mycorrhizal species colonizing roots in the litter and topmost organic layers in the prefire environment were reduced to low or undetectable levels after fire; many mycorrhizal fungi occupying deeper (mineral) soil horizons were relatively unaffected. Similar patterns have also been observed in AM communities in shrub lands (Egerton-Warburton, unpublished). Second, fungal species were not randomly distributed among seedlings or on different parts of the same root system. Inoculum for each fungal species thus behaves as a point source: spores in an extensive spore bank (*Rhizopogon*), sclerotia (*Cenococcum*), or mycelia from root tips deep within the soil profile (*Russula*) colonize root fragments (Grogan et al., 2000; Hagerman et al., 1999). Fire obviously alters the community profile, and over time, many of these early colonizing fungi will eventually be replaced by the species that previously dominated the forest community.

It remains unclear how important the effects of low-intensity fires might be on mycorrhizal community structure. Studies on the manipulation of litter on forest floor may provide clues toward an understanding of the impacts of changes in fire-related environmental parameters. Baar and de Vries (1995) reported shifts in EM community structure in seedlings following litter addition or removal treatments in Dutch *Pinus sylvestris* stands. Subsequent pure culture studies indicated that the causal factor for the observed community shifts may have been a result of differential growth rates of various EM fungi in the presence of litter or litter extracts (Baar et al., 1994). Taken together, these studies indicate that the changes in environmental parameters, such as presence or absence of litter, are likely to have profound effects on the mycorrhizal community composition even after a relatively low intensity disturbance. Accordingly, we can conclude that the environmental filter is likely to act upon the selection of the successful EM fungi in both primary and secondary successional ecosystems.

## 7.5 BIOTIC FILTERS

We will briefly discuss herbivory, bacterial fungistasis, and positive interactions among bacteria and mycorrhizal fungi, as well as competitive interactions among mycorrhizal fungi, as possible biotic filters. We stress that it is not just the presence of various biotic interactions, but the differences among the component mycorrhizal species, that are necessary for any of the possible biotic interactions to act as a selective filter that removes species from the available pool in the propagule bank (Figure 7.4 and Figure 7.5).

### 7.5.1 Herbivory as a Modifier of Fungal Communities

Herbivory acts as a biotic filter through selective grazing of fungal tissues in soil, or indirectly via changes in host physiology and carbon allocation because of defoliation by herbivores. These direct and indirect effects of herbivory influence the relative abundances

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and community composition of fungi present within the soil. The impacts of herbivory differ greatly between AM and EM fungi. For example, the positive effects of AM fungi on plant species richness tend to disappear when herbivores are present (Eom et al., 2001; Gange and Brown, 2002), and more AM propagules were recovered in plots that were not grazed by ungulates than in grazed plots (Bethlenfalvay and Dakessian, 1984). In addition, microarthropods show preferences for certain fungi, as well as certain species of EM or AM fungi present in the soil (Klironomos and Kendrick, 1996; Klironomos et al., 1992). Chronic herbivory may reduce EM species richness (Gehring and Whitham, 2002), although results and conclusions from different studies may vary greatly (Saikkonen et al., 1998). The changes in mycorrhizal community are possibly based on the selection of fungal species and propagules that are energetically less costly to the plant. Thus, not all mycorrhizal species are equally affected by herbivory. In pinyon pines, the most herbivore resistant trees supported *Tricholoma*, whereas herbivore-susceptible trees supported mainly ascomycetes. These interactions also tend to be cumulative with environmental stress so that any changes in abiotic (soil) factors further alter the mycorrhizal community within the soil (reviewed in Gehring and Whitham, 2002).

