MYCOLOGY VOLUME 17

Fungi in Ecosystem Processes

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Preface

Why did I decide to write this book? As an undergraduate student I could not make up my mind whether I wanted to be a zoologist or a botanist, so I decided to adopt ecology, in its broadest sense, as my area of interest. This led me to think about interactions among organisms and to try to look at ecosystems from a holistic, rather than from an autecological, point of view. As someone with little formal training in mycology, my interest in fungi started during my doctoral research, especially when attending university-wide lectures by C. T. Ingold, given at the University of London. My former job, at the then Institute of Terrestrial Ecology at Merlewood, UK, brought me into contact with the work on ectomycorrhizae, decomposition, and nutrient cycling in temperate and subtropical forest ecosystems. During this time, I had many fruitful discussions with fungal ecologists in both the British Mycological Society and the international world of mycorrhizal researchers. In particular, I remember animated discussions with Alan Rayner, who is a font of knowledge, inspiration, and encouragement. As a result of this history, I have been fascinated by the multifarious ways in which fungi interact with other organisms and function in moderating the processes occurring in ecosystems.

With my move to Rutgers University, I initially taught my first graduate course, Fungi in Ecosystems, during my first semester, while all my books and notes were on a ship crossing the Atlantic. The continued development of this course has been the impetus for this book. As I could find no textbook for my students that really approached the subject of mycology from an ecosystem point of view, I decided to put my ideas on the importance of fungi in ecosystem processes into a volume that could be used by upper-level students and

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researchers. This course and its variants have been the main thrust of my teaching at Rutgers. This has not been a sole venture as, along with my interactions with Jim White and Peter Oudemans, we are gradually building a strong and interactive series of mycology courses in our university.

In this book I have started with the list of functions that Alan Rayner suggests that fungi perform in ecosystems (introduction to the second edition of *The Fungal Community: Its Structure and Function*, edited by George C. Carroll and Donald T. Wicklow, (Marcel Dekker, 1992)). I have attempted to elaborate on these functional roles of fungi and tried to show how the world would function less satisfactorily in the absence of fungi. Given the vast range of fungal literature I have not been able to do much more than scratch the surface of the subject. However, I hope that the more than 1300 references that I have cited will act as a means for interested readers to delve further into the literature on any specific subject area. For the upper-level students and researchers to whom this book is targeted, I hope that it will stimulate thoughts beyond the narrow confines of their immediate research questions and allow them to place their work in the wider context of the functioning of ecosystems. I believe that it is only by the greater understanding of the linkages between organisms and the processes they control in the ecosystem that we can appreciate the beauty of the living world around us, appreciate the impacts that we are having on ecosystems, and obtain the understanding of the function of component organisms that will allow us to protect and preserve nature.

In attempting to summarize the vast literature, I have written the text in my own words, but have relied heavily on previously published literature for figures and tables to support my commentary. Most tables have been reconstructed and almost all figures have been redrawn from their original in an effort to simplify the information presented in the originals. For the statistical purist, I hope that my removal of error bars and indications of significant differences will be forgiven for the sake of simplicity of presentation. In the main, the data shown in figures represent statistically significant interactions. Although the figures and tables represent the key message I wish to convey, they are no substitute for the original data and publications. I encourage the interested reader to explore further by consulting the original publications to obtain more information that I can impart in this book.

I dedicate this book to my uncle, Wally Champkin, whose enthusiasm for natural history fueled my interest in ecology. As a child I was constantly amazed that he could put a name to most of the plants, insects, and birds we saw on our walks. I could watch for hours his cine films and stills of birds, flowers, moths, and butterflies. I owe a debt of gratitude to my parents, who encouraged and supported me in my studies and allowed me to pursue my own interests in biology. I especially thank my wife, Joan, and daughter, Gail, who have supported my career, moved with me to the United States, and encouraged me in

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the writing of this book. I could not have completed this task without them. Finally, I wish to thank Bob Evans, who commented on the first drafts of my work here, and to the students and colleagues in my research group, who have both given me encouragement and tolerated my absences during the creation of this book.

John Dighton

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Introduction

1.1 WHY FUNGI?

The first law of thermodynamics indicates that matter can neither be created nor destroyed. Within ecosystems, this law governs the transformations of energy and nutrients between compartments. Energy and nutrients are contained within the living biomass of the plants and animals forming communities within the ecosystem as energy and nutrient stores. The transformations of energy and nutrients that occur among these is a result of trophic interactions within food chains and webs and are regarded as the processes that occur in ecosystems. The nature of these stores of nutrients and energy within individual organisms and communities and the movement of material among them is the science of ecology. We will consider here the role that fungi play in some of the major ecosystem processes, namely the process of transforming carbon dioxide and nutrients into plant biomass by photosynthesis, the energy and nutrient transformations among components of food webs, and the transformations carried out by saprotrophic decomposers that use the energy and nutrients from dead plants and animals, resulting in the mineralization of nutrients for new plant growth. This latter process is referred to as energy and nutrient cycling. In addition, we will explore the interactions of human influence on the processes carried out by fungi in the ecosystem.

Fungi are a group of organisms that cannot fix energy directly, but they use the energy stored in plant and animal biomass to create their own mass. It is the vast array of interactions among fungi, and other living and dead organisms along with their interaction with the nonliving components of the environment that make fungi a key group of organisms in the regulation of ecosystem processes. Fungi are important in driving or controlling the mineral and energy cycling within ecosystems and influencing the composition of other organisms within the ecosystem.

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needed to build cytoplasm and structural components of plant biomass. Some of these nutrients come directly from mineral soil; however, much is recycled within the ecosystem. Nutrients that are locked up in plant and animal biomass become available to the saprotrophic community upon the death of the organism. The saprotrophic community, consisting largely of fungi and bacteria, utilizes the energy and nutrients contained in the dead material, but through "leakiness" of its activities, allows a proportion of the nutrients to become available to other organisms through the process of nutrient mineralization. This leakiness is a result of the inefficiencies in utilizating the end products of the activity of extracellular enzyme activity. The absorption of reaction products is never 100% efficient, and the mineralized nutrients that are not absorbed by the fungus are released into the environment and are accessible by other organisms. For example, this activity provides soil fertility for plant growth or increased nutrient content of streams for the growth of algae. We will discuss the role of fungi in both the direct support of photosynthetic activities, mainly within lichens, and in controlling the availability of mineral nutrients in the environment that can be used by autotrophs. Within this context we will discuss the role of lichen, saprotrophic, and mycorrhizal fungi.

The organisms that make up the biotic component of ecosystems coexist in communities. The interactions among members of the community can involve competition for available resources (e.g., food, light, and space) or competition among trophic levels in producer–consumer and predator–prey food web interactions. (For a review of communities, see Morin, 1999.) Within the context of population regulation of plants or animals, fungi play an important role as pathogens. Subtle interactions among fungi and plants and animals may alter the fitness of individuals or species within the community without showing the outward signs of pathogenicity. Fungal interaction with plants can be seen in the form of pathogens, which are detrimental to plant growth and fitness: mycorrhizae, which help plants obtain nutrients and provide defense against pathogens, and endophytes, which provide defense against herbivory and improve nutrient levels in the plant. In addition, fungi themselves play an important and direct role within food webs in ecosystems by being consumed by fungal grazers, and as dead organisms, by the saprotrophic activities of bacteria and other fungi within the ecosystem. Fungi are thus important in determining the population of individuals of a species in a community and the species composition or structure of that community.

The increasingly important role of humans on the landscape in most ecosystems around the world adds another dimension to the role of fungi in the environment. Because of the relatively short generation times of microbes, particularly bacteria, fungi and actinomycetes are able to more rapidly evolve resistance to disturbance than other "higher" organisms. The effects of human interactions in the environment can thus have a detrimental effect on

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the communities of fungi as well as their physiology and biochemistry. Fungi are also able to adapt to new conditions and have the capacity to utilize pollutants produced by anthropogenic activities, however. The role of fungi in heavy metal and radionuclide-polluted environments will be used as examples of the potential role of fungi in remediation of polluted ecosystems and other biogeochemical processes.

1.3 WHAT ARE FUNGI?

We will not dwell on the taxonomy and structure of fungi, as these topics are adequately discussed in other texts (Alexopoulus and Mims, 1979; Moore-Landecker, 1996; Kendrick, 1992; Hawksworth et al., 1995). We will, however, review some of the key features of the fungal body and its physiology that allow fungi to make an important contribution to ecosystem processes. The taxonomy of fungi is constantly in debate and there are continual changes in terms of the category under which species should be organized and in terms of the nomenclature of each of the hierarchical categories. For the purposes of our discussion of the role of fungi in ecosystem functions, we can say that all taxa of fungi may be involved in the processes that are described (with certain restrictions), but the details of involvement may depend upon taxonomic status and life history traits. Of these traits we will mention the general models of r-, K- and R–C–S selection strategies, as defined by Pianka (1970) and Grime (1977; 1979), respectively (Fig. 1.1). The application of these strategies has been discussed in relation to the ecology of saprotrophic fungi (Cooke and Rayner, 1984) and mycorrhizal fungi (Dighton et al., 1986; Allen, 1991). The r–K continuum contends that organisms lie along a gradient of extremes in which r-selected organisms are opportunistic, are combatitive by virtue of fast growth, have a high turnover rate, have low investment in biomass and functional attributes (e.g., enzymatic diversity), and produce many offspring, many of which will not survive. The K strategist has the opposite traits of longevity, investment into biomass, and functional attributes, is combatitive by virtue of development of defense mechanisms, and produces few offspring, each with a greater chance of survival.

The R–C–S selection strategy is possibly a more useful theoretic concept in which to discuss the behavior of fungi. In this system, the extreme positions can be considered as the apices of a triangle. R-selected organisms are ruderals, having similar survival strategies of r-selected organisms. They are quick to colonize new resources, invest little energy and resources in biomass or enzymatic function, and are outcompeted by fungal species that are more able to produce secondary metabolites for defense. The C strategists are combatitive and are equivalent to the K strategists of Pianka (1970). C strategists are slow-growing but invest resources in biomass and such functional processes as

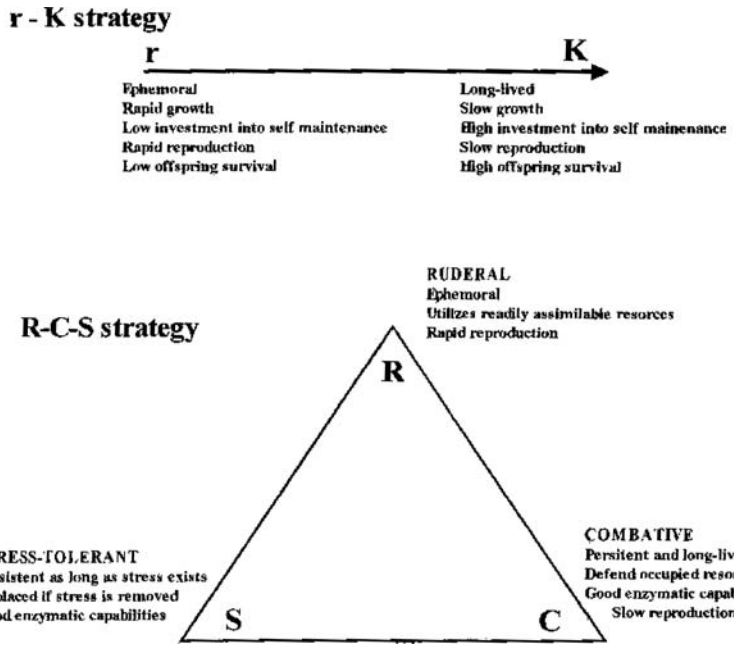

FIGURE 1.1 Life history strategies as applied to fungi, contrasting the r–K concept of Pianka (1970) with the R–C–S strategy of Grime (1977; 1979).

production of enzymes and secondary metabolites for defense. The third apex of the triangle is the S, or stress-tolerant, strategist. These exist because they are able to withstand a sustained stress within the environment (e.g., temperature, salinity, heavy metals). They resemble the C strategists in their physiological and life history traits. It is their ability to produce secondary metabolites or build defensive mechanisms in their biomass that enables them to withstand the sustained environmental stress under which they live. Upon removal of the stress, the S strategists will be less competitive against C strategists, resulting in a change in the community structure of the fungal populations. As resources in the environment become available for fungal colonization (e.g., new leaf litter during the fall) successions of fungi colonizing the resource tend to follow a trajectory from r (or R) strategists to K (or C) strategists (Andrews, 1992; Frankland, 1992). Both life history strategy simplify reality, but allow us to identify similarities and differences between fungal ecophysiology and changes in the environmental conditions in which they live. More complicated, but more realistic, models have been developed (Andrews, 1992). These simplistic

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models, however, serve a useful context in which to understand the changes in fungal communities during the utilization of resources and in the face of disturbance.

A stylized fungal organism is shown in Fig. 1.2, along with some of the properties that make it important in the context of this discussion. The mycelial portion of the fungus consists of hyphae. These hyphae, which are absent in the Chytridomycetes and yeasts, are a filamentous assemblage of tubular cells in which continuity is maintained between adjacent cells by the absence of cross-cell walls (septa) or a septum perforated by a pore. The hyphae thus develop as a coenocytic structure, consisting of continual cytoplasmic connectivity between adjacent cells. Hyphae average 5–6 μm in diameter and grow by wall extension at the tip (Rayner, 1991). Because they have a narrow diameter and long length, fungal hyphae present a large surface area, relative to volume, to the environment around them (Table 1.2). This property allows fungi to optimize the absorption of degradation products of simple carbohydrates and mineral nutrients that are derived from the action of extracellular enzymes produced by the fungi. Fungal hyphae may grow independently or coalesce to form larger and structured assemblages called rhizomorphs or strands. These

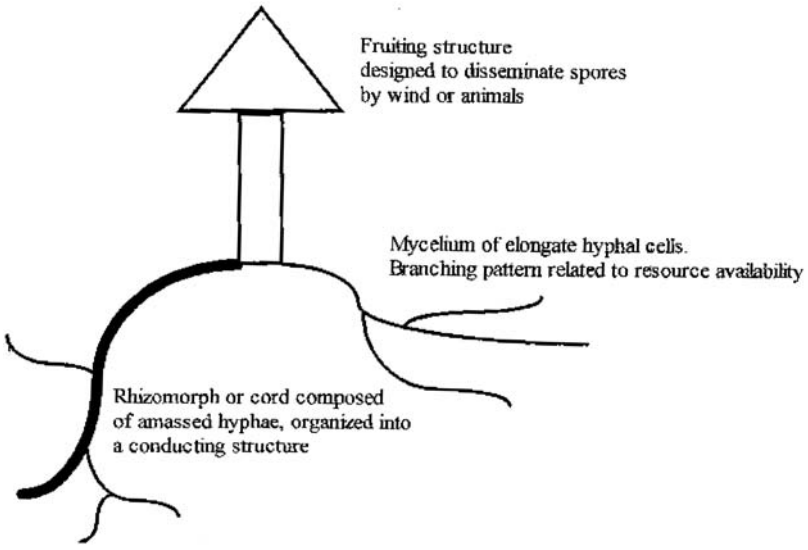

FIGURE 1.2 Diagrammatic representation of a fungus showing the branching of hyphae within the mycelium, aggregation of hyphae into cords, and the development of fruiting structures for spore dissemination.

TABLE 1.2 Characteristic of Fungal Hyphae in Relation to Their Size and Potential Effect of Their Surroundings

Hyphal diameter	5 μm
Hyphal dry weight	10% of fresh weight
1 cm^3 of packed myceium	4×10^4 m
1 g fresh weight mycelium	2.7×10^4 m
1 g dry weight mycelium	2.7×10^5 m
Surface area per g dry weight mycelium	4.2 m^2

Source: After Harley (1971).

linear structures are larger and more robust than individual hyphae and have been developed for long-distance transport of water and nutrients (Duddridge et al., 1980; Cooke and Rayner, 1984; Cairney, 1992). Nutrient and carbon translocation has important implications for maintenance of functional continuity in a heterogeneous environment (Boddy, 1999), in which resources can be reallocated within the fungal mycelium from areas of storage or excess to actively growing or functioning regions.

In this discourse on the structure and development of fungal mycelia, Rayner et al. (1986) discuss the mycelial network as a branching linear organ designed as a means of entry into and exit from a resource by a fungus. The direction of growth and the degree and direction of branching of the hyphae appear to be apically controlled. The degree of branching is controlled by feedback mechanisms between the resource quality into which the hyphae are growing and the physiology (growth and metabolic activity) of the hyphae. The concept of "fast effuse" and "slow dense" was thus coined (Rayner et al., 1986; Cooke and Rayner, 1984) to describe the patterns of hyphal growth found in favorable (nutrient rich) media and unfavorable (nutrient poor) media (Ritz, 1995; Rayner, 1996) (Fig. 1.3). Fast growth occurs when few resources are available and slow, dense growth occurs when there are abundant resources to be utilized and the fungus increases hyphal surface area to maximize enzyme release and end product absorption. The fact that the fungal hyphae appear to be ultimate fractal organisms (Ritz and Crawford, 1990) led Rayner (1996) to revise his discussion of hyphal growth in terms of nonlinear systems, fractals, and continuity of form over spatial scales. In terms of the role of fungi in ecosystem processes, fungal hyphae and rhizomorphs have resource exploitation patterns that relate to the quality of exploitable resources and the spatial distribution of the resources (Boddy, 1999).

As a result of the coenocytic arrangement of the hyphal network, there is the possibility of movement of resources within the hyphae from areas of high resource availability (sources) to areas of low availability or sites of resource demand (sinks). The movement of resources between sources and sinks is known

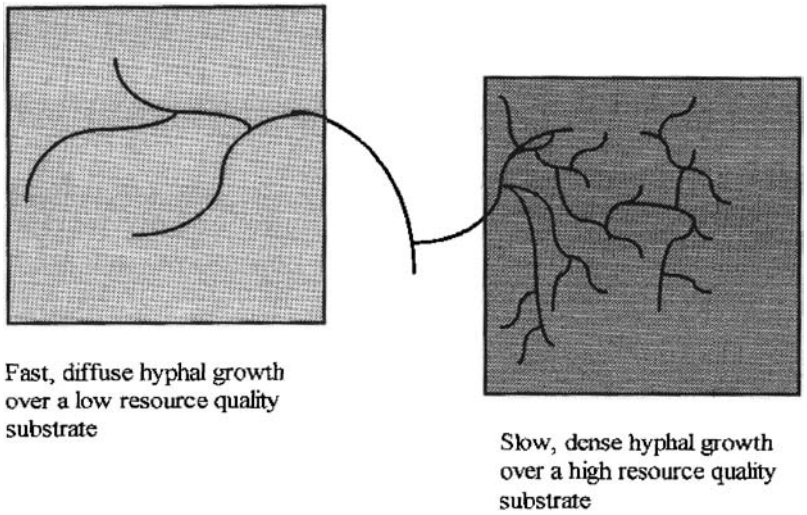

FIGURE 1.3 Representation of the exploitation of rich (right) and poor (left) resources by fungal hyphae. The fast, diffuse growth in the poor resource allows for rapid mycelial extension at minimal energetic cost to the fungus. The slow, dense growth in the rich resource allows for maximal exploitation of the resources within the substrate by the mycelium. Energy is expended to produce the extensive hyphal network to maximize the fungal surface area for the excretion of enzymes and uptake of nutrients and carbon. *Source*: After Rayner (1996) and Ritz (1995).

as translocation and has been described by Jennings (1976; 1982) and reviewed by Cairney (1992) and Boddy (1999). This attribute of the fungal mycelium, along with clonal plants, allows for the movement of resources over short (mm) to long (m) distances within the fungal mycelium, thereby reducing heterogeneity within ecosystems and connecting parts of the ecosystem in both space and time. The temporal component of this activity, immobilization, is as important as the spatial component. As mycelia grow, there is incorporation of new carbon and mineral nutrients into the biomass of the advancing hyphal front and to more proximal biomass by translocation and immobilization. While the fungal mycelium is alive and active, much of this material remains bound to structural components or in the cytoplasm. Upon the death of more proximal parts of the mycelium, however, materials incorporated into biomass may either be retranslocated from dying to living components or released into the environment via decomposition and mineralization processes. The duration of incorporation of material into biomass is regarded as an immobilization phase, whereby the material is unavailable for use by other organisms. The duration of this immobilization phase is dependent upon the turnover time of the organism. In

comparison with bacteria, which have turnover times of hours or days, some higher fungi may have hyphal turnover times of weeks or years, hence fungi may be important long-term accumulators of materials and thereby effect temporal changes in the availability of materials in the environment. The fungal mycelium is thus a sessile system of indeterminate growth. Andrews (1992) discusses the structure advantages and disadvantages of these "modular" organisms, and some of their attributes are listed in Table 1.3.

Fungi reproduce sexually or asexually (or both). In either case, new offspring can arise from spores, which are produced as dispersal agents. The production of spores often leads to the production of specialized fruiting structures on which the spores are borne. In the case of the higher fungi, Basidiomycotina and Ascomycotina, these fruiting bodies are large and visible. Because the production of spores demands energy and additional nutrients, these fruiting structures are a sink for internally translocated carbon and nutrients. The fruiting bodies are therefore an ideal food source for grazing animals. In terms of fruiting structures specifically and mycelia in general, fungi compose an important constituent of food webs by supporting secondary production

TABLE 1.3 Some Attributes of Unitary and Modular Organisms

Attribute	Unitary (discrete) organisms	Modular (non-discrete) organisms
Branching	Generally nonbranched	Generally branched
Mobility	Mobile; active	Nonmobile, sessile
Germ plasm	Segregated from soma	Not segregated
Growth pattern	Noniterative, determinate	Iterative, determinate
Internal age structure	Absent	Present
Reproductive value	Increases with age, then declines	Increases with delayed or no senescence
Environmental effects	Relatively minor hrole in development	Relatively major role in sessile forms
Effects on environment	Discrete, local effects hincreasing environmental heterogeneity	Discrete effects increasing heterogeneity and/or internal translocation allowing a soothing of environmental heterogeneity
Examples	Higher animals and plants	Fungi, bryozoans, corals, clonal plants

Source: Modified from Andrews (1992).

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(production of grazing animal biomass) in ecosystems. The functional role of fungi in a terrestrial ecosystem is represented in Fig. 1.4, which shows the interactions between above- and below-ground components of the ecosystem, plants, animals, and the abiotic environment.

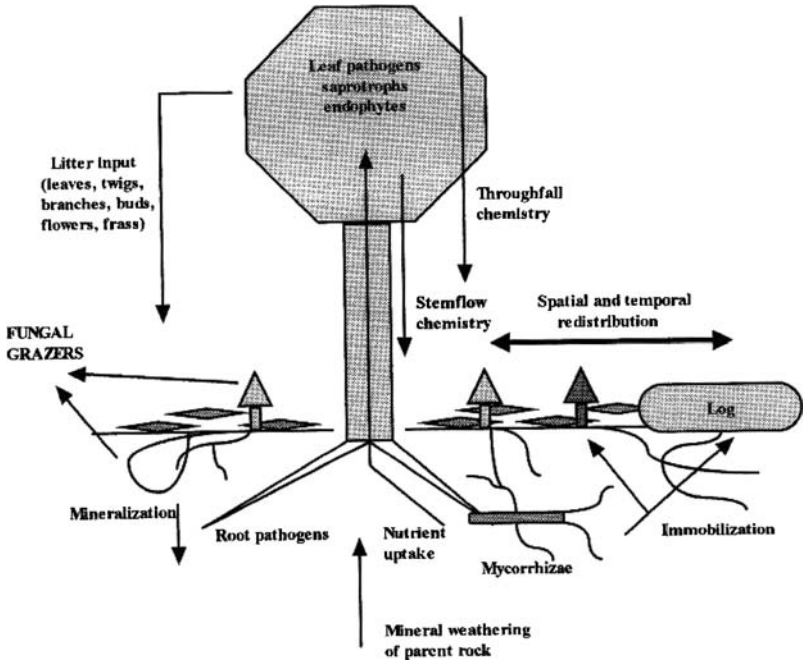

FIGURE 1.4 Representation of a plant–soil–fungal interaction in a terrestrial ecosystem. The model shows the effect of fungi in the above-ground plant parts to modify both throughfall and stemflow rain chemistry. The impact of canopy fungi is on plant fitness and may modify the chemistry of litter falling to the soil surface. At the soil surface there is litter decomposition by the saprotrophic fungal community, with the resultant mineralization of nutrients into the soil inorganic nutrient pool. Nutrients are immobilized into recalcitrant organic resources (such as the log on the right) and into fungal biomass. Here there can be both temporal and spatial redistribution of nutrients within the fungus and among resources utilized by the fungi. Mycorrhizae on plant roots aid the uptake of mineral nutrients into the plant, help to defined the plant against root pathogens, and may effect decomposition of organic residues. Both fungal hyphae and fruiting structures (represented by mushrooms) are a food source for grazing animals, thus influencing the fitness of individuals and regulating animal populations. *Source*: Adapted from Dighton and Boddy (1989).

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1.4 SPECIFIC ECOSYSTEM SERVICES CARRIED OUT BY FUNGI

1.4.1 Making Nutrients Available

As with other micro-organisms, fungi obtain their energy and nutrients by the secretion of extracellular enzymes into the environment. Degradation products, containing carbohydrates and/or mineral nutrients, are then absorbed by the hyphae and distributed within the organism by translocation. This process is termed saprotrophy and has important consequences outside the mere nutrition of the fungus. The process of extracellular degradation of resources is less efficient than ingestion of food into a gut, resulting in a fraction of the useful resources being released into the environment around the fungus. This inefficiency results in one of the key functions of saprotrophic soil fungi, the mineralization of nutrients into the soil nutrient pool (Dighton, 1997). This attribute will be discussed in more detail as it pertains to the supply of nutrients for primary productivity. In addition to the usage of organic components of the soil, leaf litter, woody debris, and animal remains, there are a number of ways in which fungi can interact with the mineral component of the soil. The secretion of oxalic acids can assist in the weathering of calcareous bedrock. In the mutualistic symbiotic association with algae, lichens produce lichenic acid, which facilitates rock solubilization and the formation of protosoils. Once a true soil has been formed, fungi are important contributors to the formation and stability of soil aggregates. These combinations of mineral soil particles and organic matter are refugia for microscopic organisms in soil, such as bacteria, protozoa, rotifera, and nematodes. Their activity at the micro scale results in the mineralization of inorganic nutrients for plant growth, and hence, soil fertility. The combination of polysaccharide secretions from bacteria and the binding property of threads of fungi assist in maintaining the structure of soil aggregates (Wright and Updahaya, 1998). Recent debates regarding the efficiency of highly intensive and mechanical agricultural practices have shown that minimal- or no-till agricultural practices reduce the disruption of hyphal networks in soil, and together with other factors improve soil aggregate stability and fertility. The pivotal role of fungi in the formation and maintenance of fertile soils for plant primary productivity will be discussed in Chap. 2.

1.4.2 Assisting Primary Production

In addition to mutualistic associations with algae, fungi also form symbiotic associations with higher plants. The root–fungal association is known as a mycorrhiza (literally fungus root). Some 90% of all higher plant species are associated with mycorrhizae (Pirozynski and Malloch, 1975), in which the association benefits the host plant by increased efficiency of nutrient uptake and

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the fungus benefits from a direct carbohydrate supply from the plant (Harley, 1969; Harley and Smith, 1983; Smith and Read, 1997). Considering that such a high percentage of plants are mycorrhizal, one might speculate that there is little interest in the study of these fungi, especially if they all perform similar functions. Evidence show, however, that these fungi have benefits in protecting the host plant from root pathogens (Marx, 1973; Duchesne, 1994; Brazanti et al., 1999). More recently, subtle effects of these mycorrhizal fungi on host plant fitness have been reported. These mycorrhizal benefits may partly be due to enhanced plant nutrition, but others are related to interactions with pathogens, in which no symptoms of the pathogen exist (Newsham et al., 1994; 1995) and in the fitness of grazers upon these plants (Goverde et al., 2000). The role of fungi in plant primary production will be explored in greater depth in Chap. 3.

1.4.3 Fungi in the Food Web

As a component of the ecosystem, fungi are available to be consumed by animals as a food resource. Indeed, fungi provide a highly nutritious form of food since it has been shown that they contain high levels of proteins and vitamins (Fogel, 1979; Grönwall and Pehrson, 1984). The production of mushrooms for human consumption in the United States currently runs at approximately 430,000 mg per year. In the natural environment, fungi form the food base for a variety of animals. Mushroom-forming species, along with lichens, are staple food items for reindeer and moose in boreal ecosystems (Cooper and Wookey, 2001; Kumpula, 2001), whereas the hyphae and spores of soil fungi are food for microscopic fungivorous mites, collembola, and nematodes (Shaw, 1992; McGonigle, 1997). The fruit bodies of hypogeous fungi, such as truffles, are food for rodents and wild boar, and adaptations of those fungi that fruit below ground are often such that spore dispersal is only possible though an animal vector (Trappe and Maser, 1976; Trappe, 1988; Cork and Kenagy, 1989). Trophic and nontrophic interactions will be the subject of Chap. 4.

1.4.4 Fungal Effects on Populations and Communities

Fungi may be selective in their source of a food base or may be restricted in terms of resource exploitation by competition with other fungal species. Providing the resource contains carbohydrates for energy and nutrients for growth, however, this resource can come from living or dead plant or animal tissue or merely from chemicals in the atmosphere (Wainwright et al., 1997). This leads to another property of fungi, their pathogenicity to both plants and animals, whereby the fungi "eat" living organisms. The role of fungal pathogens in agriculture has been

the subject of considerable research over many years. Indeed, the potato blight in Ireland (1843–1846) could be regarded as a classic example of the magnitude of the effect of a fungus on ecosystems (Austin Bourke, 1964). The fungal-induced potato crop failure not only reduced crop yield, it reduced the population of grazing fauna (humans) and caused one of the largest emigrations of fauna from an infected area (the movement of thousands of Irish to the United States). The economic loss of crops has resulted in the development of a large agrochemical industry to provide effective fungicides to combat fungal diseases of plants. In addition to the loss of plant biomass, other effects of pathogens result in the reduction of the fitness of the host organism. This fitness can be measured in terms of loss of reproductive capacity. This reduced fitness has important consequences on the population of the organism and/or its competitive abilities within the community. Fungi are thus involved in the regulation of the community structure of organisms and the population of individual species. Chapter 5 will discuss the role of fungi in influencing animal and plant populations and community structure, but will consider mainly natural ecosystems rather than the agricultural implications.

1.4.5 Fungal Interactions with Human Activities

All of the above roles of fungi in natural ecosystems are increasingly influenced by human activity. In Chap. 6 we will examine some specific interactions between anthropogenic impacts and the function of fungi, together with how fungi may be used to mitigate some of the effects of human-induced disturbance and pollution. Fungi are negatively influenced by acidifying pollutants, such as sulfur dioxide, which damages the physiological capacity of fungi (Arnolds, 1991; Dighton and Jansen, 1991; Newsham et al., 1992a, b; Shaw, 1996). Atmospheric nitrogen deposition, resulting from industrial process and automobiles, acts as an acidifying pollutant and as a fertilizer to cause changes in the nutrient cycles affected by fungal processes (Wallander and Nylund, 1991; Jonsson, 1998). Fungi may be adversely affected by heavy metals in the environment (Kuperman and Carriero, 1997; Martino et al., 2000), but are able to immobilize these metals (Morely et al., 1996; Kottke et al., 1998; Miersch et al., 2001) and effect chemical transformations of the chemicals to make them more or less toxic to other components of the food web (Byrne et al., 1997). Fungi are involved in the accumulation of radionuclides (Dighton and Terry, 1996) and are involved in the decomposition of radionuclide-containing materials (Zhdanova et al., 1991; 2000). They even have been shown to grow toward sources of radiation (Zhdanova et al., 1994).

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1.5 CONCLUDING REMARKS

In summary, the intent of the following information is to report on and speculate from the research that has been done since Jack Harley presented his presidential address to the British Ecological Society entitled "Fungi in Ecosystems" (Harley, 1971). In this address, Harley states that "It is clear from recent work that the magnitude of their [fungal] intervention in nutrient and energy cycling may be very great," and he presents a diagrammatic scheme of fungal intervention in the carbon cycle (Fig. 1.5). Harley cautions, however, that there are two difficulties in determining the roles of fungi in ecosystems. First there are difficulties in determining the identity (species) of fungi in their vegetative state, and second in being able to predict the true physiology of fungi in the natural environment from

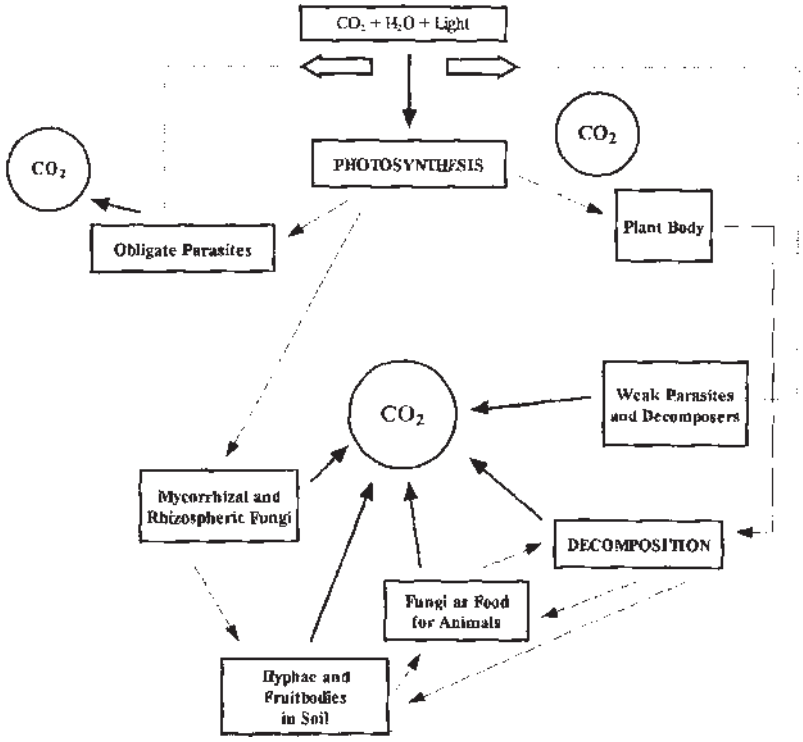

FIGURE 1.5 The role of fungi in carbon cycling as proposed by Harley (1971). The left side of the model is driven by fungal symbionts and pathogens, which directly utilize plant photosynthates. The right side of the model represents the decomposition cycle, utilizing dead plant and animal parts. Open arrows at the top indicate feedback effects on photosynthesis (plant fitness).

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the studies conducted with fungal cultures in the laboratory. The former problem is being overcome by the development of molecular tools to identify fungal species and the second is being addressed by careful manipulation studies in the field and the use of isotope tracer and natural abundance isotope studies. The links between these studies and the ecophysiology of fungi are still in their infancy, however. These studies are further hampered by our lack of understanding of the physiology of the majority of fungi in the world. Hawksworth (1991) reports that we currently have identified some 69,000 fungal species worldwide. He then calculates from the number of fungi currently known to coexist with plants and animals that with the number of new plant and animal species likely to be discovered in the future the total possible number of fungal species could be of the order of 3 million (Fig. 1.6). A browse through the species list in the back of current fungal physiology texts indicates that we probably know a little of the physiology and biochemistry of less than 1% of all possible fungal species on our planet. The debate about the role of species diversity and ecosystem function has been started by investigation of plant community structure (Tilman et al., 1996; Naeem et al., 1994; 1996). In the fungal context, there is probably greater need to separate functional diversity from taxonomic diversity (Zak et al., 1994), as many species across a number of higher taxonomic

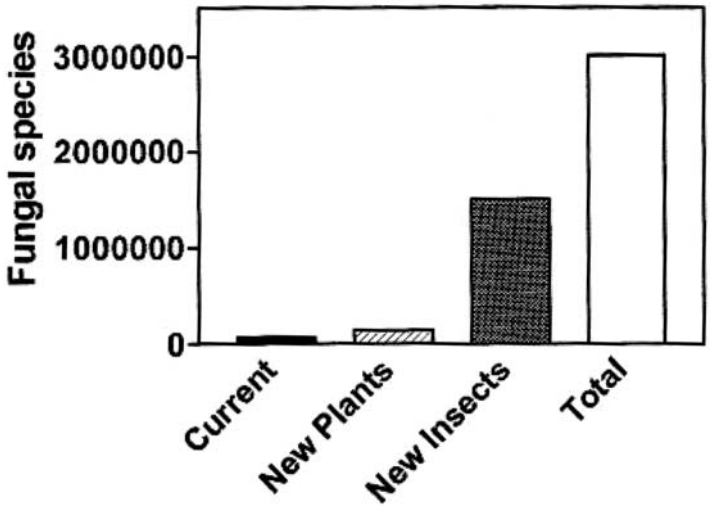

FIGURE 1.6 Actual number of fungal species known (69,000) and potential total number of fungal species in the world (3,004,800) based on new species to be found associated with yet to be discovered plants and insects. *Source*: Data from Hawksworth (1991).

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categories are capable of carrying out similar functions. It is only recently that researchers have started to investigate the functional diversity of microbial communities (Ritz et al., 1994) and started linking this functional diversity to the ecosystem-level functions of nutrient and energy flow in, primarily, terrestrial ecosystems (de Ruiter et al., 1998; Ekschmitt and Griffiths, 1998; Hodkinson and Wookey, 1999; Baxter and Dighton, 2001). We will proceed to explore the role of fungi in ecosystem processes and amplify the sentiments of Rayner (1998) with this level of ignorance. This will require a high degree of extrapolation of function between species and confront the problems of transcending spatial scales from the micro to landscape level (Friese et al., 1997) and temporal scales of seconds to decades.

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2

Fungi and Primary Productivity: Making Nutrients Available

2.1 SOILS AND NUTRIENT AVAILABILITY

Within ecosystems, primary production is carried out by autotrophic organisms. These organisms, plants, are able to fix carbon by the process of photosynthesis and build biomass by combining this fixed carbon with nutrient elements derived from the environment. The nutrients required for plant growth come from two main sources. The first source is the rock material underlying the soil. This rock may be of local origin, or of remote geology in areas that have been affected by glaciation. Rocks of the earth's crust contain a variety of the essential mineral nutrients that plants need, but the minerals are bound in complex chemical forms that make them poorly available for plant uptake. By the action of environmental factors (wind, water, and physical disturbance) along with the activities of bacteria, fungi, and plant roots, the surface of rocks can be weathered and degraded to finer particles and the mineral nutrients released in a soluble form that can be accessed by plants. Some of these minerals will be carried in water to streams, rivers, and oceans, imparting fertility to these ecosystems. The second source of nutrients is by the breakdown or decomposition of dead plant and animal remains by microbes and animals. During decomposition, mineral nutrients are released in a soluble form as inorganic ions from the breakdown of the organic complexes within the plant and animal remains. This process is called mineralization, and provides fertility to the ecosystem. Decomposition and mineralization occur in terrestrial, freshwater, and marine ecosystems. In this chapter we will investigate the role that fungi play in these processes (Table 2.1).

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TABLE 2.1 Ecosystem Services Provided by Fungi

Ecosystem service		Fungi functional group
Soil formation	**Rock dissolution**	**Lichens, Saprotrophs, Mycorrhizae**
	Particle binding	**Saprotrophs, Mycorrhizae**
Providing fertility for primary production	**Decomposition or organic residues**	**Saprotrophs, (Ericoid and ectomycorrhizae)**
	Nutrient mineralization	**Saprotrophs, (Ericoid and ectomycorrhizae)**
	Soil stability (aggregates)	**Saprotrophs, (Arbuscular mycorrhizae**
Primary production	Direct production	Lichens
	Nutrient accessibility	Mycorrhizae
	Plant yield	Mycorrhizae, pathogens
	Defense against pathogens	Mycorrhizae, Endophytes, Saprotrophs
	Defense against herbivory	Endophytes
Plant community structure	Plant–plant interactions	Mycorrhizae, pathogens
Secondary production	As a food source	Saprotrophs, Mycorrhizae
	Population/biomass regulation	Pathogens
Modification of pollutants		Saprotrophs, Mycorrhizae
Carbon sequestration and storage		Mycorrhizae, (Saprotrophs)

Note: Services to be considered in this chapter are in bold face. Fungal groups in parentheses are regarded as of lesser importance in that function.

The bulk of the chapter will deal with terrestrial ecosystems, as this is where most of the information on these processes had been derived. The impact of decomposition activity within terrestrial ecosystems has a profound effect on the fertility of streams and rivers by the process of leaching. Here, nutrient elements in water percolate through the soil into water courses, carrying soluble nutrients derived in the terrestrial environment that have not been immobilized into land plant tissue.

2.1.1 Making Soils

Soils are a complex composition of weathered mineral rock and organic material derived from dead plant and animal remains together with the living biota of bacteria, actinomycetes, fungi, protozoa, nematodes, soil

microarthropods, and other small fauna (Coleman and Crossley, 1996). To equate a soil with "dirt," which is essentially the abiotic component of soil, would be too simplistic. It is the holistic complement of abiotic and biotic components that makes the true, functional soil. Only by the close association and interaction of the component parts and the dynamic interaction between the biotic and abiotic components can the soil provide a continual source of nutrients for plant primary production. The importance of soil fertility has been known since the time of the development of agricultural practices in the Nile delta. The consequences of loss of stability of the tightly coupled interactions among the biotic and abiotic soil entities through mismanagement of agricultural soils and in combination with changes in climate result in the loss of soil fertility, as well as soil erosion and reduced crop yield. Much of this has been seen in recent years in sub-Sahalian Africa and is caused by the attempts to sustain a greater population than the carrying capacity of the land. In the historical past, we have witnessed wars and conflicts over religion, politics, and water. It is highly likely that future conflicts will be over the availability of fertile soils, especially if the predictions of global population increase are correct (Brown, 1995; Meadows et al., 1992).

Soils do not just occur; they are created by the breakdown of parent rock into mineral particles. The surface ionic exchange properties of these mineral particles give soil its fertility. The rate of exchange between ions bound to the surface of soil particles and those within the soil solution impart the fertility to soil. The greater the degree of dissociation of ions into soil solution, the more fertile the soil becomes, as plants are best able to access freely soluble nutrients. We shall see that fungi are important in creating these soil particles, modifying their chemical composition and association with organic matter and their ability to modify the physical structure of soil, which in turn influences the porosity, water-holding capacity, and overall stability of the soil. Weathering of parent rock material may be accomplished by a variety of abiotic factors. Brady and Weil (1999) describe the processes of mineral rock breakdown caused by weathering by wind and water, freeze/thaw cycles, and the effects of weak acids, formed by carbon dioxide combining with rain water. There are, however, a number of biotic factors that also influence the rate of parent rock breakdown, which in turn influences the development of soils. There is considerable literature suggesting that lichens play a significant role in the formation of soils. The soils that are formed are the substrates for the development of vascular plant communities, whose contribution to primary production through photosynthesis would be reduced in the absence of lichens. In addition, both saprotrophic and mycorrhizal fungi can be associated with mineral rock dissolution. The close and possibly synergistic association between fungi and bacteria, especially in the mycorrhizal habit, also enhances the dissolution of rock to release mineral nutrients.

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A. The Role of Lichens in Soil Formation

Lichens are a symbiotic association of algae and, primarily, ascomycete fungi. Some 15,000 species of lichen have been identified. They are often able to survive extreme environments of heat, cold, and drought that other organisms are less able to tolerate. It is in these climatically extreme or oligotrophic (nutrient-impoverished) environments that lichens become important actors in the formation of soils. Approximately 8% of terrestrial ecosystems are lichen-dominated, and in many of these systems, the ground cover by lichens is often very high, up to 100% (Honegger, 1991) (Table 2.2).