### 7.5.2 Soil Bacterial Fungistasis

Various components of soil microbial communities interact in complex ways (Cairney and Meharg, 2002; Fitter and Garbaye, 1994; Lockwood, 1977, 1992). We will consider separately the positive and negative interactions between soil bacteria and mycorrhizal fungi as well as among mycorrhizal fungi. The interactions considered here are likely to impact the mycorrhizal fungi selected from the soil propagule bank by either inhibition (fungistasis) or facilitation (mycorrhizal helper bacteria) in successional ecosystems. Negative interactions among different soil organisms are likely to result in competitive exclusion by either interference or exploitation, and affect various life stages of mycorrhizal fungi — namely, spore germination and hyphal extension (Lockwood, 1992). We will consider niche overlap in resource use and extrapolate these results to community-level changes in successional environments.

The soil environment often suppresses the germination of fungal spores and growth of mycelia (Lockwood, 1977). This phenomenon, known as fungistasis, has been suggested to protect soil-borne fungi from germinating and initiating growth under unfavorable conditions (Lockwood, 1977). The mechanisms of the soil fungistasis are unclear, but the absence of appropriate environmental stimuli, or unfavorable soil physical and chemical conditions are clearly pivotal for determining the initiation or inhibition of fungal growth. Evidence points toward microbial interactions as a possible key mechanism in the inhibition of fungal growth and spore germination in the soil. Two main factors for soil fungistasis have been proposed: (1) competition between soil bacteria and fungi for limiting resources (primarily carbon) in the soil, and (2) antagonism by production of antifungal compounds by microbes.

The direct mechanisms behind the bacterial inhibition of fungal activity are debatable. The microbial-induced fungistasis has often been explained by competition between bacteria and fungi for limited carbon supply (de Boer et al., 2003) because the immobilization of available carbon by the bacterial biomass limits spore germination and hyphal extension (Arora et al., 1983; Ho and Ko, 1986; Mondal and Hyakumachi, 1998). Correspondingly, alleviation of the carbon limitation by addition of simple carbon substrates, such as sugars or amino acids, often reduces soil fungistasis. Thus, soil nutrient resource limitations are important in soil fungistasis (Lockwood, 1977). On the other hand, an additional mechanism for soil fungistasis might be the production of antifungal compounds by microbes (Liebman and Epstein, 1992, 1994; Lockwood, 1992; Romine and Baker,

1973). A wide range of soil-inhabiting microbes produce compounds that effectively inhibit the regrowth and extension of fungal hyphae (Behal, 2000; Burgess et al., 1999; de Boer et al., 1998, 2003). It is likely that both competition among bacteria and fungi and the production of fungistatic compounds act synergistically, since the soil and rhizosphere environments contain a vast diversity of organisms with different carbon utilization potentials and metabolic pathways (Toyota et al., 2001). Thus, separation of the two different possibilities is difficult if not impossible.

Although most of the studies on soil fungistasis have focused on plant pathogenic fungi and the effects of either bacterial competition or antagonism on their growth, similar mechanisms are likely to influence germination and growth of mycorrhizal fungi. For example, AM spore germination can be stimulated by volatiles from soil-isolated actinomycetes (Carpenter-Boggs et al., 1995). Like many soil-borne fungal pathogens or saprotrophic fungi, however, mycorrhizal fungi are likely to be susceptible to bacterial antifungal compounds, although sensitivity among the fungal taxa may vary substantially (de Boer et al., 1998; Lockwood, 1977). Competition for soil carbon sources between established mycorrhizas and soil bacteria may be of limited importance because mycorrhizal fungi have direct access to host photosynthates. However, a number of EM fungi have been shown to utilize complex detrital substrates (Meharg and Cairney, 2000b; Meharg et al., 1997) and forage in litter (Bending and Read, 1996). Such taxa may be particularly sensitive to competition for available carbon. Bacterial carbon immobilization may also have significant impacts on mycorrhizae if fungal spore germination is indeed stimulated by soluble carbohydrates. Accordingly, we conclude that even in the absence of direct experimental evidence, bacterial fungistasis and different responses among mycorrhizal fungi possibly influence the selection of fungi colonizing plant roots in successional ecosystems.