The definition of a lichen is a subject discussed by Hawksworth (1988). Definitions range from Berkely's 1869 suggestion that "it is quite impossible to distinguish some lichens from fungi" to Hawksworth's 1983 definition of "a stable self-supporting association of a fungus (mycobiont) and an alga or Cyanobacteria (photobiont)." Later, Hawksworth revised the definition to "A lichen is a stable self-supporting association of a mycobiont and a photobiont in which the mycobiont is the exhabitant," which suggests that the photobiont resides within the fungal tissue. Indeed, Sanders (2001) considers lichens to be "the interface between mycology and plant morphology." The algal symbiont is usually a green or yellow-green eucaryotic alga and sometimes a blue-green procaryotic Cyanobacteria. The algae are restricted to the upper zones of fungal tissue, where light is maximal for photosynthesis. The fungal associate is usually an Ascomycete or a Deuteromycete, with occasional Basidiomyctes that are

TABLE 2.2 Taxonomic Diversity of Lichen Mycobionts and Photobionts

	(%) Lichens
Lichen mycobiont	
Ascomycotina	98
Basidiomycotina	0.4
Deuteromycotina	1.6
Lichen photobiont	
Green algae	85
Cyanobacteria	10
Green algae plus Cyanobacteria	3–4
Lichen structure	
Homoeomerous (nonstratified) thalli	55
Placodioid or sqamulose thalli	20
Foliose or fructose heteromerous (stratified) thalli	25

Source: After Honegger (1991).

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restricted to the genus *Omphalina* (Hawksworth, 1988). Fungi usually form the basal portion of the lichen, which may be differentiated into a stalklike structure or podetia. Fungal tissues form the greater proportion of the biomass of lichens and are the supporting tissue for the algal symbiont. In addition to the combination of algae and fungi, other nonphotosynthetic bacteria may also be present within the lichen (Banfield et al., 1999), also playing a role in soil biogenesis.

Brady and Weil (1999) show that biogeochemical weathering of rock is a function of water availability, the presence of organic acids, and complexation processes. Specifically, water is involved in hydration, hydrolysis, and dissolution. Hydration of oxides of iron and aluminum is an important process in rock degradation; for example, hematite (Fe_2O_3) is converted into ferrihydrate ($Fe_{10}O_{15}{\cdot}9H_2O$). Hydrolysis is important in the release of essential nutrients for plant growth. For example, potassium is released from microcline, a feldspar by the following reaction: $KAlSi_3O_8 + H_2O \Leftrightarrow HAlSi_3O_8 + K^+ + OH^-$. Dissolution allows the dissociation of anions and cations from complex materials. For example, gypsum dissolves to release calcium and sulfate ions. In dry areas, the structure of lichens acts as a point of condensation of water and a site on which atmospheric water can collect (Lange et al., 1994). They are therefore nuclei for water-related rock-weathering processes. A review of rock weathering by lichens is given by Chen et al. (2000).

The presence of living organisms increases the carbon dioxide concentration in the atmosphere because of their respiration. In the localized area around lichens and lichen communities on rocks, the condensed water mixes with carbon dioxide to form carbonic acid. This weak organic acid is an important agent of dissolution of the calcite found in limestone and marble ($CaCO_3 + H_2CO_3 \Leftrightarrow Ca^{++} + 2HCO_3^-$). Lichens and soil fungi and bacteria are organisms that produce organic acids, such as oxalic, citric, lichenic, and tartaric acids, which in turn contribute to the chemical weathering of rocks. These acids increase hydrogen ion concentration in the environment, lowering pH and increasing the solubility of aluminum and silicon. They also form chelation products (complexes between inorganic ions and organic molecules) and release inorganic nutrient elements. For example, oxalic acid dissolves solid muscovite to produce soluble inorganic potassium and soluble chelated aluminum ($K_2[Si_6Al_2]Al_4O_{20}(OH)_4 + 6C_2O_4H_2 + 8H_2O \Leftrightarrow 2K^+ + 8OH^- + 6C_2O_4Al^+ + 6Si(OH)_4^0$). Oxalic acid is known to be produced by fungal hyphae, whereas lichenic acid is specific to lichens. Crustose lichens, which are composed of a flat and crustlike thallus, are often the first organisms to colonize outcrops of bare rock. They are able to scavenge water and nutrients from the atmosphere and rain and dew to support their slow rate of growth, and are also able to tolerate complete desiccation. During their growth on the surface of rocks and in rock crevices, the acids they produce solubilize the rock and assist in its physical

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breakdown. This action of lichens has been reported to cause significant damage to both buildings and sculptures made of rock (Chen et al., 2000).

In their study of contrasting terricolous (ground-dwelling) lichen forms, Asta et al. (2001) divide the type of association between the lichen thallus and underlying substrate into three categories. Type 1 lichens, represented by the genus *Baeomyces*, have a very intimate association between the lichen body and the underlying substrate; Type 2 lichens, corresponding to the genus *Peltgera*, have a leafy thallus and an elaborate but less intimate system of attachment to the substrate. In Type 3 lichens, which correspond to the genus *Cladonia*, the primary thallus is almost absent and the podetia have little contact with the substrate. Using thin sections for light and electron microscopy, Asta et al. (2001) showed that the lichen–rock interface is primarily associated with the fungal component of the lichen and that the fungal structures consist of both individual hyphae and differentiated rhizomorphs. Although these rhizomorphs are thought to be important for translocating water and nutrients, they do not have clearly differentiated internal structures for translocation (Sanders, 1997), as do the rhizomorphs of some ectomycorrhizal fungi (Duddridge et al., 1980). Asta et al. (2001) showed that the interface between substratum and lichen *Baeomyces* was more structured and resulted in reorientation of mineral particles, biodegradation of the walls of plant debris, and bonding between these elements. In contrast, *Cladonia* had a more diffuse association with the substrate; fungal hyphae escape from the lichen body and are incorporated into the soil. The production of polysaccharides by fungal hyphae is also important in the development of organomineral complexes, which bind mineral particles together. Asta et al. (2001) also showed that the lichen complex contained lichen-specific bacterial colonies, but they did not speculate on their role in the rock degradation process.

Banfield et al. (1999) also commented that the classic concept of the structure of lichens as an upper layer of fungal hyphae containing photosynthetically active algae or Cyanobacteria ignored the fact that the fungal matrix is also a refuge for a community of nonphotosynthetic bacteria. The diversity and function of these nonphotosynthetic bacteria is largely unknown. They have elaborated the lichen/mineral rock-weathering zone model of Barker and Banfield (1998) and applied the concept to the rhizospheres of vascular plants. A representation of the zone model is shown in Fig. 2.1 and shows Zone 1 as the region of generation of lichen acids in the photosynthetic region of the lichen. Zone 2 consists of the area of biophysical disaggregation, in which the fungal and nonphotosynthetic bacteria interact closely with weathered mineral rock particles, fungal hyphae, and rhizomorphs, which penetrate into fissures in the rock. Hyphal aggregations become narrower as the hyphae penetrate deeper into the underlying rock until only single hyphae exist (Ascaso and Wierzchos, 1995). Zone 2 is the area of most intense mineral weathering with maximal

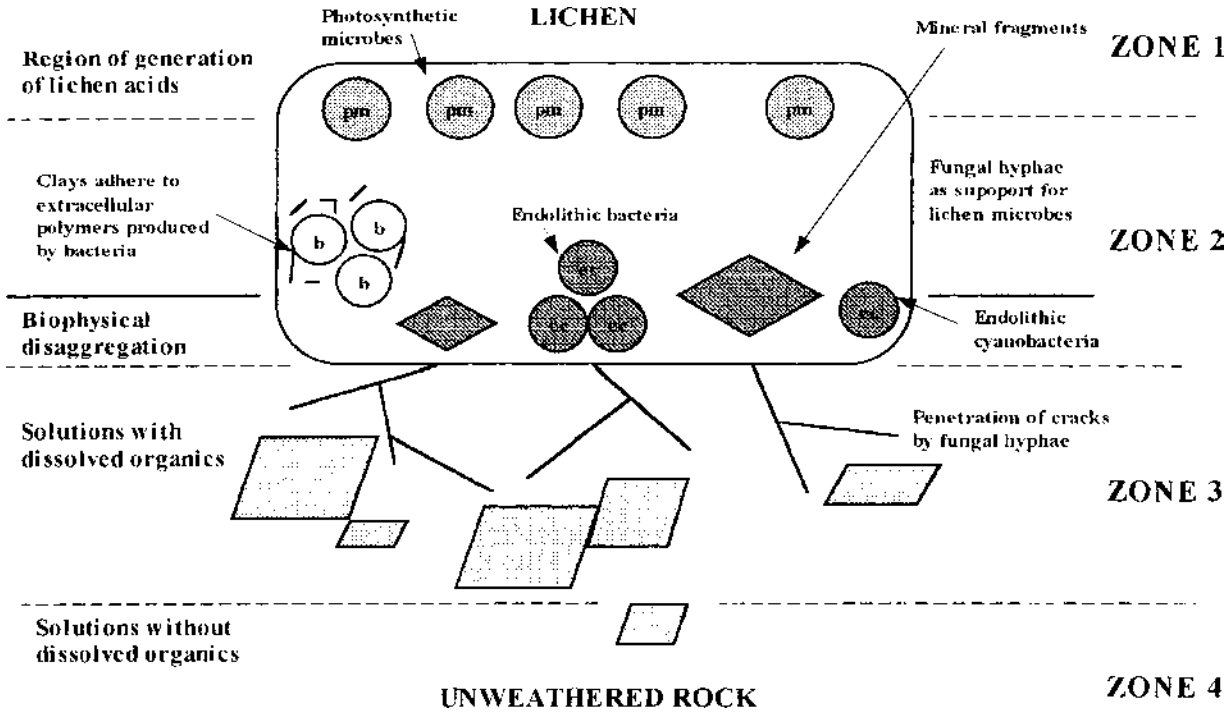

FIGURE 2.1 Model indicating the four zones of activity within a mineral-weathering lichen as depicted by Banfield et al. (1999). In zone 1, photosynthetic members generate carbon and crystalline lichenic acids. In zone 2, there is direct contact among microbes, organic products, and the mineral surface. In zone 3, organic acids act to solubilize rock in the presence of direct rock/organism contact, particularly fungal hyphal penetration into cracks. Zone 4 is characterized by unweathered rock and inorganic chemical reactions.

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contact among cells, secreted polymers, and mineral surfaces, where complexes among the minerals, clay particles, and organic polymers are formed at the nanometerscale. Here metal–lichen acid complexes occur that do not occur deeper in the rock (Ascaso and Wierzchos, 1995), such as complexes of ferric oxide in *Acarospora sinoptica*, aluminum in *Tremolecia atrata*, copper oxalate in *Acarospora rugulosa* and *Lecidia theiodes*, and complexing of copper in the cortex of *Lecidia lacteal* and copper-psoromic acid in *Lecidella bullata*. In the underlying Zone 3, solutions containing lichen-derived organic acids effect chemical solubilization of the parent rock material. This is primarily a biogeochemical interaction and is not mediated by direct microbial contact. Finally, the bottom of Zone 3 represents the unweathered rock, which water can penetrate but not carry organic acids. Ascaso and Wierzchos (1995) point out that there is a temporal component to the development of the lichen–soil interaction, which microbial populations and diversity increase as the weathering continues and a more diverse soil structure develops.

In contrast to this evidence of the role of lichens in the weathering of rock and the destruction of buildings and monuments made of rock, Mottershead and Lucas (2000) present evidence to suggest that the cover of *Aspicilia calcarea* and *Diploscistes diacapsis* lichens on calcareous stonework in Europe can protect against rock solubilization. They show evidence that lichen-protected areas of gypsum were 15 mm higher than adjacent uncovered areas, where the lichen layer increases the rate of shedding rainwater containing acidic pollutants that would have eroded the rock surface.

In addition, the aerial parts of the lichen trap particles of dust, which together with dead parts of the lichen (Crittenden, 1991) contribute to the organic component of the protosoil produced, thus after a period of time (usually years), lichens contribute significantly to the formation of the mineral component of a new soil and to some degree to the organic component.

B. The Role of Fungi in Rock Breakdown

Fungi alone produce organic acids that are capable of breaking down rock. Ascaso and Wierzchos (1995) cite studies by Eckhardt (1985) that show that yeasts and filamentous fungi, such as *Aspergillus niger*, alone are involved in rock solubilization, releasing cations from amphibolite, biotite, and orthoclase. *Penicillium* and yeasts were also found to be able to dissolve calcium-rich rocks, such as limestone, marble, and calcium phosphate (Chang and Li, 1998). In addition, Connolly et al. (1998) showed that the white rot wood decay fungus *Resinicium bicolor* could solubilize strontianite sand to release the strontium contained within. This fungus was then able to translocate strontium through mycelial cords and secrete it, along with calcium oxalate crystals, in newly advancing zones of the mycelium in decaying wood. This activity demonstrates that not only does strontium behave similarly to calcium in fungal metabolism

but that this saprotrophic fungus can move strontium from the parent mineral substrate into a decomposing wood resource. The importance of translocation of nutrients, carbon, and water will be raised again throughout this book. This ability of fungal hyphae—on their own or as differentiated translocatory organs (rhizomorphs, strands, or cords)—is an important physiological trait of fungi that provides them with a mechanism to move materials within their own bodies (thalli) in relation to gradients of supply and demand. This movement of materials may occur at very small scales (μm to cm range), or in differentiated organs over distances of meters to tens of meters. At the ecosystem scale of resolution, this long-distance movement of nutrients, carbon, and water can have a profound effect on ecosystem function and the modification of heterogeneously distributed resources.

Hirsch et al. (1995) showed a loose relationship among fungi, bacteria, and coccal cells (thought to be algae) that together form an endolithic community in sandstone and granite. Fungal species present included *Alternaria*, *Aspergillus*, *Aureobasidium*, *Candida*, *Cladosporium*, *Paecilomyces*, *Phoma*, *Penicillium*, and *Sporobolomyces*. The production of organic acids by this assemblage of organisms was suggested to be responsible for the dissolution of rock, allowing the invasion by bacteria and other fungal species. In culture, *Aspergillus niger* has been shown to effect the solubilization of fluorapatite (Nahas et al., 1990). In a similar study, fungi were found in small holes (3–10 μm diameter) in feldspars and horneblende (Jongmans et al., 1997). It was shown that these holes were produced by micromolar concentrations of organic acids (succinic, citric, oxalic, formate, and malate) secreted by saprotrophic and ectomycorrhizal fungi associated with the overlying pine forest ecosystem. Thin sections of feldspars observed under the microscope have revealed fungal hyphae bearing cross walls in hyphal-generated tunnels in the rock (Hoffland et al., 2001, 2002).

Fungi in symbiotic association with plant roots, mycorrhizae, have also been shown to play a role in the dissolution of parent rock material in more established soils. Sometimes fungi alone are capable of this activity, but often it is an evolved partnership between the mycorrhizal fungi and bacteria that work in a consortium. Azcon et al. (1976) showed that there were interactions between bacteria and arbuscular mycorrhizae of lavender, allowing the acquisition of phosphorus by the host plant from that released from rock phosphate by the rhizospheric microbial community. They showed there was a degree of synergism between the bacteria and mycorrhizal fungi and differences in behavior between the two mycorrhizal fungal species selected (Table 2.3). In their study of maize root systems, however, Berthelin and Leyval (1982) compared the ability of arbuscular mycorrhizal root systems of maize to nonsymbiotic rhizospheric microflora and combinations of the two in the weathering of micas. In experimental systems, measures of maize growth (biomass) and potassium, calcium, and magnesium uptake (derived from the breakdown of biotite) were

TABLE 2.3 Interactions Between Bacteria and Arbuscular Mycorrhizae of Lavender in the Acquisition of Phosphorus from Rock Phosphate

	Plant growth	Phosphorus uptake into plant
Bacteria[a]	>Control[d]	>Control
AM (E3)[b]	>Control	>Control
AM (E3) + bacteria	>AM (E3)	>Bacteria alone
AM (YV)[c]	>Control, >AM (E3)	>Control, >AM (E3)
AM (YV) + bacteria	>AM (YV)	>AM (YV)

[a] Mixture of *Pseudomonas* spp. and *Agrobacterium* spp.
[b] Isolate E3 was thought to be *Glomus fasciculatus*.
[c] Isolate YV was thought to be *Glomus mosseae*.
[d] Control consisted of heat-killed bacteria and filtered mycorrhizal fungal washings.
Source: Data from Azcon et al. (1976).

similar in plants with nonsymbiotic rhizospheric microflora and arbuscular mycorrhizal root systems, but there was no synergistic effect of the combination of mycorrhizae and bacteria. Suggesting the role of arbuscular mycorrhizal fungi alone in rock breakdown, Mojallala and Weed (1978) showed that mycorrhizal soybeans used weathered potassium from the biotites, phlogopite, and muscovite. The potassium released, however, was insufficient to sustain the enhanced growth of the mycorrhizal plants so that the tissue concentration of potassium was less in mycorrhizal than nonmycorrhizal plants.

Electron microprobe analysis of the biotites showed that arbuscular mycorrhizal fungi increased the rock weathering with extensive potassium and some aluminum release from the edges of the phlogopite but not from muscovite (Hinsinger and Jaillard, 1993). The rate of release of potassium from phlogopite by ryegrass roots is related to the potassium demand by the plant. They did not, however, attribute these changes in parent rock chemistry and physics directly to the action of fungi or bacteria. Plant acquisition of nutrients from insoluble or poorly soluble sources is also enhanced by consortia of mycorrhizae, saprotrophic fungi, and bacteria. Singh and Kapoor (1998) showed that mung bean plants in association with a consortium of phosphate-solubilizing organisms could better obtain phosphorus from rock phosphate than each organism alone. The consortium consisted of the arbuscular mycorrhizal fungus *Glomus fasciculatum*, fungal saprotroph *Cladosporium herbarum*, and the bacterium *Bacillus circulans*. A field demonstration of the effect of rhizospheric microbial communities (including arbuscular mycorrhizae) on the release of phosphate from rock phosphate comes from the study of Vanlauwe et al. (2000) in Nigeria. The addition of rock phosphate to crops planted on low-P soils showed an immediate response in terms of increased mycorrhizal colonization and enhanced growth. This increase in growth showed a combined effect of the mycorrhizae

and associated rhizospheric bacteria in dissolving the rock phosphate to make it available for plant uptake. The pivotal role of mycorrhizae in this process was demonstrated by the fact that in the presence of high fungiverous nematode populations the effect of added rock phosphate was significantly reduced because of grazing of the mycorrhizal mycelia.

April and Keller (1990) demonstrated changes in the mineral physical and chemical composition of soil in the rhizosphere of forest tree roots. They showed that in the presence of roots, phyllosilicate grains were fragmented and aligned with the long axis of the root, exposing a larger surface area for chemical attack. In addition there was precipitation of amorphous aluminum oxides, opaline and amorphous silica, and calcium oxalae deposits in the roots. Also, kaolin in the rhizosphere had a higher thermal stability compared to kaolin in the bulk soil. These causative agents were potassium enrichment in the rhizosphere soil or preferential dissolution of biotite at the root–soil interface. Gobran et al. (1998) reviewed the effects of rhizospheres on forest biogeochemistry. They showed that the rhizosphere:bulk soil ratio for bacterial populations is 10–50 and that for fungi is 5–10, showing that the rhizosphere is an important focus for the activities of micro-organisms and that this can effect considerable physico-chemical changes in the soil (Table 2.4). They also showed that the abundance of weatherable minerals near the root surface was consistently less than in the bulk soil (Table 2.5), which they attribute to increased hydrogen ion and carbon dioxide content and the presence of complexing organic acids. Chang and Li (1998) investigated the ability of seven ectomycorrhizal fungal species to solubilize limestone, marble, and calcium phosphate. From plate-clearing studies, only *Hysterangium setchellii*, *Rhizopogon vinicolor*, and *Suillus bovinus* formed halos around the colonies, indicating a degree of solubilization. In contrast, *Cenococcum geophilum*, *Hebeloma crustuliniforme*, *Laccaria laccata*, and *Piloderma croceum* did not clear the medium. Nonmycorrhizal fungi, including *Penicillium*, three species of *Azospirillum*, three isolates of

TABLE 2.4 Composition Between Rhizosphere and Bulk Soil Physicochemical Characteristics in the E Horizon of Forest Soils

Characteristic	Rhizosphere soil	Bulk soil
Cation exchange capacity ($cmol_c\,kg^{-1}$)	4.41	12.16
Exchangeable base cations ($cmol_c\,kg^{-1}$)	0.33	1.93
Soluble base cations ($cmol_c\,kg^{-1}$)	0.10	0.46
Titratable acidity ($cmol_c\,kg^{-1}$)	4.08	10.23
Base saturation (%)	7.47	16.13
Organic matter (%)	9.80	23.03

Source: After Gobran et al. (1998) with kind permission of Kluwer Academic Publishers.

TABLE 2.5 Comparison Between Rhizosphere and Bulk Soil Content of Weatherable Minerals Expressed as Mineral Intensity as a Percentage of the Quartz Peak at 100

Mineral	Rhizosphere soil	Bulk soil
Amphibole	0.03	0.12
Interstratified vermiculite	0.54	1.14
Plagioclase	1.73	2.24
K-feldspar	1.28	1.29

Source: After Gobran et al. (1998) with kind permission of Kluwer Academic Publishers.

Pseudomonas fluorescens, and a yeast, also cleared the substrate. The effectiveness of these isolates in mineralizing calcium showed that the pseudomonads were most efficient, along with the yeast and *Penicillium*. Of the mycorrhizal fungi, *Laccaria laccata* showed no activity, but *Rhizopogon* and *Suillus* showed a slight increase in calcium release over the control, along with the *Azospirillum* isolates. In pure culture conditions, Paris et al. (1996) showed that the two ectomycorrhizal fungi, *Paxillus involutus* and *Pisolithus tinctorius*, produced oxalate in the presence of the mica phlogopite, and that this process was not influenced by the availability of potassium or magnesium. *Pisolithus* produced oxalate in the presence of phlogopite with either ammonium or nitrate nitrogen being available, however, the production of oxalate was greater in the presence of ammonium nitrogen in the absence of phlogopite. On the other hand, *Paxillus* did not accumulate oxalate in the presence of ammonium or nitrate nitrogen in the absence of phlogopite. Similarly, *Paxillus involutus* and *Suillius variegates* in mycorrhizal symbiosis with Scots pine seedlings were found to mobilize potassium from biotite and microcline by production of citric acid, which was produced in proportion to fungal hyphal biomass (Wallander and Wickman, 1999). The role of ectomycorrhizal fungi in rock dissolution and the ability to mobilize K, Mg, and Ca for tree nutrition has recently been reviewed by Landeweert et al. (2001). Subsequently, Thompson et al. (2001) showed that in certain circumstances NH_4-N could be derived by ectomycorrhizal activity on feldspars in Miocene shales and possibly other rocks. Gobran et al. (1998) suggest that in addition to regulating nutrient fluxes and pools, the presence of abundant ectomycorrhizal hyphae in the rhizosphere of trees acts as a source of organic matter. This could act as a source and sink of available nutrients, and possibly toxic elements. The ionic exchange sites on the surface of organic matter regulate the movement of these ions. Where ionic exchange forces are high, the elements are closely bound to the organic matter. Where ionic forces are less, the nutrients become more available in soil pore water for plant growth.