### 7.5.3 Positive Interactions among Mycorrhizal Fungi and Bacteria

Ecto- and arbuscular mycorrhizas have been shown to have bacterial associates. For example, bacteria colonize EM mantle and Hartig net, as well as mycelium and fruiting bodies of EM fungi (Danell et al., 1993; Mogge et al., 2000; Nurmiaho-Lassila et al., 1997). Similarly, AM hyphae have been shown to host both superficial and intracellular colonization by bacteria (Bianciotto et al., 1996, 2000). Although these associations are relatively common, their function and significance have remained largely unknown. Some may simply represent an opportunistic colonization of damaged hyphae (Mogge et al., 2000), whereas others may constitute endosymbiotic associations (Bianciotto et al., 1996, 2000). These associations are likely to have a wide variety of impacts on mycorrhizal fungi and their ability to colonize host roots, ranging from positive to negative (Garbaye, 1994). In this section, we concentrate on how bacteria associated with mycorrhizal fungi might influence the process of root colonization and, in turn, influence the community of fungi colonizing roots in successional ecosystems.

Facilitation among rhizosphere organisms is one possibility. For example, bacteria have been reported to adhere superficially or intracellularly to fungal hyphae on root surfaces and in soil, or be generally associated with the rhizosphere of mycorrhizal plants (Bianciotto et al., 1996, 2000; Minerdi et al., 2002; Mogge et al., 2000; Poole et al., 2001). Although AM fungi are exclusively biotrophic, organic matter can facilitate the growth of extramatrical mycelium — a response that has been attributed to bacterial activities within organic matter (Green et al., 1999; Ravnskov et al., 1999). Some bacterial genera have also been shown to stimulate mycorrhizal colonization (Budi et al., 1999; Garbaye, 1994; Poole et al., 2001). Ruiz-Lozano and Bonfante (2001) hypothesized that bacterial associations with AM fungi may positively influence nutrient uptake by the host plant and nutrient transport from the AM fungus to the plant. The possibility of intimate association between

fungi and helper bacteria exists (Garbaye, 1994; Minerdi et al., 2002), but the precise mechanisms of the bacterial stimulation of mycorrhiza formation remain unclear.

Garbaye (1994) hypothesized that the bacteria may either facilitate recognition between the host and mycorrhizal fungus, stimulate propagule germination, or stimulate mycelial growth. The variety of possible largely unknown interactions in the rhizosphere of mycorrhizal plants leaves much to speculation. We propose, nonetheless, that some fungal taxa may benefit more than others. For example, root colonization of various EM plants by *Laccaria laccata* was stimulated by strains of *Pseudomonas fluorescens* (Dunstan et al., 1998; Duponnois et al., 1993; Garbaye and Duponnois, 1992). However, these results are not universally supported (e.g., Duponnois and Plenchette, 2003), suggesting that host species or environmental conditions may impact the EM fungus responses to bacterial facilitation.

#### 7.5.4 Interactions among Mycorrhizal Fungi

In the previous sections, we concentrated on interactions and associations among organisms that fulfill functionally different positions within successional ecosystems. However, the interactions and competition among organisms are likely to intensify the closer their functional and environmental niches are (Figure 7.4 and Figure 7.5). Although saprotrophic and mycorrhizal fungi can have positive and negative interactions (Cairney and Meharg, 2002; Lindahl, 2000; Lindahl et al., 1999), saprobic fungi are unlikely to impact the ability of mycorrhizal fungi to establish or maintain host root colonization. We are not aware of any examples of facilitation among mycorrhizal fungi. In truth, Fleming (1985) observed neither a direct nor an indirect facilitative mechanism between early- and late-stage fungi. We acknowledge, however, that there are only limited data available on a number of candidates for positive interactions in successional communities of mycorrhizal fungi, as well as on the great variety of direct and indirect possible facilitative mechanisms. Given the paucity of available information, in this section we concentrate on resource exploitation and negative interactions among the mycorrhizal fungi. As only few examples of competition among mycorrhizal fungi are available, we will highlight the available examples and extrapolate those results to community dynamics of mycorrhizal fungi.

Several examples for antagonism or competitive exploitation among different types of fungi are available. Janisiewicz (1996) showed that selection of yeasts with carbon and nitrogen utilization abilities (fundamental niche), similar to those of apple-scab-causing *Penicillium expansum*, greatly improved the yeasts' abilities to minimize apple colonization by *P. expansum*. These results were attributed to substantial niche overlap among the organisms and exploitative competition between the biocontrol yeasts and *P. expansum*.

Different types of fungi may colonize roots simultaneously (Jumpponen and Trappe, 1998). For example, AM and EM fungi may colonize roots of various EM hosts (e.g., Cázares and Trappe, 1993; Chen et al., 2000; Egerton-Warburton and Allen, 2001; Harley and Harley, 1987) and establish functional mycorrhizas (Lapeyrie and Chilvers, 1985). AM and EM have been suggested to be negatively associated (Lodge and Wentworth, 1990; Neville et al., 2002), as they appear to occur rarely in the same root segments (Egerton-Warburton and Allen, 2001). It remains unclear whether the observed negative associations among mycorrhizal fungi are due to antagonism or competition, or merely to different environmental tolerances. However, the poor seedling performance in oaks that were highly colonized by AM and EM fungi indicated competition between mycorrhizal types for carbon (Egerton-Warburton and Allen, 2001). Alternatively, as suggested by Chen et al. (2000), there may be a temporal replacement of AM by EM fungi as the plants age (Egerton-Warburton and Allen, 2001), especially if AM fungi are functionally more important in younger than older seedlings. Local microsite characteristics may also be critical

in determining the success of fungal colonization (Wöllecke, 2001). Both AM and EM fungi may possess different environmental tolerances. For example, AM fungi were more likely to colonize sites with low moisture content, whereas EM tended to colonize roots in moister soils (Lodge, 1989).

Competition also can be linked to variation in fungal life history strategies. 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” (Hart and Reader, 2002). 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. In addition, ontogenetic shifts in fungal biomass or turnover result in concomitant increases in the quantity of C, N, and P accrued within fungal tissues.

Although multiple fungi simultaneously occur within a single root system and root fragments (Marks and Foster, 1967; Vandenkoornhuysen et al., 2002a, 2002b), their relative efficiencies in retrieving host carbon or the acquisition of mineral nutrients from soil or soil-borne detritus will also determine and govern their respective abilities for hyphal extension, root colonization, and, ultimately, dispersal and reproduction. Uncolonized roots may be subject to intense competition among mycorrhizal fungi (Deacon and Fleming, 1992). When Wu and coworkers (1999) studied the competitive interactions of EM fungi (*Pisolithus tinctorius* vs. *Suillus luteus* or unknown mycorrhizal fungus), they observed that *P. tinctorius* was progressively replaced by the unknown EM fungus, although it remained unclear whether *P. tinctorius* was replaced from already colonized root tips. The competitive interactions among mycorrhizal fungi were attributed to differences in relative growth rates among the competing fungal taxa (Wu et al., 1999). Alternatively, the competing species may inhibit mycorrhiza formation or hyphal extension in one another, as has been proposed generally for fungus soil microbe interactions (see above). Because the competitive interactions are likely to occur at a local microscale, it is unlikely that a single fungus would be able to dominate an entire site or even an entire root system. Similarly, if no clear dominance can be established and all competing fungi remain in the root system, multiple, equally competitive fungi may remain in the root system and coexist — a situation called combative deadlock (Cooke and Rayner, 1984).

The outcomes of the competition are not solely determined by the competitive abilities of the component fungi, nor are the competitive abilities static in time or space (Figure 7.4). Environmental heterogeneity and the dynamics of the critical environmental factors can influence the competition among mycorrhizal fungi. Studies of grain storage fungi have indicated that temperature and water, or nutrient availability, are important determinants (Armstrong, 1976; Magan and Lacey, 1984; Marin et al., 1998). Depending on the environmental conditions, different suites of component fungi were able to establish dominance in inoculated grain. Similarly, the outcomes of competition among mycorrhizal fungi will be modified by different environmental conditions that differ in space and time. This is particularly important in successional ecosystems where localized resource patches are distributed along extended (continuous) gradients, which change over time (temporal dynamics in successional environment) and space (space-for-time substitution in successional seres and accumulation of organic resources).