These results suggest that the fungal component of mycorrhizae have slight rock-weathering capacity. This activity is probably less efficient than that of bacteria, is very species-dependent, and is dependent upon environmental conditions. The interactions between the mycorrhizal fungi and mycorrhizaspheric bacterial community appear to vary from a loose association to something near a symbiosis. The nature of the interactions of component organisms in the mycorrhizasphere is far from fully described, however, and the physiological attributes and biogeochemical changes effected by these communities are not completely understood. It does seem, however, that the action of mycorrhizae and root surface bacterial communities may access a greater variety of nutrient elements from rock than had previously been thought (Thompson et al., 2001; Hoffland et al., 2001), and the relative contribution of nutrients derived in this fashion, compared to other sources, for plant growth in a variety of ecosystems has yet to be determined.

C. Fungal Contribution to the Organic Matter Pool in Soil

In addition to the formation of soils, fungi in the form of lichens and cryptogramic soil crusts are important primary producers and contributors to the soil carbon pool (Lange et al., 1998), especially in arid ecosystems. Soil crusts can be formed by a diverse group of organisms, including mosses, lichens, fungi, and green and blue-green algae (Cyanobacteria), as well as other bacteria. States and Christensen (2001) identified 33 species of fungi associated with the lichens, bryophytes, and graminoids of the surface crusts of semidesert grassland ecosystems of Utah and Wyoming. These included a new species of basidomycetes, five new loculoascomycetes, and three mitosporic species that had not previously been identified from soil crusts communities. These crust communities are an essential part of the soil formation and control the nutrient content and availability of soils for the invasion by other plant species. The mat-forming lichens (*Cladonia*, *Cetraria*, *Stereocaulon*, and *Alectora*), which grow in elevated microsites of boreal Arctic peatlands, grow upwards and die off at the base. The dead bases input a considerable amount of organic matter into the developing soil (Crittenden, 1991; 2000). These lichens form up to 60% of the winter food for caribou and reindeer and are resistant to trampling effects. In the oligotrophic, sandy soils, vascular plants need to invest energy into root growth for water and nutrient acquisition. Mat-forming lichens, however, trap both water and nutrients from the air, making them less dependent on roots and soil for their supply of water and nutrients. The carbon cost of nutrient acquisition is thus reduced (Crittenden, 2000). This benefit allows lichens to be primary colonizers. In addition to adding organic matter in the form of lichen biomass, the nitrogen fixation by the Cyanobacteria photobiont of *Stererclaulon paschale* has been shown to be approximately $20\,\mathrm{kg\,ha^{-1}\,y^{-1}}$ N. This rate of fixation could

provide a large proportion of the 10 to 40 kg ha^{-1} y^{-1} plant demand for nitrogen in the upland spruce boreal forecast of Canada and Russia (Crittenden, 2000).

The ability of fungal mycelia to form an extensive, long-lived network that is more resilient to the vagaries of rapid changes in climatic conditions than bacteria may allow components of the ecosystem that rely on fungal mycelia to respond more readily than systems that rely on the growth of populations of bacteria to carry out an ecophysiological function. A good example of this homeostasis can be seen in the study of Lange et al. (1994), who explored the role of soil crust lichens in carbon sequestration in the Namibian desert. In desert conditions, the main limitation to the survival of organisms is the scarcity of water. As was suggested earlier, the structure of lichens can act as a nucleus for water condensation, and lichens are able to survive periods of desiccation. Lichens are thus well adapted as primary producers in the stressed conditions of deserts and periodically dry environments.

Lange et al. (1994) showed that the soil crust lichens *Acarospora schleicheri*, *Caloplaca volkii*, and *Lecidella crystalline* perform this ecosystem function in response to pulses of water and light availability in the Namibian desert. Following the development of nocturnal dew or fog, the lichens in the soil crust rapidly absorbed water, carried out photosynthesis, and then shut down as daytime temperatures reduced water availability again. By close observation of environmental conditions, lichen respiration, and photosynthesis, Lange et al. (1994) were able to show that after a night fog lichens were respiring at a temperature of 11°C. As the water content of lichen crust increased, respiration continued to increase to a maximum of about 0650 h when the sun rose. At this time the hydrated lichens were able to photosynthesize, but the dense fog cover restricted light levels so that photosynthesis only occurred at suboptimal levels, so that compensation point was only reached at 0740 h. After this period, photon flux density increased to about 520 μmol m^{-2} s^{-1} and photosynthesis continued to a peak of activity at 1000 h. After the fog dissipated, evaporation of water was rapid and the lichens dried to the compensation point 45 min after maximal photosynthesis, thus due to the large amount of water produced by the fog, photosynthesis was sustained for only 3 h 20 min on that particular day. Depending upon the amount of water available as dew or fog, these short pulses of photosynthesis produced a carbon dioxide exchange between zero and about 4 μmol m^2 s^{-1} for short periods in the morning. The amount of carbon fixed during these periods was often no greater than the loss due to respiration; however, on average the net carbon gain was calculated to be approximately 126 mg C m^2 day^{-1}. Using a factor of approximately 250 foggy days per year at their research site, they calculated an annual gross primary production of 32 g C m^{-2}; however, by factoring in respiration carbon loss the figure for net carbon gain by 100% lichen cover is on the order of 16 g C m^{-2} y^{-1}. Similarly, fast photosynthetic responses for cyanobacterial soil crust lichens have been found

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in the arid soils of Utah (Lange et al., 1998) in response to pulses of available water. The rapid response of lichens to short-term pulses of optimal environmental conditions to support photosynthesis, together with the ability of fungi to survive long periods of inhospitable conditions (S strategists), provide lichens with a competitive advantage over vascular plants in extreme environments.

Once lichen communities have become established and their action has developed a soil to support their growth, their effect on the production of adjacent plant communities can be considerable. In a study of the mosaic of land cover in an Alaskan taiga ecosystem, Lamontagne (1998) demonstrated that net nitrogen mineralization was seven times higher and nitrate nitrogen 40 times higher in lichen patches than adjacent forest islands, although nitrogen fixation in lichen communities was not an important source of nitrogen into the system. These higher figures are likely due to the lower nitrogen immobilization into lichen tissue than into tree tissue. In this landscape, consisting of a mosaic of forest islands covering 27% of the area, lichen patches cover 24% and bedrock with crustose lichen cover occupy 49% of the catchment area, respectively. Lichen-dominated areas of the upper slopes of the catchment are important producers of soluble mineral and dissolved organic nitrogen that runs off into the adjacent lower-lying forest islands. In these forest islands, the nutrients are utilized by immobilization into tree biomass.

2.1.2 Keeping Soils Together

Soils are prone to erosion by a number of factors. Intense rainfall can literally wash soil away, especially on sloping ground. Dry soils can be displaced by wind erosion. In the development of a soil, the balance of inorganic, organic, and biotic components is thus of great importance to the physical stability of soils and their ability to support plant life.

The risk of erosion is greatest where bare mineral soils are exposed. In these conditions the primary colonizers are an important component of stabilizing the mineral particles. In addition to the development of soils, lichens and fungi are often important constituents of cryptogamic crusts on nutrient-poor or sandy soils in dry areas (States and Christensen, 2001). The role of fungi in these communities of bacteria, algae in lichen symbioses, is to physically hold the mineral soil particles together. The fungal hyphae penetrate between the soil mineral particles and act as a web to physically retain soil particles. Polysaccharide secretions of both fungi and bacteria aid this process, acting as a glue to bind mineral particles together. In these highly exposed conditions, the longevity of fungi, compared with the rapid turnover of bacterial cells, is also beneficial, as this property allows a greater degree of permanency to the soil-stabilizing function. The hydrophobic nature of some fungal hyphae alters the flow of water through soil colonized by cryptogramic crusts. Water tends to flow

laterally across the surface soil in the presence of these crusts rather than downward in uncolonized soil surfaces. This prevents the downward movement of soil particles and organic matter and reduces the risk of erosion of the developing soil structure. Recently formed nutrients are also retained in the upper soil horizons by the hydophobicity of the lichen community, and the leaching of essential plant nutrients is thus reduced. As discussed above, however, the runoff of nutrients from crust communities may be of importance for the growth of surrounding plant communities. Fungi involved in the mat-forming communities are subject to a variety of environmental stresses that occur on the soil surface compared to more buffered parts of the ecosystem. They are exposed to rapid and wide changes in water availability, temperature, and light. Certain adaptations of the fungal species having a lichen habit make them fit for existence in a stressful environment. In a recent study of melanins in fungal tissue, Gauslaa and Solhaug (2001) showed that the melanin content of fungi tissue within lichens reduced ultraviolet B (UVB) and ultraviolet A (UVA) light penetration into the lichen, acting as a natural sunscreen. Their study shows that these pigments shift the wavelength of light entering the lichen to higher wavelengths, which do less structural damage to the organisms. In previous studies, Solhaug and Gauslaa (1996) demonstrated that removal of the orange pigment parietin in the lichen *Xanthoria parietina* increased the damage caused by the excessive light that was allowed to enter the lichen tissue. The photosynthetic capability of microalgae in freshwater systems can also be damaged by exposure to UV- and visible wavelengths of light (Xiong et al., 1999). It is therefore probable, that the evolution of melanin-containing fungal symbionts in soil surface colonizing lichens could be important in protecting the function of the algal symbiont.

The development of crust communities on soil also adds dead organic material to the soil (Crittenden, 1991). This organic material contains complex forms of nutrients and is utilized as a food resource by saprotrophic fungi and bacteria, effecting mineralization of inorganic nutrients for plant uptake. This will be the subject of discussion in the next section. It should be noted here, however, that this organic material is an essential component of soil and is combined with the mineral component of soil to form aggregates. Crittenden (1991) shows evidence that in two mat-forming lichens, *Cladonia stellaris* and *Stereocaulon paschale*, the nitrogen concentration in dead tissue at the base of the lichen is significantly lower than in the upper living portion. This, he suggests, shows the presence of retranslocation of nutrients from the dead tissue into new growth. This could also be interpreted as the development of a soil to which dead material is added and from which nutrients are derived, because of the decomposition of organic residues (lichen necromass) and mineralization of nutrients. In this scenario, the decrease in necromass N concentration, compared to live tissue, could be caused by mineralization and the combined effects of uptake into new lichen growth and loss through leaching to deeper soil horizons.

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In more highly developed soils, soil aggregates are formed by a physical combination of soil mineral particles, dead and living microbial components, and organic material derived from dead plant and animal remains (Tisdall and Oades, 1982). Microaggregates are classified as being less than 250 μm in diameter and combine to form macroaggregates (>250 μm diameter). An aggregation of aggregates is referred to as a soil crumb, the size and structure of which determines the texture and porosity of soil. In addition to the development of aggregates, soil organisms and their products are important in the stability of aggregates—their resistance to being physically disrupted.

The role of fungi and bacteria in the formation and stability of soil aggregates is of fundamental importance to both the fertility of soil and carbon storage and sequestration within soils. Coleman and Crossley (1996) summarize the development of soil aggregates by citing the work of Tisdall and Oades (1982). This process spans five orders of magnitude, from the cementation of clay particles, each on the order of 0.2-μm diameter, through their interaction with microbial debris and interactions with living bacteria and fungi (20 μm scale), making aggregates in the 200-μm range to soil crumbs are at 2000 μm in diameter (Table 2.6). The importance of bacteria and fungi in the development and stability of soil aggregates is further discussed in a review by Tisdall (1994). She concludes that bacteria play a major role in the formation and stabilization of

TABLE 2.6 The Interaction of Soil Mineral Particles, Organic Matter, Bacteria, Fungi and Root Material Spanning Five Orders of Magnitude in the Formation of Soil Microaggregates

Scale of interaction	Interaction between components	Strength and nature of interaction
0.2 μm	Amorphous aluminosilicates, oxides, and organic polymers sorbed onto clay plates with electrostatic bonding and flocculation	Permanent, inorganic
2 μm	Microbial and fungal debris (humic material) encrusted with inorganics	Persistent, organic
20 μm	Plant, fungal, and bacterial debris encrusted with inorganics	Persistent, organic
200 μm	Roots and fungal hyphae aggregated with mineral particles	Medium term, organic
2000 μm	Major binding of aggregate units to form a solid perforated with pores	Variable term, organic

Source: After Coleman and Crossley (1996).

microaggregates. The capsule surrounding many bacteria, especially Gram-negative bacteria, is composed of polysaccharides. This polysaccharide layer physically causes clay particles to adhere to the bacteria, and together with polyphenols attracted by ionic charges protects the polysaccharide from microbial attack. This collection of clay particles and bacteria forms a microaggregate of about 20 μm in diameter. Additionally, saprotrophic fungal hyphae can grow between these microaggregates and continue the accumulation of material to produce larger aggregates, possibly by cation bridges between the hyphal polysaccharides and the clay particles.

The presence of plant roots in soil adds another dimension to the complexity of the microbial communities and the soil's physical components. The presence of mycorrhizal symbiotic fungi adds a greater density of fungal hyphae in the soil. In both ectomycorrhizal and arbuscular mycorrhizal associations, the external (extramatical or extraradical) hyphae also perform the same function. The presence of ryegrass in an alfisol increased the content of stable macroaggregates from 36–78% in 6 months. In contrast, conversion of pasture (90% stable macroaggregates) into tilled tomato crop reduced the aggregates to 58% due to the physical disruption of the soil by the agricultural practices adopted. Among the hypotheses for increased aggregate stability in the presence of arbuscular mycorrhizal fungi are that these fungi produce more mucilage than other fungi, produce stickier mucilage, and form more cation bonds with clay particles and other organic matter. The discovery, however, of copious production of a glycoprotein called glomalin from arbuscular mycorrhizal fungi suggested that this compound was key to the enhanced aggregate-forming abilities of arbuscular mycorrhizal fungi (Wright and Upadhyaya, 1996). Using 16 soils from the Middle Atlantic states and one from Scotland, Wright and Upadhyaya (1998) used a monoclonal antibody technique to detect the glomalin content of soil aggregates. The glomalin content was then correlated with measures of aggregate stability. Across all sites the relationship between the logarithm of glomalin content, expressed as mg g^{-1} soil and percentage of aggregate stability, was positive, with a correlation coefficient of 0.86 (Table 2.7). In addition, there is evidence that arbuscular mycorrhizal hyphal growth is stimulated by the presence of organic matter (i.e., sloughed material from root surfaces). This increased fungal growth and the presence of organic matter increased bacterial populations. (St. John et al., 1983; Wright and Upadhyaya, 1998). There thus appears to be a synergistic effect among the presence of organic matter, mycorrhizal hyphae, bacteria, and the development of stable soil structure.

The close juxtaposition of the mycorrhizal hyphae with the decomposing organic matter optimizes the ability of the mycorrhizae to capture mineralized nutrients for plant uptake. The interaction between mycorrhizal and nitrogen-fixing, nodulating bacteria on soil aggregate formation has been studied by

TABLE 2.7 Correlation Coefficients for Measures of Glomalin and Total Soil Carbon with Soil Aggregate Stability for a Range of Soils and Cropping History

	Soil C (%)	Easily extractable glomalin	Immunoreactive easily extractable glomalin	Total extractable
Easily extractable	0.49			
Immunoreactive easily extractable	0.61	0.94		
Total extractable	0.82	0.73	0.78	
Aggregate stability (%)	0.65	0.69	0.84	0.70

Note: All correlations are significant at less than 0.1%.
Source: After Wright and Upadhyaya (1998) with kind permission of Kluwer Academic Publishers.

Bethlanfalvay et al. (1999). Using soybeans inoculated with *Bradyrhizobium japonicum* and/or arbuscular mycorrhizae in a range of applied nitrogen fertilizers, they showed that maximal water-stable aggregate formation occurred in nodulated plants with ammonia fertilization. Nitrogen-deficient plants had sparse root development, and the integrity of soil aggregates was maintained by arbuscular mycorrhizal fungal hyphae. They suggested that water-stable soil aggregate formation occurred in three phases. During phase 1, mean aggregate size decreased because of an increase in bacterial numbers, while mycorrhizal fungi were in a lag phase of growth. It was suggested that this was caused by the cohesion of small aggregates being weakened by the metabolic activity of the increased bacterial population. During phase 2, the rapidly developing network of mycorrhizal hyphae increased entanglement of small aggregates into larger aggregates because of the production of glomalin. In phase 3, compaction of soil by increased root growth was thought to possibly contribute to aggregate stabilization. In combination with other factors, it has thus been shown that glomalin from arbuscular mycorrhizal fungi is an important component in aggregate formation and stability. Miller and Jastrow (1990) also studied the interactions among roots, mycorrhizae, and soil aggregation. In their study of changes in soil characters under prairie restoration, they used path analysis to understand the interactive links between plant communities, their rooting characteristics, their mycorrhizal associations, and the formation of stable aggregates in soil. The path of fine root length to root colonization and abundance of extra radical hyphal length gave the greatest correlation to aggregate size. It was of interest to note that this pathway was more strongly associated with fine roots, common to the native plant species, than the abundance of very fine roots, associated with nonindigenous plant species (Fig. 2.2). This suggests that there could be some degree of coevolution of soil development and plant community type.

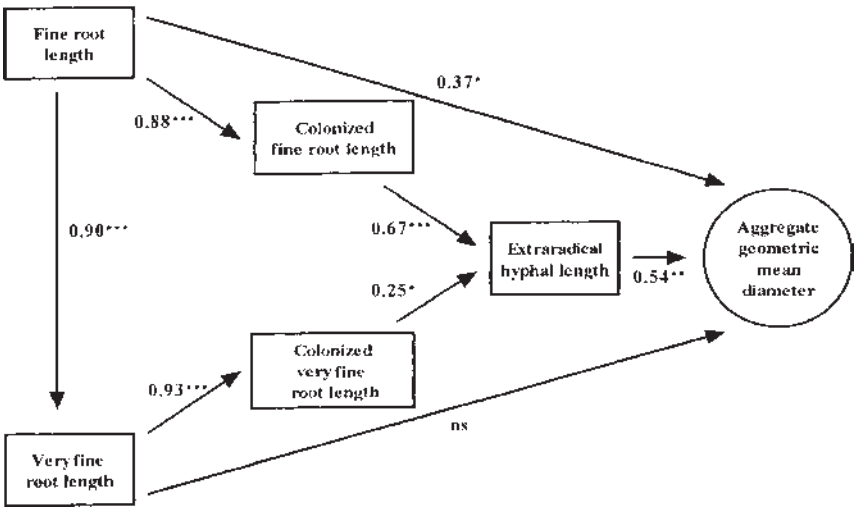

FIGURE 2.2 Path model relating the influence of root diameter class, arbuscular mycorrhizal infection, and their relative contribution to the development of water-stable soil aggregates. Arrows indicate path coefficients, where * is significant at $P < 0.05$, **$P < 0.01$, and ***$P < .001$. *Source*: After Miller and Jastrow (1990).

In addition to the presence of mycorrhizal fungi, roots release their own carbohydrates that act as foci for bacterial and fungal activity in soil. The development of links among bacteria, fungi, and soil organic matter to form soil aggregates is greatly enhanced by the presence of readily utilizable carbon. The addition of starch to soils provided an easily obtained source of energy for the growth of bacteria and provided "hot spots" for fungal growth and an increase in the density and mean size of aggregates (Guggenberger et al., 1999). The importance of residual islands of plants and their mycorrhizae or the ability of animals to move mycorrhizal fungal propagules between established and developing plants is thus important during the initial stages of plant recolonization of a highly disturbed system to effect rapid soil accretion and stabilization. These factors were found to be important contributions to the re-establishment of vegetation on Mount Saint Helens after pyroclastic disturbance (Allen et al., 1984; Allen, 1987; 1988).

The changes in soil caused by agricultural practices are manyfold. One of the main effects is that of physical disturbance caused by plowing and other mechanical disruption of soil. This disturbance can lead to direct damage to fungal hyphae, resulting in a shift of fungal community structure of favor those species that can withstand mycelial disruption. In a study of the effects of cultivation of steppe soils, Kurakov and Mirchink (1985) showed that

TABLE 2.8 Changes in the Frequency (Percentage of Sample Containing Fungal Species) of Dominant Mitosporic Fungal Species in Steppe Soil of the Former Soviet Union When Converted into Agriculture

Species	Virgin steppe	Cotton (year 1)	Cotton (year 2)	Corn	Lucerne
Aspergillus fumigatus	26	43	46	33	23
A. ustus	3	63	73	86	76
Cladosporium cladosporioides	10	53	56	60	100
Fusarium spp.	0	50	30	53	30
Mucor spp.	3	56	40	43	60
Penicillium claviforme	33	30	26	30	60
P. funiculosum	3	26	30	43	43

Source: After Kurakov and Mirchink (1985).

of the mitosporic fungal community, *Penicillium* spp. was more abundant in cultivated soils than in virgin steppe (Table 2.8). The change in species composition caused by the initiation of agricultural practices cased a greater shift in fungal community structure than subsequent changes in crop species. As a result of the continual physical disturbance of soils under highly mechanized agricultural practices, soils become less stratified, with organic matter incorporated more evenly and to greater depth. The dependence of soil fertility on the number, size, and stability of soil aggregates increases, as nutrients are more associated with protected organic matter locked within the aggregate structure. Agricultural soils are therefore primarily fertile due to the availability of inorganic nutrients in soil pore water rather than being under fungal control of mineralization from organic material stocks (plant litters and their decomposition products). Such soils become increasingly dependent upon exogenous sources of added nutrients (fertilizers) to maintain their fertility under continuous cropping systems. Recently, interest has been raised regarding the return to less intensive agricultural practices. Minimal- or no-till agricultural practices require a reduction in the physical disturbance of the soil structure, planting of crop species in and among native plant species, and a reduction in the use of herbicides and pesticides. The plant community of crop and native plants supports a greater diversity of natural predators for pests, and the return of dead plant parts to the soil surface is a source of endogenous, slow-release fertilizer. The agricultural system therefore returns to a system that mimics natural ecosystems. The decomposer community shifts from a primarily bacterial-dominated system toward one dominated by fungi. The impact of this fungal-driven decomposer community is that a great variety of factors come into play in controlling the rates of release of mineral nutrients from an organic nutrient store. The temporary

nutrient immobilization in fungal biomass, binding of organic material with mineral material in soil to increase aggregate formation and aggregate stability as well as the decomposition of organic matter, are integrated functions carried our by fungi in association with other soil organisms (Beare et al., 1994a,b).

2.1.3 Breaking Down the Dead: Adding Fertility

Primary productivity (plant growth) is dependent on adequate sunlight, moisture, temperature, and essential nutrients in soil solution. The nutrient component of soil comes partly from the dissolution of parent rock (see above) and secondarily from the decomposition of dead plant and animal remains. Dead plant parts (above- and below-ground) are returned to the soil, where the activities of bacteria, saprotrophic fungi, and soil fauna degrade the complex organic components. They utilize the carbon skeletons for energy, and in the process, cleave off mineral elements that they incorporate into their biomass and release into the soil water. These organisms rely on extracellular enzymes (Sinsabaugh and Liptak, 1997) to degrade the complex organic molecules contained in the litters. By virtue of their high surface area to volume ratio (bacteria) or filamentous form (fungi) the degradative products of this enzyme activity can be absorbed into the cytoplasm of the organisms. The activity of these saprotrophic fungi is neatly summarized by Forsyth and Miyata (1984, p. 19): "under the silent, relentless chemical jaws of the fungi, the debris of the forest floor quickly disappears."

Reliance on extracellular enzymatic activity, however, is less efficient than the digestive process of animals, in which enzyme activity occurs within a gut. Some of the nutrients mineralized from the decomposing organic matter escape absorption by the micro-organisms and are released into the soil inorganic nutrient pool in soil water. In addition, the rapid turnover of these organisms means that nutrients temporarily locked up or immobilized within their biomass soon become available as new, dead, organic resources for decomposition. Nutrient elements are thus released into the soil solution as simple inorganic compounds through the process of mineralization (Fig. 2.3) and give the soil its fertility. These nutrients are taken up by plants, and the cycle is completed. Figure 2.3 gives a diagrammatic representation of nutrient cycling in forest ecosystems. The principle components are the same in any terrestrial ecosystem, in which any other plant form (grass, forb, herbaceous shrub, cactus, etc.) could be substituted for the tree.

A. Input/Output Ratios: The Link Between Plant Production and Decomposition

The balance between rates of decomposition and mineralization and the rate of input of dead plant parts to soil determines the type of soil profile developed over

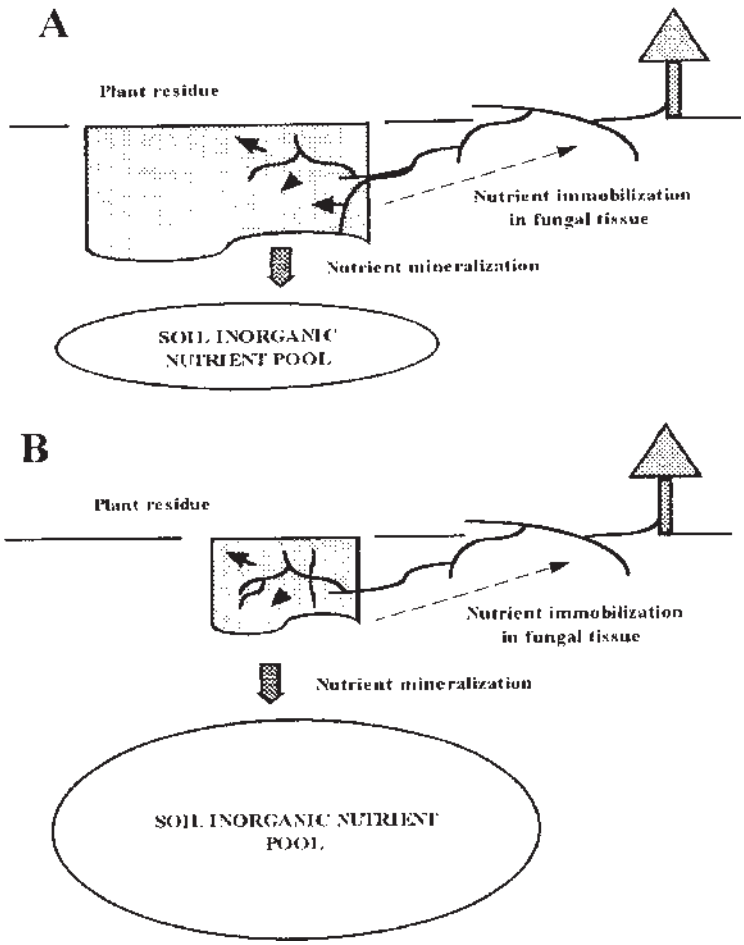

FIGURE 2.3 Diagrammatic representation of the decomposition of plant residues by fungal enzymes, the mineralization of inorganic nutrients to the soil nutrient pool, and the immobilization of nutrients into fungal biomass. At time A, the fungal hyphae colonize the plant resource, secrete extracellular enzymes (arrows within the resource), and mineralize nutrients from the organic resources in the plant litter. Much of the mineralized nutrient is immobilized by the fungal biomass and converted to growth; however, the system is leaky and some mineralized nutrient is lost to the soil nutrient pool. As time continues, the plant resource is utilized and more nutrient accumulates in both fungal biomass and the soil nutrient pool. The latter accumulation in soil gives rise to soil fertility as it is available for plant growth.

time. Where decomposition is very slow, organic matter accumulates as peat. Where decomposition is rapid, as in agricultural soils and grasslands, a mineral soil profile is developed with low organic matter content that is often incorporated to a greater degree into the mineral component of the soil. The organization of soil structures in different ecosystems and the general description of soil structure are well described by Brady and Weil (1999) and are summarized in Coleman and Crossley (1996). They show that the addition of plant and animal litter to the surface of soils is of greater importance in forest and woodland soils than in grassland soils, in which the addition of dead root tissue to deeper soil layers is the most important organic input. This results in different soil profiles developing under different vegetation communities. Forest ecosystems have a clearly defined A horizon of progressively decomposing plant remains, underlying an A_o horizon of relatively undecomposed plant remains. In contrast, in grassland communities the input of aerial plant parts is less important than below-ground plant parts, so the development of an A_o layer is reduced and organic matter is more intimately mixed with the mineral soil. The role of fungi in the process of decomposition and mineralization is greatest in the A_o and A horizons.

The relationship between the input of dead plant and animal parts, climatic conditions, and the rate of decomposition dictates the fertility of the soil and the nature of both nutrient and carbon stores within the soil. Indeed, when there are great imbalances between the rate of input of dead plant and animal remains and the rate of activity of saprotrophic organisms, due to climatic constraints, large, long-term carbon stores can be created. With the rapid demise of the Carboniferous forest and subsequent climatic limitations for complete decomposition of the forest residues, huge deposits of carbon were accumulated, now in the form of coal and oil. The ecological implications of these deposits can be seen worldwide as they fuel our industrialized nations, stimulating human population growth and the environmental pollution associated with it. Here is an example in which the lack of fungal activity, among other factors, had enormous and long-term repercussions on ecosystems.

As will be seen in the next chapter, the nature of the nutrient store is important for plant community development because the soils in which plant litter decomposes rapidly contain most of the nutrients in an inorganic form in soil pore water. Soils that support poor rates of plant litter decomposition lead to an accumulation of partly decomposed, raw humic material in which the nutrients are trapped in an organic form, with slow rates of release of nutrients in an inorganic form into pore water. The former soils are generally more fertile, being able to provide plant growth with a readily accessible source of nutrients. The latter soils are regarded as nutrient-poor (although they may contain more total nutrient than the "fertile" soils), as most of the nutrients are in a plant-unavailable form or only available to plants with specific adaptations to these conditions.

TABLE 2.9 Trends in Primary Production and Litter Input to the Decomposer System in Relation to Latitude

Ecosystem	Plant primary production ($t\,ha^{-1}$)	Litter biomass ($t\,ha^{-1}$)
Tundra	30 to 130	1 to 4
Temperate forest	180 to 200	7.3 to 8.2
Tropical forest	400 +	44

Source: After Rodin and Bazilevich (1967).

(See ericoid and ectomycorrhizal association in the following chapter.) Data from Rodin and Bazilevich (1967) show that the rate of plant litter input into soil of different ecosystems is partly related to plant biomass (Table 2.9), but the amount of litter resident on the soil surface is related to the rate of decomposition (a combination of resource quality and environmental factors). The fertility and structure of soils is thus a function of climate, physicochemical composition (resource quality) of the plant litters, and the soil biotic (bacteria, fungi, and soil animals) composition and activity (Dighton, 1995).

In cold and wet climates, plant growth and biomass is low, being constrained by low temperatures and short photoperiods. Plant litter fall is comparatively high to the plant standing biomass, but often contains many secondary plant compounds, such as polyphenols and tannins. Consequently, the rate of decomposition is low, resulting from the combination of poor litter quality for microbial decomposition and narrow windows of environmentally favorable conditions for microbial activity. This leads to accumulation of organic components of the soil and evolution of peaty soil profiles. These systems tend to be dominated by fungi as the main saprotrophic micro-organism (Heal and Dighton, 1986). Kjøller and Struwe (1982) measured the abundance of fungal hyphae in different ecosystems, and the values (Fig. 2.4) vary, depending upon the metric used. Hyphal length appears to be a more important fungal investment of energy than biomass in cooler environments and where the available resources for decomposition are more recalcitrant. Biomass, with less hyphal extension, appears to be more important in warmer environments and where resources are of a higher quality. Schmidt (1999) shows the importance of fungal biomass in the high-organic-matter-content soils of the tundra ecosystems of Siberia. Hyphal lengths of 393 and 27 $m\,g^{-1}$ dry weight soil were found in the Levinson-Lessing Valley, supporting typical tundra plant communities of dwarf willow communities and polygon soils, whereas low values of 9 $m\,g^{-1}$ dry weight soil can be found in the more fertile, lower-organic-content brown earth soils at Labaz.

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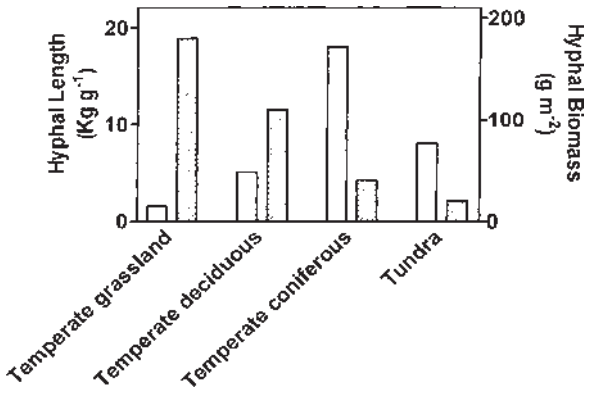

FIGURE 2.4 Maximum estimates of fungal hyphal length (open bars) and fungal biomass (hatched bars) in soils from a range of ecosystems. *Source*: From Kjøller and Struwe (1982).

In coniferous forests, plant biomass is high and litter fall is low, but accumulation occurs, mainly because of the recalcitrance of the litter to decomposition (low resource quality). Harborne (1997) describes the nature of plant phenolics, suggesting that external leaf phenolics are admixed with leaf waxes and have antifungal properties that reduce germination and growth of phyllosphere fungi (Table 2.10). The degree to which these phenolics inhibit or regulate rates of fungal colonization of leaf litter and interact with mycorrhizal fungi is an area of current research.

TABLE 2.10 Anti-fungal Phenolics Obtained from Plant Surfaces

Phenolic	Source
Kaempferol 3-glucoside	Oak leaf
4-Coumaric acid ester	Birch leaf
6-Isopentenylnaringenin	Hops resin
5-Pentadecylresorcinol	Mangifera fruit peel
Chrysin dimethyl ether	Heliochrysum leaf
Quercetin 7,3′-dimethylether	Wedelia leaf
Sakuranetin	Ribes leaf gland
Lueone	Lupin leaf
Pinocembrin	Poplar leaf

Source: After Harborne (1997).

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In tropical forests, plant biomass is very high, and litter fall is high, but the litter on the soil is sparse, indicating a combination of climatic conditions conducive to decomposition and high resource quality. Hedger et al. (1993) showed that in tropical forest ecosystems the input of litter is more important than in temperate forests as a nutrient return to the system. Tropical forests have a continuous rather than seasonal litter input and the quantity of litter can be triple that of temperate forests ($9\,t\,ha^{-1}\,y^{-1}$ tropical; $3\,t\,ha^{-1}\,y^{-1}$ temperate). The importance of litter in tropical regions is so great that some 75% of phosphorus and 41% of potassium flux occurs in the litter in tropical regions. One of the reasons for reduced resource quality in forested ecosystems compared with grassland or herbaceous ecosystems is the diversity of litter types produced within a forest. Quantities cited by Dighton and Boddy (1989) show a forest litter composition of some 55% leaves, 10% fruits, buds, and flowers, 20% twigs, 10% branches, 5% insect frass, and so on. The wood component may be underestimated and may be nearer 40%. This woody component has a high lignin content and high C:nutrient ratio, making it much less degradable by fungi (Melillo et al., 1982). Ranges of carbon to nitrogen and carbon to phosphorus ratios in different plant residues are shown in Table 2.11. The diversity of chemical constituents in these resources results in a general reduction in the overall resource quality and a temporal distribution with respect to the input of litters of differing qualities between seasons. Some resources are pulsed into the decomposer community (flowers and buds), whereas others are of more continual input (twigs, branches) and lower resource quality. The continuous presence of fungal mycelia in the decomposer community thus provides a stable and constantly available mechanism for the decay of these resources whenever they become available. The rate at which the resources are utilized depends upon the diversity of the fungal community available to colonize the resource, their enzymatic competence of that fungal assemblage, the nature of the available resources, and the climatic conditions.

Boddy and Watkinson (1995) show the importance of woody debris in the return of nutrient elements to terrestrial forest ecosystems (Table 2.12),

TABLE 2.11 Range of C:N and C:P Ratios in a Variety of Plant Residues

Component	C:N	C:P
Herbaceous leaf litter	15:1 to 160:1	25:1
Tree leaf litter	20:1 to 300:1	
Woody litter	300:1 to 500:1	1850:1
Fungi	6:1	15:1

Source: After Dighton (1995); Swift et al. (1979).

TABLE 2.12 Relative Contribution of Woody Debris and Nonwoody Litter to the Forest Floor in Temperate Woodland Ecosystems

	Nonwoody litter fall ($kg\,ha^{-1}\,y^{-1}$)			Woody litter fall ($kg\,ha^{-1}\,y^{-1}$)		
	Biomass	N	P	Biomass	N	P
Warm temperature						
Broadleaf deciduous	4236	36	3.8	891	2.6	0.8
Broadleaf evergreen	6484	55	3.7	—	—	—
Needleleaf evergreen	4432	28	2.7	1107	2.5	0.2
Cold temperature						
Broadleaf deciduous	3854	43	4.6	1046	3.7	0.2
Broadleaf evergreen	3590	—	—	—	—	—
Needleleaf evergreen	3144	26	3.2	602	1.1	0.1

Source: From Vogt et al. (1985); Boddy and Watkinson (1995).

where wood can represent 30–40% of the total biomass and 1 to 4 and 0.1 to $0.8\,kg\,ha^{-1}\,y^{-1}$ of N and P, respectively. Decomposition of woody debris and the mineralization of the nutrients contained within is effected primarily by basidiomycete fungi. Often these fungi produce rhizomorphs or cords, which provide long-lived connections between islands of woody residues and allow reallocations of resources within an extensive fungal network. Movement of phosphorus was measured over distances of 1 m. This network is also an ecological compartment for immobilization of nutrients, which are released by death and decomposition or through grazing by invertebrates.

Although climatic conditions dictate to some degree the mass and composition of plant material entering the decomposer system, climatic limitations do not necessarily relate to lack of diversity of the fungal community, rather, they relate to the lack of activity in that community. Indeed, Zak (1993) showed that there is great diversity in the fungal communities of desert ecosystems. This is because of the temporal heterogeneity imposed on the environment by pulses of water availability and the rapid response to "windows of opportunity" by fungi. Fungi are better adapted to this periodic stress than bacteria, as fungi are perennial, nondiscrete organisms that are able to smooth out spatial heterogeneity. Fungal biomass may maintain a permanent presence rather than having the peaks and troughs of populations seen in bacteria. Fungi are able to maintain links between microsites of optimal and suboptimal physicochemical conditions. The diversity of fungi is not only in taxonomic diversity, but more important, in terms of the diversity of functional groups. Citing the work of

Gochenaur (1975), Zak described the greater enzymatic diversity in desert fungal communities than in less xeric ecosystems. He suggests that "fungi from desert and semiarid environments may have evolved a greater functional diversity to cope with the extreme spatial and temporal heterogeneity characteristic of these ecosystems than that of fungi from more mesic environments."

B. Fungal Interactions: Resource Quality and Enzyme Production

The rate at which a resource is decomposed is dependent on its chemical composition (Heal and Dighton, 1985; Heal et al., 1997), edaphic factors (available moisture and temperature), and the colonization of the resource by appropriate saprotrophic organisms. Many of these factors are discussed by Cooke and Rayner (1984). The input of different types (chemical composition and hence resource quality) of plant litters varies with ecosystem type (Dickinson and Pugh, 1974; Cadish and Giller, 1997). The general consensus is that the carbon:nitrogen and lignin:nitrogen ratios can be used as determinants of the resistance of resources to decomposition and ultimate mineralization of nutrients (Melillo et al., 1982). Where the C:N or lignin:N ratios are high there are reduced rates of decomposition, compared to resources containing lower ratios. Other secondary chemicals produced by plants, however, particularly polyphenols and tannins, also inhibit the rates of decomposition of plant material by soil microorganisms (Harborne, 1997). Vanlauwe et al. (1997) showed that there often was little negative relationship between the mineralization of nitrogen from leaf litter and either the polyphenol:N or lignin:N ratio of the resource. Both rates of decomposition (mass loss) and nitrogen mineralization rates are strongly correlated to the (lignin + polyphenol):N ratio (Table 2.13), however.

Because of the variability in chemical composition of plant and animal remains, not all materials can be utilized by all fungal species. Differences exist

TABLE 2.13 Regression Analysis (Regression Coefficients) of Decomposition (Mass Loss) and Nitrogen Release Rate and Determinants of Leaf Litter Resource Quality

	Litter mass loss	N mineralization
C:N ratio	0.74[a]	0.61
Lignin:N ratio	0.68	0.42
Polyphenol:N ratio	0.54	0.76[a]
(Lignin + polyphenol): N ratio	0.77[a]	0.68[a]

[a] Indicates a significant regression ($\alpha = 0.05$).
Source: After Vanlauwe et al. (1997) with permission from CABI.

in the ability of species to access simple or complex forms of carbohydrate and mineral nutrients. Decomposition is a product of enzyme activity, in which the types of enzymes required are dependent on the substrates (chemical constituents) of the resource. Sinsabaugh and Liptak (1997) give a description of the various ectoenzymes produced by fungi and their biochemical effects on organic resources in plant litters (Table 2.14). The ability of different species of fungi to produce specific enzymes dictates in part the succession of fungi as they colonize resources. In addition to enzymatic competency, there are other factors, such as relative growth rates, the production of antibiotic secondary metabolites, and environmental constraints, that influence the ability of specific fungi to colonize resources in the face of competition against other fungi (Cook and Rayner, 1984; Lockwood, 1992; Wicklow, 1992; Frankland 1992; 1998). Linkins et al. (1984) discussed some of the factors affecting the activity of extracellular cellulase, particularly the positive influence of temperature and the cellulose: lignin ratio. Cellulose appears to become unavailable for microbial use when the cellulose:lignin ratio declines below 0.5.

Sinsabaugh et al. (1993) studied the extracellular enzymes that are involved in wood decomposition. Most of these enzymes are derived from fungal activity. Using standardized wood as a resource, they showed that the production of lignocellulase enzyme did not differ between different locations in a temperate forest ecosystem. The rate of immobilization (mainly fungal) of total nitrogen

TABLE 2.14 Fungal Enzyme Systems Associated with the Degradation of Specific Plant Compounds

Plant compound/ fungal resource	Fungal enzyme system
Lignin	Lignin peroxidase, manganese peroxidase, glucose oxidase, cellobiose oxidase, arylalcohol oxidase, glyoxaloxidase, laccases
Cellulose	Exo-1,4-β glucanase, endo-1,4-β glucanase, 1,4-β-glucosidases
Hemicellulose	Endo-1,4-β xylanases, endo-1,4-β mannases, 1,4-β xylosidases, 1,4-β-D mannosidases, 1,4-β glucosidases, α-L arabinosidases, α-glucuronidases, α-galactosidases, acetylxylan esterases, acetyl galactoglucomannan esterases
Pectin	Polygalacturonases, endo-1,4-α polygalacturonase, exo-1,4-α polygalacturonase, pectinlysases, pectinesterases

Source: Information compiled from Sinsabaugh and Liptak (1997).

and total phosphorus into decomposing wood, however, ranged from 2.2 to 4.4 $\mu g\ g^{-1}$ wood for P and 43 to 139 $\mu g\ g^{-1}$ for P at the time when 80% mass loss was achieved. The spatial variability of this parameter was much greater than that for lignocellulase, but much less than for acid phosphatase and N-acetylglucosaminase activity. The process of decomposition is governed by the production of enzymes, which are in turn regulated by the availability of nitrogen or phosphorus. Where nutrient elements are less available, the fungi thus expend greater amounts of energy to produce enzymes to sequester the nutrients from organic sources. These results suggested a large degree of edaphic (soil condition) control over enzyme expression, which is closely related to the availability of inorganic N and P supplies in soil water. Sinsabaugh et al. (1993) thus developed a model that contains both fungal (microbial) and soil nutrient controls over the expression of enzymes. Use of models like this can help us to better understand the complexities of decomposition and nutrient-cycling processes by allowing hypothesis development, leading to the design of experiments that can logically alter single or multiple parameters to investigate the key processes and organisms that are responsible for driving ecosystem processes.