Can a superior competitor outcompete an already established fungus in a root fragment? We speculate that an established fungus can rarely be expelled from a root unless uncolonized space is exposed. If we assume that in successional ecosystems initial colonization is always established by an allochthonous propagule with limited access to host photosynthate by the established mycorrhizal fungi, drastic community changes would



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be unlikely. Observations in primary successional ecosystems (Helm et al., 1996; Trowbridge and Jumpponen, 2003) indicate that the entire root systems are rarely completely colonized during the earliest stages of primary succession. Accordingly, although time and order of mycorrhizal fungus arrival may be important in later stages of succession, they are unlikely to exclude establishment and dominance by less competitive fungal species in early succession (see Figure 7.4).

The biotic interactions discussed here operate on various levels in successional ecosystems. Interactions among trophic levels may influence mycorrhizal colonization via facilitative and inhibitory mechanisms acting upon propagule activation, spore germination, or processes involved in early mycorrhiza formation, such as partner recognition. Although experimental evidence for interactions among mycorrhizal fungi is scanty, we propose that at least competition for space, carbon, and mineral nutrients is acting within successional communities. Additional biotic interactions that may be similar to territorial strategies to exclude invading genotypes may also function in the course of successional dynamics. However, these biotic interactions may be of lesser importance in early primary successional environments, where only limited root space is colonized by mycorrhizal fungi. Later in these primary successional systems, and especially in secondary succession and as root space becomes more limiting, the biotic interactions are likely to increase in their relative intensity and importance (Figure 7.4 and Figure 7.5). In other words, competitive interactions are likely to increase over time in successional environments. We hypothesize that competition occurs in various forms, ranging from simple exploitation for space and nutrient resources to complex metabolic and molecular inhibitory effects. The bottom line is that competition intensifies as the overall available niche space becomes more tightly packed (Figure 7.5) and its impacts become more severe over successional time (Figure 7.4). It is most likely that competition operates mainly via differences in fungal growth rates (see Wu et al., 1999) after accounting for realized niches and possible inhibitory interactions among component organisms.

## 7.6 SYNTHESIS

### 7.6.1 Synopsis of the Proposed Model for Succession of Mycorrhizal Fungi

We have incorporated general central themes from community ecology into a simple filter model that focuses on mechanisms of successional changes in mycorrhizal communities. This includes both in- and out-of-site propagule availability into a local propagule or available species pool from which various component species are selected (INPUT). We considered the disturbed landscape patches as islands differing distinctly from the surrounding nondisturbed units. Depending on the level to which the local propagule pool was removed by the disturbance (i.e., the disturbance severity), the relative contributions of allochthonous and autochthonous propagule sources would vary (Figure 7.2). The environmental selection criteria (ENVIRONMENTAL filter) are based on the niche theory: any species unable to perform in any given environment would not be included in the active mycorrhizal community even if its propagules were available (Figure 7.3). In our community assembly model, host–fungus compatibility (HOST filter) is an essential selection criterion, especially for more host specific EM species. Fungi in the local species pool that establish and survive in the environment at any successional stage will, in turn, interact with other components of the soil community and likely compete for limiting resources. At a BIOTIC filter level, these competitive interactions are likely to eliminate the species occurring in the marginal areas of their environmental tolerances (Figure 7.4).

We suggest that the filters we propose allow greater accuracy in identifying critical factors in fungal community dynamics within a general framework for testable hypotheses. Which of the proposed filters act upon the fungal community in any given environment or successional system? One way to visualize the result of mycorrhizal community filtering is to show how different parameters change community composition. For example, one can test hypotheses on whether the community composition from one species pool changes with different levels of soil fertility following a disturbance event.