It is important to remember at the outset that saprotrophic fungi involved with decomposition and nutrient cycling in soil do not perform that function in isolation. Plant and animal remains may be comminuted by soil fauna and subjected to enzyme attack by bacteria and actinomycetes. Interactions among these organisms are important in determining the rate of decomposition and the diversity of soil biota. The decomposition process is also dynamic; for example, the same suite of organisms is not present on the plant or animal remains (resource) for the duration of the process of decomposition. It will be seen that different fungi have different enzymatic capabilities, so their appearance on a resource will be dictated by (1) their ability to utilize the resource, (2) their rate of arrival at the resource either by growth or by such transport as spores, and (3) their ability to compete against other fungal species with similar physiological competence.

The colonization of resources by fungi is a function of the quality of the resource, rate of arrival of the fungal propagule (spore or hyphal fragment), and the competitive interaction among fungal species on the resource. The role of plant litter quality on the pattern of fungal colonization of resources has been discussed in Dickinson and Pugh (1974), who give many examples of the change in species composition of fungal communities as different plant substrates undergo the cascade of decay. In general, there appears to be a succession of fungi utilizing different resources within the litter. The classic assumption is that the initial colonizers used soluble carbohydrate sources (sugars) and were later replaced with fungal species having greater enzymatic competence, which are able to break down organic sources of carbon, such as cellulose, and lignin. There

are few clear distinctions in the succession, however, and in fact many of the species overlap in time and space. The successional trends of fungi colonizing decomposing plant material have been described in more detail for the litter of the fern *Pteridium aquilinum* by Frankland (1992) in her discussion of fungal successions (Frankland, 1998). She describes changes from lesion-forming *Rhizographus* and *Aureobasidium* on standing dead litter, through the colonization by basidiomycetes in relation to the rate of loss of cellulose and lignin, and the consequential decrease in C:N ratio from some 200:1 to 30:1. By microscopic observation of small samples of forest floor leaf litter, Ponge (1990; 1991) characterized the colonization of *Pinus sylvestris* needles into four stages (Fig. 2.5). The first stage is characterized by the decomposition of freshly fallen leaves by fungal species, *Lophodermium*, *Ceuthospora*, and *Lophodermella*, that were probably present on and in the leaf at the time of abscission. These fungi cause browning of the leaf and decomposition of relatively available resources. This is followed by greater invasion of the leaf tissue by decomposing microfungi, such as *Verticicladium* (stage 2), and basidiomycete fungi, such as *Marasmius* and *Collybia* (stage 3). Finally, along with the entry of soil arthropods is invasion by mycorrhizal fungi. The close association between the presence of mycorrhizal fungi and decomposing organic matter has also been shown for arbuscular mycorrhizae (St. John et al., 1983). The fine scale examination by Ponge (1990; 1991) allowed him to identify both fungal and faunal components and their interactions. This work also suggested that phylloplane fungal species are present and act as saprotrophs on freshly fallen leaf litter.

A model proposed by Swift et al. (1979) presents the changes from "sugar" fungi to basidiomycetes in relation to the changes in available resources and the influence of climatic stresses. The model suggests that during initial decomposition the carbohydrate component is used as an energy source until such time that the C:nutrient ratio approaches that of the decomposer organism (around 15:1 for P and 6:1 for N in fungi). Only then is there net conversion of organic nutrient to inorganic nutrient (net mineralization). In general, initial resource structure is chemically heterogenous, thus supporting a variety of fungal species. As decomposition proceeds, recalcitrant chemicals are left that can be degraded only by a fungal flora capable of producing the enzymes necessary to degrade the complex resources. Diversity is thus reduced. From these studies, the windows of opportunity for decomposition may be determined and the rate of substrate decomposition mapped. The colonization of decomposing plant material in relation to resource quality has only been presented in reference to the chemical composition of the whole leaf, however. As fungal hyphae are of a small diameter ($\sim 5\,\mu m$), their pattern of growth, enzyme expression, and the subsequent changes in leaf litter chemistry occur at a scale of resolution much smaller than that of a whole leaf. In recent studies (Mascarenhas et al., 2000; Dighton et al., 2001) using microscopic Fourier transform infrared (FT-IR)

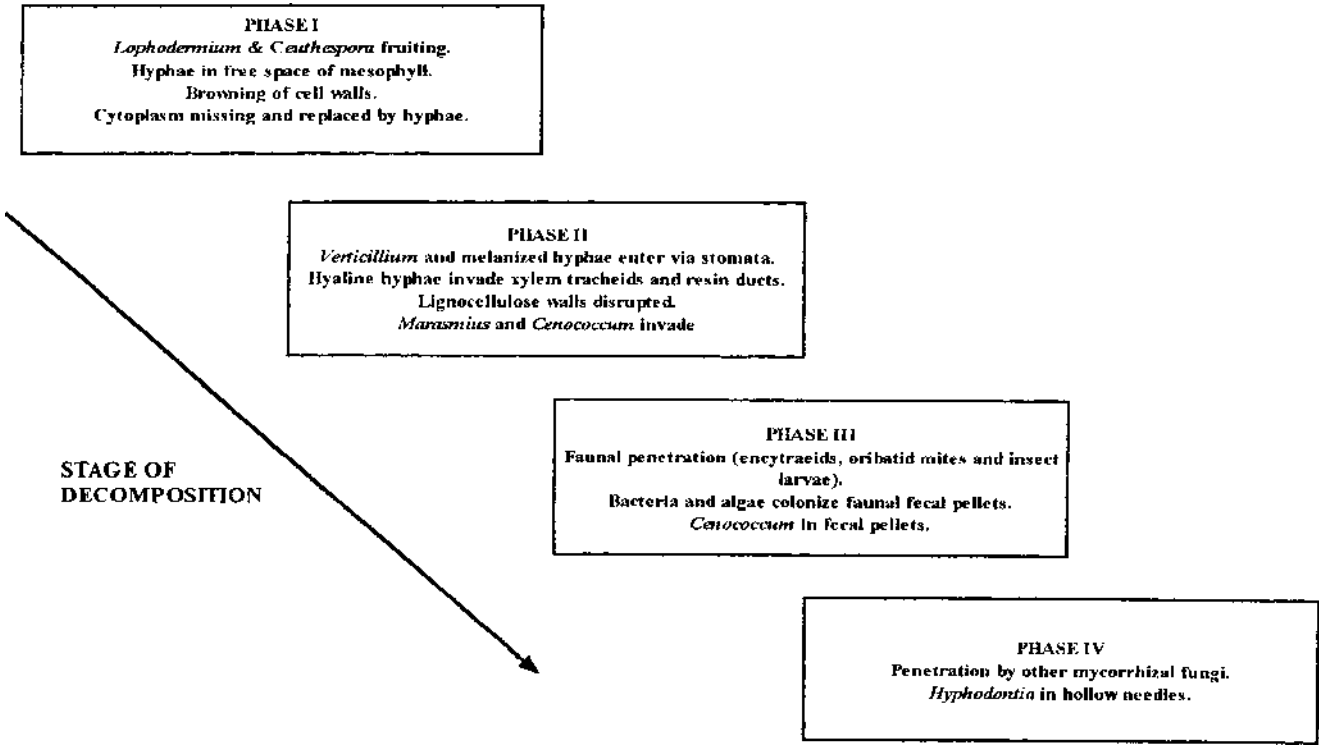

FIGURE 2.5 Schematic of the pattern of fungal colonization of individual pine needle leaf litter as observed by microscopy. *Source*: The information is compiled from Ponge (1991) with kind permission of Kluwer Academic Publishers, and the diagram modified from Dighton (1997).

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spectrometry, real-time microscale ($100 \times 100\ \mu m$) multichanges in leaf surface carbohydrate chemistry caused by fungal colonization are beginning to be revealed. It has yet to be shown how this can be scaled up to ecosystem scales and related to nutrient cycling.

In addition to the changes in fungal species during colonization of a resource unit (leaf, twig, branch, etc.) the dominant fungal species in communities can be a function of the dominant type of resource entering the decomposition system. During seral succession of vegetation from herbaceous to forest ecosystems, there is a change in dominant plant species and plant form (Heal and Dighton, 1986). Along with this change in plant form, there is a general change in the diversity and complexity of resources entering the decomposer system. The initial seral stages are marked by an addition of high-quality resources to the decomposer community, consisting mainly of cellulose and a high C:N ratio and a low lignin content. Following forest canopy closure, woody resources and more recalcitrant leaf litters dominate (Attiwill and Adams, 1993). These litters have high lignin content and low C:N ratios, and therefore decompose at a slower rate. In addition to changes in the dominance of the fungal species or group with ecosystem succession, the degree of interaction between fungi and animals increases. There are more and more intimate associations between fungi and fauna in the exploitation of the more recalcitrant plant residues (Table 2.15).

In forested systems, much deadwood remains in the canopy prior to recruitment to the forest floor. This standing dead material may have a different fungal community than wood on the forest floor. The work of Boddy and Rayner (1983) on oak wood in canopies showed that 12 basidiomycete fungal species dominated in the community. Of these, *Phellinus ferreus*, *Sterium gausapatum*, and *Vuilleminia comendens* were pioneer species of partially living branches, *Phlebia adiata* and *Coriolus versicolor* were secondary colonizers, and *Hyphoderma setigerum* and *Sterium hirsutum* were related to insect activity. In wood, the interactions among fungi can be most clearly observed. The zones of interaction among adjacent, competing fungal colonies have been mapped in three dimensions using wood as a resource (Rayner, 1978; Rayner and Boddy, 1988). Clear demarcation zones are set up when genetically incompatible strains or species meet in a relatively homogenous resource. In an environment in which resources are patchily distributed, such as mixed litter on the forest floor, the colonization of individual resource units is more difficult to map. The colonization pattern of individual straw resource units by a range of fungal species was correlated to relative growth rates of the fungi on agar (Robinson et al., 1993a). These rates of growth allowed four species to be ranked in combative order. Mixtures of fungal species caused significant reductions in the rate of growth of less combative fungal species in the presence of combative species. The cascade of decomposition is thus related to colonization of

TABLE 2.15 Changes in Plant Forms, Their Residues, the Dominant Fungal Groups Effecting Plant Litter Decomposition and the Interactions Between Fungi and Animals During Plant Seral Succession from Herbaceous Ground Cover to High Forest

Ecosystem succession and the increasing contribution of component of plant residues					
	Lower plants	Herbaceous plants	Angiosperm leaves	Coniferous leaves	Wood
Cellulose (%)	16 to 35	20 to 37	6 to 22	20 to 31	36 to 63
Lignin (%)	7 to 36	3 to 30	9 to 42	20 to 58	17 to 35
C:N	13 to 150	29 to 160	21 to 71	63 to 327	294 to 327
Changes in dominant fungal groups					
	"Sugar fungi," ascomycetes, mitosporic, fungi	Yeasts, "sugar fungi," ascomycetes, mitosporic, fungi, basidiomycetes	Ascomycetes, mitosporic fungi, basidiomycetes		Basidiomycetes, ascomycetes, mitosporic, fungi
	Fauna less important		Fauna more important		
	Enchytraeids	Enchytraeids, oligochaetes, diptera	Oligochaetes, collembola, acari	Acari, collembola, oligochaetes	Insecta, arthropoda

Source: After Heal and Dighton (1986); Dighton (1997).

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a substrate by fungi based on their enzymatic competence in relation to the chemical resources available and also by the outcome of interaction with other potential colonizers of that resource. In a companion paper on straw decomposition, Robinson et al. (1993b) showed that where fungal interactions were taking place on straw respiration was greater than where only one fungal species was present. This indicates that the maintenance of combative activities is energy-demanding and may affect the rate of decomposition.

There is evidence that both ectomycorrhizal and ericaceous mycorrhizal fungi are able to access organic forms of nutrients (N and P) and thus may compete with saprotrophic fungi for resources in forested ecosystems. (See Chapt. 3.) The importance of this interaction is not well understood, although negative interactions between saprotrophic and ectomycorrhizal fungi in terms of mycorrhizal colonization of roots have been found (Shaw et al., 1995). The interactions between fungi and bacteria in the decomposition of leaf litter may also not always be synergistic. In an incubation study of beech leaves, Møller et al. (1999) showed that the cellulolytic fungus *Humicola* sp. caused double the carbon utilization from leaves than in combination with a mixed inoculum of soil bacteria. This increase in carbon utilization was positively related to greater β-*N*-acetylglucosaminidase and endoexocellulase activity of the fungus alone than in combination with bacteria.

C. Immobilization and Movement of Nutrients by Fungi

During the course of decomposition, mineral nutrients are sequestered by decomposer soil organisms by being incorporated into the organism's biomass. The residence time of these elements is usually equivalent to the turnover time (lifespan) of that organism. During this period, the element is not in a soluble form in the soil solution, but is immobilized in microbial tissue. The amount of accumulation within the fungal component varies among ecosystems, depending on the chemical composition of the plant parts available for decomposition and the main fungal groups involved in the process. Shorter-lived, ephemeral molds, utilizing simple carbohydrates, thus have lower investment in biomass than longer-lived basidiomycetes growing on woody resource; the potential accumulation in basidiomycetes is therefore greater. Unlike bacteria, fungi are larger organisms and their rate of turnover is lower, particularly in the long-lived Basidiomycotina. A discussion of the role of basidiomycetes in decomposition is given by Frankland et al. (1982).

Where the C:nutrient ratio of a resource is very high, as in wood, the model of Swift et al. (1979) proposes initial immobilization and the import of free nutrient into organic form (fungal thallus) during the initial stages of decomposition until the fungal resource C:nutrient content is equivalent to that of the fungus. Fungal immobilization of nutrients can be considerable. Stark (1972) showed that hyphae had 193–272% greater N content and 104–223%

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TABLE 2.16 Allocation of Standing Crop Organic Matter in a Second Growth Douglas Fir Forest Ecosystem

Forest component	Total standing stock (%)	Tree component	Total tree standing stock (%)
Tree biomass	78 to 79	Bole	64 to 66
Soil organic matter	17	Branches	7 to 8
Forest floor litter	4	Foliage	4
Fungi	2	Nonmycorrhizal roots	17 to 18
		Mycorrhizae	6

Source: After Fogel and Hunt (1983).

greater P content than the pine needle litter on which they were found, suggesting immobilization of these elements into fungal biomass. Fungi are also important as temporary nutrient immobilizers. Fogel and Hunt (1983) demonstrated the importance of fungal biomass in a temperate Douglas fir forest ecosystem (Table 2.16). For all nutrients except calcium, roots and mycorrhizae contained greater stocks than the forest floor of fungi, but the amounts of Ca in fungi and the forest floor were twice those for mycorrhizae and roots. Return of N, P, and K by mycorrhizae to soil was about 83–87% of the total tree return and 25–51% of the Ca and Mg return. Evidence for elevated nutrient concentrations in fungal tissue above that of the underlying substrate comes from Clinton et al. (1999). Their measures of nutrient content of fungal fruit bodies (mushrooms of both mycorrhizal and saprotrophic basidiomycetes) in a *Nothofagus* forest show that all elements other than calcium are more concentrated in fungal tissue than in forest floor material (Table 2.17). In practical forestry, particularly in fast-growing trees, there is competition for essential nutrients between the fungi decomposing woody residues from logging and for growth by second rotation tree crops. To alleviate this competition, burning protocols have been established to rid the site of both woody debris and (incidentally) leaf litter, as well as the nutrients they contain (Dighton, 1995). A greater understanding of the interactions between nutrient availability, temporary nutrient immobilization, and alternative applications for postharvest residues could lead to a more rational use of residues to provide sustainable forestry without the loss of nutrients from the ecosystem from burning and without the need for exogenous nutrients in the form of fertilizers (Jones et al., 1999).

Decomposition of the fruit body material will be faster than that of surrounding forest floor material, providing localized spots of high rates of mineral nutrient release. The duration of immobilization of those nutrients into fungal hyphae before translocation to the fruit body, however, could be an important aspect of the control fungi have on the rates and timing of release of

TABLE 2.17 Nutrient Concentrations ($mg\,kg^{-1}$) and C:N Ratio of Fungal Fruit Bodies and Underlying Forest Floor Substrates in a *Nothofagus* Forest Ecosystem

	Forest floor mushrooms	Forest floor substrate	Deadwood mushrooms	Deadwood substrate
N	35	8.7	31	1.5
P	4	1.0	5	0.2
K	22	3.5	19	0.1
Mg	0.8	0.1	1.6	0.4
Ca	0.5	7.0	2.6	2.9
Si	95		37	
Na	97		34	
Al	45		24	
C[a]	446		446	
C:N	13		19	

[a] Carbon measured as $mg\,g^{-1}$.
Source: After Clinton et al. (1999) with permission of *N. Z. Journal of Botany*.

pulses of nutrients within the forest ecosystem. In temperate zones, the spring and fall abundance of fruit body production may coincide with the high root growth and high nutrient demand by trees at these periods, a correlation that has yet to made by observation and measurement. Marumoto et al. (1982) suggested a longer turnover time for fungi than bacteria in their experimental decomposition study of killed bacteria, fungi, and combined bacteria and fungal cells. Using ^{14}C and ^{15}N labeling techniques for each of the cells, they showed that the rate of carbon loss as CO_2 was similar between microbe sources, but that the rate of mineralization of nitrogen as both NH_4 and NO_3-N was slower in the decomposition of fungal cells.

Lodge (1993) discussed the role of fungi in nutrient cycling in tropical forest ecosystems (Table 2.18). These systems have large nutrient capital in plant biomass but are frequently limited by nutrient supply from soil. Much of this is caused by phosphorus binding to aluminum and iron oxides, and thereby being less plant-available. Due to high rainfall, other plant essential nutrients, nitrogen and potassium, are likely to be leached from the rooting zone. Fungal biomass (5 to 5 $mg\,g^{-1}$ litter and 2.5 to 3 $mg\,g^{-1}$ soil; reports of 8 to 333 $g\,m^{-2}$) in these soils contains a large reservoir of nutrients that can be slowly released on death and decomposition. This is especially true for phosphorus, where the concentration in fungal tissues can reach 5 to 36 $mg\,g^{-1}$ and the phosphorus content of leaf litter can increase 10-fold due to immobilization by fungi. Lodge (1993) also showed that the biomass of fungi in wet tropical forest soils is significantly and positively correlated with soil moisture and the amount of rainfall in the preceding week.

TABLE 2.18 Proportion of Nutrient Elements Contained in Fungal Biomass in Wet Tropical Soil Systems Demonstrating the Importance of Fungi as Nutrient Reservoirs

Element	Fungal as percentage of leaf litter	Fungal as percentage of soil extractable
N	1.6	
P	22.2	10.5
K	3.7	3.6
Ca	2.0	23.6
Mg		3.2
Na		3.1

Source: After Lodge (1993).

She thus attributes the effects of fungi to immobilization of nutrient elements at a time when there could be maximal loss due to leaching. Fungi are therefore an important control on nutrient retention and release. Many of the fungi are basidiomycetes that form rhizomorphs and are associated with decomposing wood. Many of these have the ability to translocate nutrients from decomposed leaf litter to freshly fallen leaf litter to improve resource quality (lower the C:nutrient ratio) and enhance rates of decomposition. Due to activities of cord-forming fungi, Lodge demonstrated that the phosphorus content of recently fallen leaf litter could increase by 120–140% during the first 6 weeks of decomposition. Similarly, nitrogen could increase by 110–160%. Behera et al. (1991) found 36 species of fungi in the soils of a tropical forest site and showed that the composition and biomass of this community changed between seasons. Greatest biomass and species number occurred in January, following the rainy season, showing a positive correlation with both soil moisture and soil organic matter content.

The accumulation of nutrients into fungal biomass makes fungi a good source for animals. In addition to the direct food chain interaction, other soil fauna–fungal interactions occur. Grazing of fungal hyphae by soil animals has been shown to affect both colonization of resources (litter) and rates of nutrient mineralization. Newell (1984a,b) showed that the effect of fungal grazing collembola altered the vertical distribution of competing mycelia of *Mycena galopus* and *Marasmius androcaceous* in a spruce forest floor. Preferential grazing of *Marasmius* restricted its growth to lower depths and *Mycena* dominated in the A soil horizon. Coleman et al. (1990) showed that reduction in microbial predators in ecosystems with high densities of soil fauna (forests) led to increased decomposition of litter (relief of grazing pressure). In contrast, in

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systems with low densities of soil fauna (agricultural soils) the effect of faunal reduction was to reduce decomposition (suggesting a synergistic interaction). In a comparison of tilled and untilled agricultural soils, Beare et al. (1992) showed that the exclusion of fungiverous soil arthropods reduced litter dry mass loss by only 5%, but significantly altered nitrogen dynamics in surface litter of no-till soil. Saprotrophic fungi were responsible for as much as 86% of net nitrogen immobilization ($1.8\,g\,m^{-2}$) into surface litters with the exclusion of fungiverous microarthropods. These trophic interactions will be discussed further in Chapt. 4.

Different nutrient elements—and in particular, metal ions—may be immobilized for long periods in fungi (bioaccumulation). Fungi are nondiscrete organisms (having an extending hyphal network) and are able to translocate elements within the fungal thallus (Cairney, 1992). This could account for the spatial redistribution of elements. For example, if an element were always translocated away from dying regions, translocation would increase the length of time of immobilization into fungal components. Olsson and Jennings (1991) demonstrated that translocation of ^{14}C and ^{32}P through hyphal systems of *Rhizopus*, *Trichoderma*, and *Stemphylium* occurred by diffusion. The rate of translocation of carbon within the fungal thallus has been shown to react in real time to provide directional flow to the building phases of the hyphae (Olsson, 1995). In the face of high demand for nutrients and carbon at advancing hyphal fronts, nutrients and carbon are translocated acropetally through cytoplasmic flow and diffusion in the cytoplasm and apoplasm. In contrast to the diffusion of C and P, however, Gray et al. (1995) demonstrated that translocation of ^{137}Cs through hyphae of *Schizophyllum commune* was slower than diffusion, suggesting incorporation of the element into structural components of the cytoplasm or hyphal wall, reducing the rate of movement. This presents a plausible mechanism for accumulation of radiocesium in basidiomycete fungi by Dighton and Horrill (1988) and others (data from Yoshida and Muramatsu, 1994). These studies suggest that accumulation levels could be high and long-lived.

The translocation of solutes through fungal tissues colonizing wood has been measured by tracer studies and has been shown to be of importance in allowing the colonization of low resource quality substrates. Wells and Boddy (1990) showed that 75% (*Phanerochaete velutina*) and 13% (*Phallus impudicus*) of the phosphorus added to a decomposed wood resource is translocated to newly colonized wood resources through mycelial cord systems. Maximum rates of P translocation are given as $7225\,nmol\,P\,cm^{-2}\,d^{-1}$ through cords. Using the radioisotope ^{32}P, Wells and Boddy (1990) demonstrated translocation of phosphorus through cords of the wood-decomposing fungi *Phanerochaete velutina* and *Phallus impudicus*. They showed that cords were only formed in unsterile soil, suggesting the trigger for cord formation is derived from other organisms and that the rate of translocation of phosphorus from decayed wood

blocks to new wood blocks is on the order of 7 μmol cm^{-2} d^{-1} through cords. In field experimental manipulations, Wells and Boddy (1995a) showed that this translocation could be conducted over distances of up to 75 cm between decomposing resources on the forest floor and into living wild strawberry and moss plants. Translocation of phosphorus in mycelial cords is temperature-dependent, with greater rates of movement at higher temperatures (Wells and Boddy, 1995b). The effect of change from wet to dry soil conditions induces a thickening of the cord system of *Phanerochaete velutina* and a reduction in the translocation of phosphorus to a new wood resource. Wetting appears to have no effect on cord structure or P movement (Wells et al., 2001).

Fungi therefore are major contributors to the fertility of soil by their action of decomposing organic residues derived from dead plant and animal remains. The activity of their exoenzymes removes the mass of dead remains and mineralizes the nutrients contained within, providing a source of nutrients for further primary production. During this process, however, fungi can perform the important function of regulating the release of nutrients in both space (translocation) and time (immobilization). These activities smooth out some of the heterogeneity seen in the distribution of resources to the decomposer community in the soil system. Patch accumulation of leaf litters on the forest floor of pine barrens ecosystems has been shown to be related to the density and distribution of stems of understory herbaceous vegetation (Dighton et al., 2000). The study by Dighton et al., they showed that the size of leaf litter patches was dependent upon the density of leaf-trapping ericaceous stems. In addition, the quality of resources within patches depended upon the litter patch size, as the proportion of litter material composing the patches differed among patches of different sizes. The interpolation of the process rates occurring within different patches from the leaf litter patch scale to an ecosystem-level scale of resolution, however has yet to be made.

In addition to plant litter, the remains of animals and their dung form specific organic resources that select for specific groups of fungi (Richardson, 2001). In a literature review, Richardson (2001) showed that there were highly significant differences in the fungal community structure among the dung of six animal species. These fungi are often specific to their niche, but provide food for a variety of fungiverous animals (Hayashi and Tuno, 1998) and are therefore of significance in the ecosystem. We will not dwell on the autecology of these fungi here, but will return to their importance in fungal–faunal interactions in Chap. 4.

D. Where Does Soil Begin and End?

In wet tropical forests it may be difficult to determine where soil starts and ends. Due to the high rainfall, nutrients are leached from leaves and twigs in the canopy. These nutrients are added to rainfall percolating through the canopy and thus cause changes in the chemical composition of throughfall and stemflow.

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This modifies the nutrient availability in the forest floor. Additionally, some 7% of the total expected leaf litter fall never reaches the forest floor, but is trapped in the canopy of the tree or in the canopy of the understory shrub community (Hedger et al., 1993). Plant litter trapped in the canopies is held there by fungal hyphae and particularly by rhizomorphs formed by species of the genera *Marasmius* and *Marasmiellus*, which effect the decomposition of the plant litter. These rhizomorphs and hyphae have become adapted to desiccating environments by their ability to produce copious amounts of mucilage and to be able to grow at low moisture potentials (-4 to -8 mPa). In an experimental litter manipulation in the canopy, Hedger et al. (1993) investigated the development of the contact zone between freshly added leaf litter and the fungal hyphae. Hedger et al. (1993) concluded that a large proportion of the hyphae invading new leaves originated from live leaves in the canopy. These fungi grow upwards and away from previously trapped litter at a rate of $3-6\,\mathrm{mm\,d^{-1}}$. The authors suggest that the fungi are endophytes within or saprotrophs on the surface of living leaves. The balance between the amount of leaves trapped is a function of leaf weight, tensile strength of the retaining fungal structures, and weight loss due to decomposition. As the leaves decompose, mineralization will release nutrients that will wash to the forest floor in throughfall rain, thus the formation of "soil" in the tree canopy is a reality, and probably has a significant impact on the fertility of the tropical forest ecosystem.

Lodge and Asbury (1988) demonstrated that the ability of fungi hyphae and cords to bind leaf litter together on the forest floor is important in preventing downslope loss of leaf litter in tropical forest ecosystems. The potential loss of organic matter containing nutrients for plant growth is mainly prevented by the action of a number of basidiomycete fungi that bind the leaf litter together. Species of *Collybia*, *Marasmiellus*, *Marasmius*, and *Mycena* are the main fungi involved in forest floor litter trapping. The effect of litter binding by fungi increases with increasing ground slope. Lodge and Asbury (1988) concluded from field manipulation experiments that loss of litter was reduced by 35% from shallow slopes ($<75\%$ of angle) and 45% at greater slopes (75–90%). The reduction in leaf litter loss and subsequent incorporation of organic matter into the mineral soil is thought to prevent soil erosion during high rainfall periods.

The magnitude of the effects of rainfall volume and leaching rates from canopy plant parts in wet tropical forests is much greater than that of other ecosystems. Even in temperate forest ecosystems, however, the changes occurring in the stemflow water chemistry is enough to provide a suitable habitat for epiphytic lichen communities. Knops et al. (1996) demonstrated that the presence of the epiphytic lichen, *Ramalina menziesii* on blue oak also altered throughfall chemistry, thus altering nutrient availability in the forest soil. They measured $590\,\mathrm{kg\,ha^{-1}}$ of lichen biomass in the forest, in comparison with a standing crop of $958\,\mathrm{kg\,ha^{-1}}$ of oak leaves. Trees with lichens had a higher

deposition of total N, organic N, Ca, Mg, Na, and Cl in throughfall rain than trees without lichens. Tress with lichens had a lower throughfall of SO_4, and the concentration of NO_3, NH_4, K, and total P was not different. Lichen litter reduced the decomposition of oak leaf litter, in such a way that release of N and P were reduced by 76% and 2%, respectively. The increased mineralization from lichen litter more than compensates for the reduction in oak litter decomposition, however, leading the authors to conclude that the impact of both lichen leachates and effect on decomposition was unlikely to affect intrasystem or forest productivity. The evolution of a stable interaction between the forest and epiphytic lichen community has, however, not been contemplated.

2.2 NUTRIENT AVAILABILITY IN AQUATIC AND MARINE ECOSYSTEMS

2.2.1 Marine Ecosystems

The diverse taxonomic fungal groups found in marine ecosystems suggest that they should be regarded as an ecological rather than a taxonomic, group (Hyde et al., 1998). The ascomycete order of *Halosphaeriales* is well represented in this ecosystem by some 43 genera and 133 species. A lower diversity of basidiomycete and mitosporic fungi are found in marine ecosystems, but the distribution of species may be related to environmental conditions. Jones (1993) reports on fungal communities that are restricted to tropical and subtropical marine systems, and thus are distinct from those fungal species with cosmopolitan distribution. Many of these tropical species are associated with mangrove. The majority of species are saprotrophs, particularly involved in the role of decomposition of wood and the plant litter derived from mangrove swamps. All marine fungi show physiological adaptations that allow them to survive under the stress of a high saline environment (Jennings, 1983; Clipson and Jennings, 1992), especially in their regulation of their osmotic potential. Fungi even exist in the hypersaline conditions of the Dead Sea at total salt concentrations of $340\,g\,l^{-1}$, where the number of species isolated has been reported to be 55 (Kis-Papo et al., 2001). Kohlmeyer and Kohlmeyer (1979) characterize marine fungi in terms of their habitat and function. Arenicolous, or sand-inhabiting fungi, are mainly decomposers, which utilize algae, leaves, and detritus as their resources. Lichen fungi form associations with algae and have ecological functions similar to terrestrial lichens in the formation of soil and so on as we previously discussed. Additionally, primitive lichen associations are formed with loose associations between fungi and mircoalgae. Of these, *Leiophora pelvetiae* is thought to be parasitic on the seaweed *Pelvetia canaliculata*. A range of ascomycete fungi appear to be true parasites of seaweeds, imparting a range of effects from minor discoloration of the thallus to

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the formation of galls and malformations that limit the photosynthetic function of the algae. Newell (1996) suggests that there are four basic strategies adopted my marine decomposers (organo-osmotrophs), that adapt them for a marine life. First, they maximize their surface area and have a high substrate affinity to allow enzymes to easily diffuse into solid particles to effect mineralization. This trait is particularly seen in prokaryotes. Penetration of the decomposing resource by tunneling or surface erosion into solid organic substrates is common in both bacteria and labyrinthulids and involves chains or series of single cells. Penetration of solid material by adsorptive "ectoplasmic nets" or rhizoids is a strategy adopted by true chitrids, thrasusochitrids, and hyphochytrids. Colonization of solid substrates by networks of "self-extending tubular reactors" (tube of chitil–laminarin or cellulose–laminarin), however, signify the activity of mycelial eumycotic fungi and oomycte protoctists.

Although fungi compete with marine borers as wood decomposers, their ability to survive in sediments of low oxygen tension give fungi a competitive edge. Indeed, wood is a major resource for fungi in marine ecosystems (Rohrmann and Molitoris, 1992). Wooden breakwaters, jetties, and piers provide resources for the saprotrophic fungal community, whose effects cause large economic repercussions. Kohlmeyer and Kohlmeyer (1979) show a table of 107 fungal species isolated from decomposing wood in marine habitats. These include 73 Ascomycotina, two Basidiomycotina, and 29 mitosporic species. As in terrestrial ecosystems, the low resource quality of wood appears to encourage tight linkages between fungi and fauna for its decomposition. Evidence suggests that wood-boring marine mollusks preferentially settle and feed on wood that has previously been colonized by fungi and partially decomposed rather than invading fresh wood. The associations have become so tight that, for example, the wood-boring crustacean the gribble (*Limnoria tripunctata*) has increased longevity when feeding on wood colonized by fungi. More important, it is incapable of reproduction on any substrate unless marine fungi are included as part of its diet. This may be due to the enhanced availability of proteins, essential amino acids, and vitamins, which are unavailable in the absence of fungi.

In salt marsh ecosystem, the decomposition of the salt marsh grass *Spartina* relies on a community of fungi to decompose leaves separate from those effecting decomposition of the roots and rhizomes, which make up more than half of the plant biomass. Live fungal biomass is low ($< 20\,\mathrm{mg\,g^{-1}}$ substrate), and their strategy is to grow rapidly within the substrate and immobilize nutrients into the fungal biomass. Fungi in this situation can contain some 75–100% of the total N of decaying cordgrass leaves. Leaves are mainly decomposed by ascomycetes, of which *Phaesosphaeria spartinicola* is dominant. The role of oomycetes (e.g., Halophytophthoras) is unknown. Kohlmeyer and Kohlmeyer (1979) report a range of both ascomycete and mitosporic fungi involved in the decomposition of salt marsh vegetation, but only a single basidiomycete species, *Nia vibrissa.*

In salt marsh sediments, aerobic conditions quickly give way to anaerobic conditions with increasing depth. In the anaerobic environment, fungi cede to the abilities of bacteria to derive energy form chemoautotrophic processes. In the anaerobic zones, bacteria dominate over fungi. Mansfield and Bärlocher (1993) found that fungal biomass, measured as ergosterol content, was negatively related to redox potential in *Spartina* salt marshes, showing a rapid decline of fungal activity with increasing sediment depth, although fungi are a major agent in the decomposition of *Spartina* plant parts (Meyers, 1974). When balsa wood panels were buried in an anaerobic salt marsh, however, they were colonized by fungi within 12 weeks. Many of the fungal species colonizing these wood blocks could not grow in entirely anaerobic conditions, but were able to grow down from aerobic to anaerobic zones over distances of 5–10 mm in 15 days from resources in the aerobic zone. This evidence shows that fungi have the ability to conduct oxygen from aerobic region, through hyphae, to advancing mycelial fronts, which are physiologically active in decomposition in the anaerobic zones. (Padgett and Celio, 1990).

Fungal biomass in the decomposing material in salt marsh ecosystems is also important for the sustaining invertebrate herbivore populations. The amphipod *Ulorchestia spartinophila* has been shown to have complex dietary requirements and appears to grow best and produce the most offspring when fed on decaying leaves containing a high fungal biomass.

Mangrove swamps are the tropical equivalent of salt marsh habitats in the temperate world. They occur in more sheltered areas, however, away from the direct impact of wave action. The litter from these ecosystems is more diverse than that of salt marsh systems, and the high rate of primary production produces copious detritus supporting a large population and diversity of detritivore fungi, bacteria, and fauna (Kohlmeyer and Kohlmeyer, 1979). The mangrove fungi are almost exclusively saprotrophic, consisting of some 23 species of ascomycete, 17 mitosporic species, and two basidiomycetes. Fungi, including ascomycetes, mitosporic fungi, the chytrids, and the chromistan group (oomyetes), are important decomposers of this plant material. The composition of mangrove fungal communities has been shown to be distinct from those associated with decomposition in salt marsh ecosystems (Newell, 1996). The fungal biomass in decaying mangrove leaves is much lower than that in decaying salt marsh vegetation ($< 1\,\mathrm{mg\,g^{-1}}$ compared to $60–85\,\mathrm{mg\,g^{-1}}$, respectively) (Newell and Fell, 1992; Newell, 1996), and bacteria represent a very small percentage of the decomposers ($0.7\,\mathrm{mg\,g^{-1}}$). Newell and Fell (1992) also showed that there were significant changes in fungal biomass during decomposition of red mangrove leaves. They suggest that the actual fungal biomass is greater than $1\,\mathrm{mg\,g^{-1}}$, as many marine oomycetes (e.g., *Halophytopthora*) do not contain ergosterol (Table 2.19). Mangrove leaves rapidly accumulate a large population of oomycete fungi (*Halophytophthora* spp.), but ascomycete fungal species,

TABLE 2.19 Sequential Development of Fungal Biomass as Determined by Ergosterol Content on Decaying Red Mangrove Leaves

Stage of leaf decomposition	Mass loss (%)	Ergosterol content ($\mu g\, g^{-1}$ organic mass)
Live or senescent	0	<1
Red-brown stage	30	19
Black, submerged	40 to 60	85

Source: Data from Newell and Fell (1992).

dominated by *Lulworthia grandispora*, may comprise 50% of the fungal community.

Export of plant detritus from mangrove ecosystems to the oceans is an important contribution to the nutrient loading of oceans (Lee, 1995). Lee demonstrated the importance of the decomposition of plant litter in coastal communities and the consequent nutrient mineralization that supplied nutrient to the ocean. Outwellings of water from mangrove swamps to the ocean can result in a transfer of between 60 and $260\, t\, y^{-1}$ of carbon, which is exported mainly as dissolved organic carbon (DOC). This may be an important component of nutrient additions to near-shore waters and a process in which fungi play a major role. Hyde and Lee (1995) point out, however, that there are still many gaps in our knowledge of the role of fungi in nutrient cycling in mangrove ecosystems. They suggest that the rates of chemical transformations are dependent upon the age of the mangrove stand, the diversity of mangrove and terrestrial tree flora, and the proportion of the various microhabitats within an area. They also suggest that the end product of fungal decomposition is likely to be dissolved organic matter rather than particulate organic matter, of which there is scant understanding of its origins and movement in distribution in marine estuarine ecosystems. In addition, fungi are exported from mangrove ecosystems. The mangrove tree (*Rhizophora mangle*) produces viviparous seedlings. These seedlings develop as the fruit germinates on the tree, falls off into the water, and is carried by water currents. These drifting seedlings are vehicles for the dispersal of marine fungi. Kohlmeyer and Kohlmeyer (1979) report occasions where *Keissleriella blepharospora* and *Lulworthia* spp. have been transported in this manner from the tropics to the coast of North Carolina by the Gulf Stream.

2.2.2 Freshwater Ecosystems

According to Wong et al. (1998) there are more than 600 species of aquatic fungi, many of which have specific morphological and physiological adaptation to allow them to live in aquatic ecosystems. Fungi have been isolated from spores

suspended in the water column of streams, ponds, and lakes, growing on decaying vegetation and utilizing suspended organic matter in deep aquifers (Kuehn and Koehen, 1988). Aquatic hyphomycetes occur on almost all substrates in freshwater systems (Bärlocher, 1992). Fungi biomass is usually greater than bacterial biomass on decomposing leaf litter in aquatic ecosystems. Plant litter inputs into headwater streams in forested catchments can be on the order of 500 g dry mass m^{-2} and reach peaks of over 100 g m^{-2} (Weigelhofer and Waringer, 1994). The success of fungal species that are adapted to live in aquatic habitats is that terrestrial fungi entering the system along with the plant material are unable to macerate the resources when submerged, and colonization of plant litter by tetraradiate and sigmoid spores of aquatic fungal species is more efficient than by rounded spores of terrestrial fungi, which are adapted for wind dispersal (Wong et al., 1998). Measures of rates of decomposition of plant litters by aquatic fungi suggest that a range of carbohydrate resources can be utilized (Bergbauer et al., 1992), but also that the rate of decomposition is reduced in mixed-species fungal assemblages compared to single species. Bergbauer et al. (1992) attribute this reduction in decomposition to the production of antimicrobial compounds that result in nonnutritional competition between fungal species. Wood is an important resource, representing up to 20% of the total plant litter input (Table 2.20). Shearer (1992) estimates that some 250–800 tons ha^{-1} of woody debris enters stream systems of old-growth temperature coniferous forests and 40 to 130 tons ha^{-1} in mixed hardwood forests. This woody material is important in that its residence time is much greater than leaf litter, and therefore forms a more stable environment for fungal community development. Despite the lack of white and brown rot fungi, which occur in terrestrial ecosystems, lignolytic aquatic hyphomycetes of the genera, *Tricladium*, *Anguillospora*, and *Dendrospora* are dominant colonizers of woody material in streams. The main addition of woody material to a stream ecosystem occurs in the winter as a result of windthrow and weather damage to branches and twigs. It is thus available for fungal colonization in the spring and throughout the year, whereas deciduous leaf litter enters as a pulse in the fall and is usually degraded before the next leaf fall or has already been exported downstream. Approximately one-third (86 species) of aquatic hyphomycetes have been isolated from wood. Shearer (1992) also shows that many species express a wide range of enzymes related to the decomposition of woody material. Of 20 species, seven were shown to produce enzymes to degrade carboxymethyl cellulose, cellobiose, amylose, xylan, xylose, lignin, and pectin, while another four species could utilize five or more resources. The community of fungi colonizing woody resources alters along the length of a water course (habitat selection) and over time at the same location (resource succession). Gessner et al. (1997) provide a review of the role of fungi in plant litter decomposition in aquatic ecosystems. They provide a conceptual model of the interactions among the internal controls (litter quality), external controls

TABLE 2.20 Annual Total Coarse Particulate Organic Matter Entering a Variety of Streams in a Beech-Dominated Austrian Forest

Site	Input location	Leaves (%)	Wood (%)	Miscellaneous (%)	Total (g dw)
1	Aerial	76	6	18	545
	Right bank	68	16	15	105
	Left bank	71	11	18	328
2	Aerial	89	9	2	362
	Right bank	85	15	1	47
	Left bank	81	17	2	213
3	Aerial	80	12	9	473
	Right bank	85	5	10	194
	Left bank	80	17	3	413
4	Aerial	70	17	13	680
	Right bank	80	17	3	595
	Left bank	86	9	5	380
5	Aerial	73	16	11	716
	Right bank	72	15	13	141
	Left bank	68	27	6	164
6	Aerial	93	4	3	422
	Right bank	83	17	1	484
	Left bank	88	10	2	432

Note: The relative contributions of leaf, wood, and miscellaneous plant material entering the stream directly (aerial) and via the right or left stream bank are given in percentages.
Source: Data from Weigelhofer and Waringer (1994).

(environmental variables), and the metabolic activity of fungi that determines the possible outcomes of decomposition in the aquatic system (Fig. 2.6).

Fungi are not the only organisms that effect leaf litter decompositions in freshwater ecosystems. Gaur et al. (1992) identified 13 bacteria and 24 fungal species associated with the decomposition of water hyacinth leaves. They demonstrated that the bacteria were involved with the breakdown of polysaccharides and proteins and the fungi with the decomposition of cellulose and lignocellulose. Litter decomposition in the first few days, comprising some 30% of litter mass loss, was predominantly nonmicrobial (faunal comminution). Bacteria were then the most important components of the microbial community, where they accessed dissolved organic matter. Fungi became important as the leached organic matter availability declined and they were capable of entering the intact structural components of the leaf litter. Within the fungal community, Gaur et al. (1992) showed that there were successions of fungi, with fungi having greater enzymatic capabilities sharing a larger proportion of the community in later stages of decomposition and utilizing the more recalcitrant resources.

FIGURE 2.6 Schematic representation of decomposition in aquatic systems based on a fungal-dominated system. *Source*: After Gessner et al. (1997).

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Bacteria account for approximately 30% of the respiration from decomposing leaf litter of the dominate plant species in the Florida Everglades. The remaining 70% comes from fungi (Hackney et al., 2000). Ergosterol measures of fungal biomass showed an increase on decaying leaves during the course of decomposition, but the fungal biomass was not related to nutrient levels in the water.