In our model, mycorrhizal propagules arrive as an allochthonous input (airborne spores, INPUT) at a barren site (no residual organic legacies, primary succession) after the disturbance event. Availability of compatible or physiologically receptive hosts in the pool of host plants will filter out certain mycorrhizal fungi from the species pool (HOST filter), with the remaining species labile within the propagule bank. The dominant mycorrhizal fungi will also likely be generalists with broad host ranges. The fungi establishing from the available propagule bank should show comparatively high (mineral) nutrient uptake and tolerance to various environmental stresses, excluding competition (ENVIRONMENTAL filter). The most abundant fungi will likely be positively correlated with mineral N and negatively correlated with organic N. Biotic interactions (BIOTIC filter) among the various components in the soil microbial assemblies interact with the mycorrhizal fungi either positively or negatively, facilitating establishment of some while inhibiting others. Competition among mycorrhizal fungi will be limited at the initial stages due to the abundant uncolonized root space (Figure 7.4). As a result, the capacity for fungal expansion into neighboring roots will be moderately high. Although competition for root space is low, the dominant mycorrhizal fungi may take long to establish and contribute to the autochthonous propagule bank. Eventual propagule production by the dominant colonizers will shift the relative contributions from allochthonous and autochthonous sources in the propagule bank, providing a feedback mechanism for community change (Figure 7.2). From a successional perspective, these root communities will be far less complex than in adjacent (nondisturbed) communities or secondary successional systems. Subsequent vegetation and mycorrhizal colonization will further modify the soil nutrient status, and thus result in changes in the ENVIRONMENTAL filter. One item to consider is the persistence (or inertia) of the initial colonizing mycorrhizal taxa and rate of colonization by other mycorrhizal fungi or saprobes (BIOTIC filter). These differences may lead to time lags between the ENVIRONMENTAL and BIOTIC filters.

In summary, the general principle of our proposed model is that species are selected from a larger regional or local species pool (here, a propagule bank) based on their abilities to pass through a series of environmental and biological filters. Only those species that pass through the entire set of filters prevail and establish under a given set of conditions. These component species will also be able to contribute to the local propagule pool via vegetative, mycelial expansion, as well as via deposition of propagules into the local spore bank.

## 7.6.2 Applicability of the Proposed Model

### 7.6.2.1 *Can These Assembly Rules Be Applied across Ecosystems?*

Although data for some components of our proposed conceptual model are minimal, we argue that the proposed model is sufficiently general to allow development of testable hypotheses upon which the search of universal rules of mycorrhizal community assembly in successional ecosystems can be based. Importantly, autochthonous and allochthonous dispersal factors, as well as relative importance of environmental tolerances and competitive interactions, are likely to vary substantially among communities. We are currently unable to make clear predictions on the relative importance of the different components

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in our model across different communities in various successional stages. However, we believe that our model serves as a starting point for developing hypotheses on the specific drivers of mycorrhizal community change.

### 7.6.2.2 On What Scale Is the Proposed Model Applicable?

The components that we have presented and proposed above operate mainly on small, local scales. For example, competitive interactions are likely to take place on the scale of a root fragment, possibly a proportion of the root system. Similarly, resource patches may be very limited in their size, confining the fungal niche to small spatial units. Although the model components may be limited in their scale, the outcomes of the various filters will influence the community composition not only on local, but also on larger, possibly ecosystem, scales. We argue that incorporation of the local and allochthonous propagule production expands the scale of our proposed model. Our aim is to account for both out-of-site and local contributions to the potential species pool in any successional ecosystem or community. The general, underlying question is: What are the component species that comprise mycorrhizal fungus communities in successional ecosystems? If we consider successional ecosystems as islands demarcated by distinct disturbance events within which various environmental pressures and biotic interactions define successful component species, we should be able to utilize this model to identify controls of community composition on an ecosystem scale.

## ACKNOWLEDGMENTS

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