The rate of leaf litter decomposition is strongly influenced by water chemistry. Suberkropp (1995) showed that fungal biomass was higher in streams with higher nitrogen content, but also that the effects of additional nitrogen had a more pronounced effect on the production of spores than on mycelial biomass. This, he suggests, demonstrates the ability of the fungi to allocate resources to either growth or reproduction, depending on environmental factors. Suberkropp and Chauvet (1995) performed reciprocal exchange of yellow poplar leaves between streams differing in pH and nutrient composition. They showed that the rate of leaf decomposition varied by a factor of 9 between streams, the microbial activity (measured as ATP production) by a factor of 8, and fungi sporulation by a factor of 80. A summary of the interactions among stream characteristics, leaf litter decomposition, and measures of fungal activity are given in Table 2.21. Litter decomposed faster in hardwater streams, with higher availabilities of nitrate–nitrogen and phosphorus and higher temperatures. The greater availability of nutrients in hardwater streams stimulated more abundant fungal biomass and fungal activity and resulted in a more diverse fungal species assemblage. About six species of fungi were common throughout all hardwater streams, whereas the softwater streams used in this study had only two species in common with the hardwater streams. Also, the species that occur among the streams were different, with *Anguillospora filiformis* and *Flagellospora curvula* being the two dominant species in softwater and not occurring in the hardwater

TABLE 2.21 Pearson Correlation Coefficients Among Stream Variables, the Decomposition of Yellow Polar Leaves and Fungal Activity in Contrasting Soft- and Hardwater Streams

		NO_3-N	PO_4-P	Temperature
All streams	Decomposition constant (k)	0.97	0.83	0.77 NS
	Maximum ATP	0.95	0.86	0.91
	Maximum sporulation	0.90	0.46 NS	0.72 NS
Hardwater streams	Decomposition constant (k)	0.96	0.75 NS	0.51 NS
	Maximum ATP	0.92	0.70 NS	0.84
	Maximum sporulation	0.97	0.66 NS	0.85 NS

Note: NS shows that correlation is not statistically significant.
Source: Data from Suberkropp and Chauvet (1995).

streams. The occurrence of different species of fungi in aquatic systems is dependent upon season, however. Both Gupta and Mehrota (1989) and Thomas et al. (1989) identified seasonal changes in fungal species composition of the community. Thomas et al. (1989) reported the greatest conidial abundance in early autumn (500–600 conidia l^{-1}) and the lowest during the winter (300–500 conidia l^{-1}). Using stepwise multiple regression analysis of the conidial abundance and a variety of environmental measures, they showed that spore abundance was significantly related to temperature ($R^2 = 0.62$) and somewhat related to a combination of both temperature and rainfall. Species composition, however, was not related to temperature, but to rainfall and conductivity.

These studies, however, do not relate to the impact of seasonal variations in plant litter composition and changes in the physicochemical composition of that litter that occur during succession. In a study of the comparative decomposition of yellow poplar (*Liriodendron tulipifera*), red maple (*Acerrubrum*), and white oak (*Quercus alba*) leaf material in streams, Griffith et al. (1995) demonstrated differences in decomposition constants between leaf species and between sites, with pH and temperature being major variables between sites. In general leaf litters decomposed more readily in streams of higher pH and higher temperature (Table 2.22), but some of the between-site differences were less obvious if the data were temperature-corrected, suggesting that this was a primary driving variable. The temporal pattern of production of pectinase enzyme was also different among leaf litter types and may be related to differences in chemical composition, as observed by the physical changes among leaf litters during decomposition. Both white oak and red maple exhibited skeletonization, whereas yellow poplar leaves just became increasingly softer. Similar observations have led Gessner et al. (1993) to demonstrate temporal successions of aquatic fungi as leaf litters decompose. Their findings are analogous to the successions observed on terrestrial leaf litter. Fungal communities on alder leaf litter were dominated by five to six species during early colonization at 2 weeks of incubation (*Flagellospora curvula*, *Tetracahetum elegans*, *Lemonniera centrospharea*, *L. aquatica*, and *L. terrestris*). At 4 weeks, the species composition was more

TABLE 2.22 Decomposition constants (-*k*) of Leaf Litters in Three Streams of Differing pH and Temperature

Site	pH	Cumulative degree days	White oak -*k* (day^{-1})	Red maple -*k* (day^{-1})	Yellow poplar -*k* (day^{-1})
SFR	4.3	233	0.0020	0.0037	0.0058
WHR	6.2	424	0.0059	0.0106	0.0068
HSR	7.7	393	0.0038	0.0091	0.0081

Source: Data from Griffiths et al. (1995).

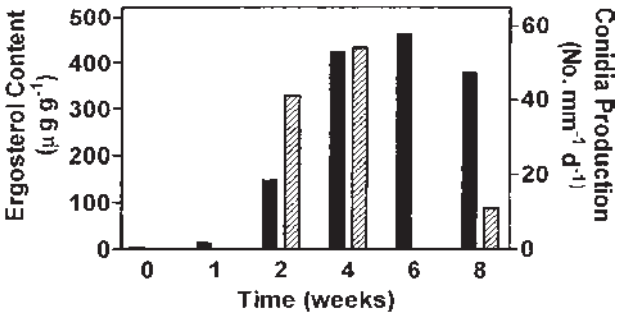

FIGURE 2.7 Fungal biomass expressed as ergosterol content (solid bars) and conidial production (hatched bars) during the successional development of fungal communities colonizing alder leaf litter in streams. *Source*: Data derived from Gessner et al. (1993).

equitable and consisted of a larger species assemblage (11 species), which persisted, with some differences in dominance, at 8 weeks. It is in the middle of this succession that fungal biomass (measured as ergosterol content) and conidial production peak (Fig. 2.7).

Initial efforts to relate fungal activity during the decomposition of plant litters in aquatic and salt marsh systems to the nutrient and carbon budgets are reviewed by Gessner et al. (1997). They showed that fungal biomass increases at an early stage of the decomposition of the plant material and forms a significant proportion of the total detrital mass (up to 15%). The effects of fungal and bacterial action on the carbon flux in decomposing plant residues in aquatic and marine systems is given in Fig. 2.8, in which the rate of decomposition is greatest in salt marshes and the importance of a high mycelial biomass is highest. Concomitant to a faster decomposition rate of *Spartina* than *Plantanus*, a higher percentage of the carbon is released as dissolved and fine particulate organic matter from *Spartina*. The effect that these end products have on nutrient dynamics and the support of primary and secondary productivity within the ecosystem is as yet unknown. Regulation of fungal degradation of plant residues in aquatic and salt marsh ecosystems are positively enhanced by increased fungal biomass, which is reflected in the production of conidia, and activity (measures of adenosine triphosphate ATP activity). As in the terrestrial ecosystem, the high lignin content of the resource reduces its rate of decomposition, which can be ameliorated by the exogenous supply of nitrate nitrogen in the system, (Gessner et al., 1997).

Aquatic fungi form an important food source for invertebrates and alter the physical structure of the wood substrate to allow faunal penetration (Suberkropp, 1992), Graca et al. (1993) have demonstrated that some faunal shredders prefer to feed on leaves that are already colonized by fungi, while others consume fungal mycelia selectivity. It is likely that the palatability of the resource is enhanced

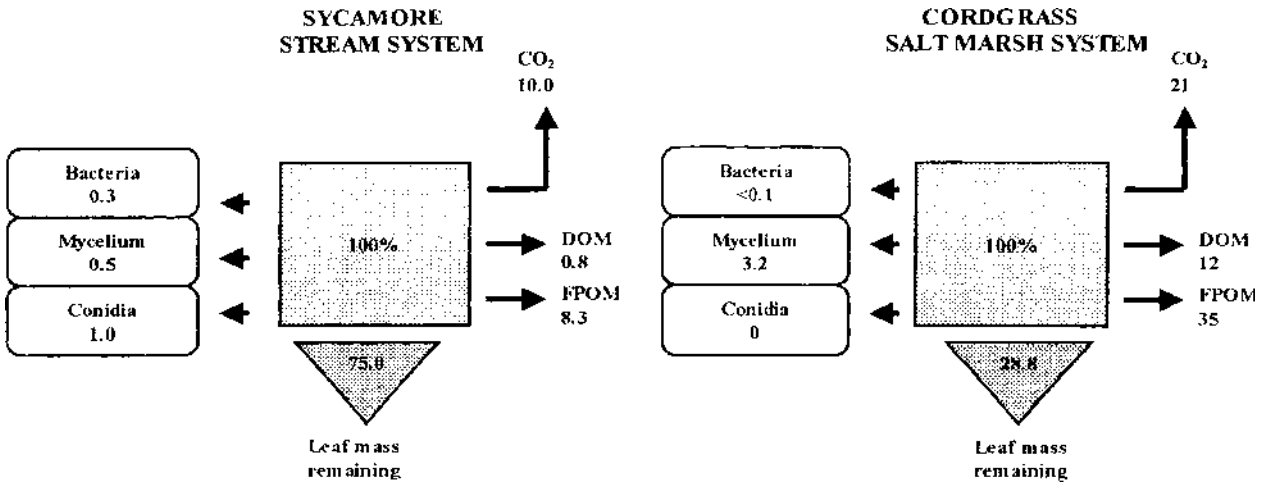

FIGURE 2.8 Field carbon budgets of sycamore (*Plantanus occidentalis*) in a freshwater stream system and cordgrass (*Spartina alterniflora*) in a salt marsh system, showing the proportion of carbon lost to dissolved organic matter (DOM), fine particulate organic matter (FPOM), and incorporation into bacterial and fungal biomass. *Source*: Modified from Gessner et al. (1997).

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during fungal decomposition by the increase in nitrogen content during the initial stages of fungal attack (Gessner et al., 1997).

The role of fungi in aquatic ecosystems has not been studied as intensively as it has in terrestrial ecosystems. Wong et al. (1998) reiterate this in their review, saying that although fungi are the dominant decomposers in these systems we know little about the mechanisms of decomposition or the interactions between fungi and between fungi and other organisms. Resource succession by saprotrophic fungi has been identified (Gessner et al., 1993), however, but we know very little about the relationship between fungal biodiversity and ecological function. It would appear, however, that resource quality of plant material dictates the community structure of the aquatic saprotrophic fungi colonizing it, and there may be many parallels between aquatic and terrestrial systems in the way in which materials are processed and utilized (Wagener et al., 1998). Gulis (2001) performed a multivariate analysis of 146 samples from 92 aquatic systems to show that the fungal species assemblage on wood and grass leaves has a different composition from those on tree leaf litter (Fig. 2.9). He did not, however, correlate the differences in fungal communities, resource quality, and rates of decomposition, nor any of these factors with physiological function (enzyme function, etc.) of the individual species or communities. This information is one of the aquatic decomposition system functions that is still to be explored.

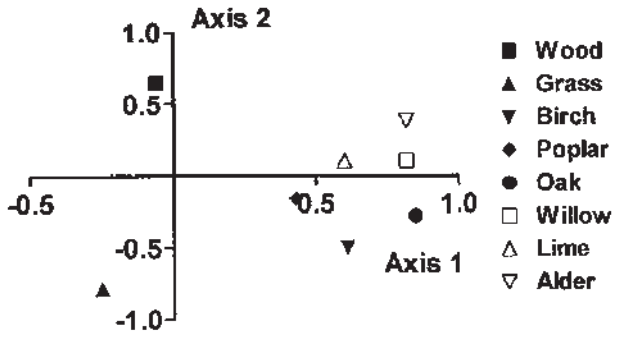

FIGURE 2.9 PCA analysis of the aquatic fungal community structure on a variety of plant resources in an variety of aquatic ecosystems. The community structure separates significantly along axis 1, where the tree leaf litter communities show similarity between each other but are different from communities developed on wood and grass leaves, which lie to the left of PCA axis 1 and are separated from each other along PCA axis 2. *Source*: Data from Gulis (2001).

2.3 CONCLUDING REMARKS

Fungi are a diverse group of organisms. A range of taxonomic groups is involved in the process of decomposition and mineralization of nutrients from organic sources. It has been shown above that these fungi differ in their enzymatic capabilities (their ability to decompose certain resources), their rate of growth (competitiveness), and their interactions with other organisms in the ecosystem. We have concentrated mainly on terrestrial ecosystems, as here we have the greatest information regarding the role of fungi in decomposition, the measures of rates of nutrient mineralization from organic matter, and the effects of fungi on rock dissolution and soil development. We can see from the discussions of the activities of fungi in aquatic and marine ecosystems that they are involved in similar processes of decomposition of organic resources and that the interactions between fungi and their changing environment during decomposition of these resources leads to similar patterns of resources succession, limitation of decomposition by resources quality, and impacts of environmental constraints upon their activity in the same manner as in the terrestrial environment. Information regarding measure of the amount of nutrient mineralization, however, and the importance of this to plant primary production is less available than for terrestrial ecosystems. Soil development and stability is a unique feature of terrestrial ecosystems. Lichens are abundant on rocky coastlines, but there is little information regarding their input to the nutrient content of oceans by the process of rock dissolution. In salt marsh sediments, fungi probably play a role in binding particles together and reducing the possibility of erosion caused by tidal and wave action. We know that approximately 50% of aquatic and salt marsh plants are mycorrhizal (Khan and Belik, 1995; Cooke and Lefor, 1998), but we have little information about the extent of mycorrhizal hyphal development into sediments in either aquatic or salt marsh habitats or their roles in nutrient acquisition, sediment stabilization, or interactions with other biotic components.

Thus, although we can make generalized statements about the role of fungi in decomposition, nutrient cycling, and nutrient accumulation and the similarity of action in different ecosystems, it must be remembered that there are other external influences on communities and function. For example, Hackney et al. (2000) showed that the external supply of nitrogen significantly influenced the ratio of fungi and bacteria colonizing plant leaves in the Everglades (Fig. 2.10). In addition, Hawksworth (1991) has suggested that we may be able to identify some 5% of the possible total number of fungal species in the world. Of these, we may have isolated and investigated the physiology of a mere handful. We must ask how confident we are in extrapolating these findings to fungi as a whole. Soil is an opaque medium in which most of the fungal-mediated nutrient-cycling processes occur in terrestrial ecosystems. Bodies of water represent the aquatic and marine ecosystems that require specialized equipment to enter, in which to conduct

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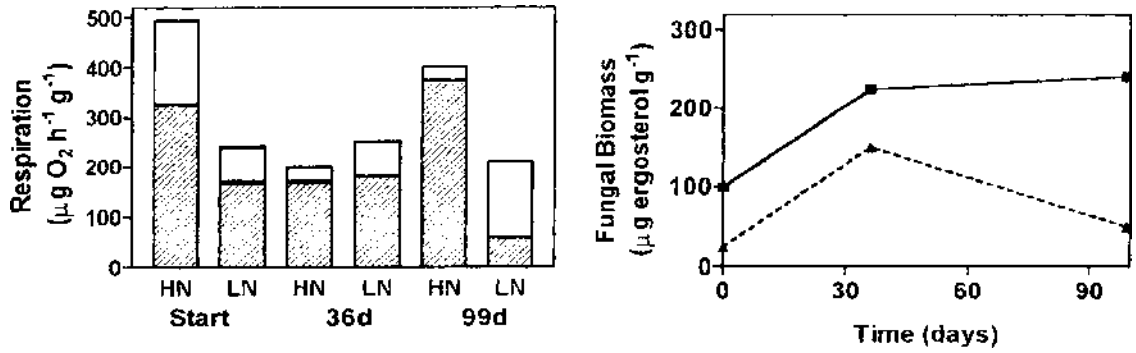

FIGURE 2.10 Relative contribution of bacterial (open bar) and fungal (hatched bar) respiration to total respiration of decomposing *Cladium* leaves in the Everglades at high (HN) and low (LN) levels of external nitrogen supply (left panel) and time course of changes in fungal biomass (measured as ergosterol content) on decomposing *Cladium* leaves at high (squares) and low (triangles) levels of N availability. Data from Hackney et al. (2000).

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experiments, and from which data may be collected. These are not easy habitats in which to study the activities and roles of fungi. Additionally, we are limited by our methodologies of study, especially in determining active fungal biomass and in situ measures of activity, enzyme production process rates at the scale at which they are performed by the fungal hyphae. Our level of knowledge is constantly growing, but it is far from complete.

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3

Fungi and Primary Productivity: Plant Growth and Carbon Fixation

The role of fungi in primary production goes beyond making nutrients available to plants. There are intimate associations between the photosynthesizing components of the ecosystem and fungi, many of which are symbiotic. Such interactions between fungi and other organisms enhance nutrient availability for primary production and include mycorrhizae and associated rhizospheric microbial communities. In addition, some of these synergistic interactions between plants and fungi are involved in the prevention of plant disease and inhibiting herbivory. The latter is an important trait of endophytes, and has economic importance. In the form of lichens, the whole symbiotic association among fungi, algae, and bacteria is involved in primary production. Here, as we saw in the last chapter, the fungal partner acts as a supportive network for photosynthetically active algae and bacteria. In the mycorrhizal habit, fungi form a close association with plant roots and are physiologically and morphologically adapted to assist in the transport of nutrients into root systems. The diversity of mycorrhizal morphologies, the range of fungal taxa associated with mycorrhizal associations, and their range of degrees of dependency upon the association has led scientists to investigate their biology and ecology for more than 100 years. Indeed, Setälä et al. (1998) accumulated evidence to show that the diversity of organisms in soil has significant effects on primary production, especially when the number of trophic levels is low. They also suggest that the inclusion of ectomycorrhizae into the models of diversity and function of forested systems is of fundamental importance in understanding the mechanisms regulating primary production. As endophytes, fungi can be important in defending plants against herbivory, thus indirectly influencing primary productivity by negating or

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minimizing plant biomass loss through grazing. In addition to these direct effects of fungi on regulation of primary production, fungi are important in regulating the individual fitness of a plant or animals, and thus can influence the standing of individual species within a community and the community composition. These indirect effects will be explored in greater depth in Chap. 5. Table 3.1 shows the ecosystem services promoted by fungi that will be discussed in this chapter.

3.1 THE ROLE OF LICHENS IN PRIMARY PRODUCTION

The role of lichens in soil formation was discussed in Chap. 2. The fact that these organisms are able to access mineral nutrients from the dissolution of parent rock material and that the symbiotic bacteria and algae are able to photosynthesize make it logical to assume that lichens can be important components of total primary productivity. The importance of this process to net primary production is most important in a number of ecosystems in which lichens compose a large proportion of the plant biomass. Crustose and foliose soil lichens are major components of the plant biomass in many cold, wet environments, in which vascular plants are less able to survive. Beymer and Klopatek (1991) showed that approximately $28\,\mathrm{kg\,C\,ha^{-1}}$ was fixed by the lichen crust community in a pinyon pine and juniper forest in a semiarid environment in the Grand Canyon. Using radioactive tracer techniques, they estimated that approximately 34–36% of this fixed carbon becomes incorporated into soil organic matter. In mat-forming lichens, Crittenden et al. (1994) showed that lichen growth was limited by the availability of nitrogen in oligotrophic environments. They showed significant and positive relationships between nitrogen availability and chitin content (a measure of fungal biomass) of the lichen. Crittenden (1989) reported that there is very little nitrogen available in the substratum on which these lichens grow and that they are very dependent upon intercepting nitrogen in precipitation. The efficiency of nitrogen interception can often be close to 100% (Table 3.2), but at certain times lichens can be a source of leached nitrogen and potassium for other plants. Indeed, this form of nitrogen capture can be equivalent to the N fixation capacity of those lichens containing nitrogen-fixing bacterial phycobionts (Table 3.3). This information suggests that within limits, increased atmospheric N deposition will stimulate growth of lichens in nutrient-poor environments.

Growth of mat-forming lichens can be severely limited by the availability of nitrogen. In some cases, as in the soil crust communities, bacteria, in association with lichens and fungi, may fix significant quantities of nitrogen. Belnap (2002) showed that between 1 and $13\,\mathrm{kg\,N\,ha^{-1}\,y^{-1}}$ could be fixed by crust communities in the deserts of Utah. Terricolous lichen species have been shown to have growth rates of 0.2 to $0.4\,\mathrm{g\,g^{-1}}$ dry weight (30 to $70\,\mathrm{g\,m^{-2}}$) in

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TABLE 3.1 Ecosystem Services Provided by Fungi

Ecosystem service		Fungal functional group
Soil formation	Rock dissolution	Lichens Saprotrophs Mycorrhizae
	Particle binding	Saprotrophs Mycorrhizae
Soil fertility	Decomposition or organic residues	Saprotrophs (Ericoid and ectomycorrhizae)
	Nutrient mineralization	Saprotrophs (Ericoid and ectomycorrhizae)
	Soil stability (aggregates)	Saprotrophs Arbuscular mycorrhizae
Primary production	**Direct production**	**Lichens**
	Nutrient accessibility	**Mycorrhizae**
	Plant yield	**Mycorrhizae** **Pathogens**
	Defense against pathogens	**Mycorrhizae** **Endophytes** **Saprotrophs endophytes**
	Defense against herbivory	
Plant community structure	Plant–plant interactions	Mycorrhizae Pathogens
Secondary production	As a food source	Saprotrophs Mycorrhizae
	Population/biomass regulation	Pathogens
Modification of pollutants		Saprotrophs, Mycorrhizae
Carbon sequestration and storage		Mycorrhizae (Saprotrophs)

Note: Services and Fungal Groups discussed in this chapter are boldface. Fungal groups in parentheses are regarded as of lesser importance in that function.

Sweden (Palmqvist and Sundberg, 2000). These authors also report that epiphytes in the same locality only produce 0.01 to 0.02 $g\,g^{-1}$ (1 to 4 $g\,m^{-2}$). The greater biomass accumulation of ground-inhabiting species is attributed to their better water-holding capacity and greater light levels than arboreal habitats. As epiphytes, lichens are able to successfully utilize the mineral nutrients that are intercepted by or leached from tree canopies and that run down the branches and trunks as stem flow. Again, the combination of fungal sequestration of mineral nutrients and photosynthesis by the symbiotic algae provides another source of carbon fixation in the tree canopy.

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TABLE 3.2 Range of Nutrient Retention by Mat-Forming Lichens from Rainfall

	Nutrient retention (%)		
Mat lichen species	NO_3-N	NH_4-N	K
Stereocaulon paschale	86–100	40–99	−37– + 90
Cladonia stellaris	62–99	50–97	−978– + 65

Source: Data from Crittenden (1989).

In the Norwegian high arctic, Cooper and Wookey (2001) measured the rate of growth of the fruiticose lichens *Cetraria* spp., *Cladonia* spp., and *Alectoria nigricans* (Fig. 3.1) as between 2.4 and 10.6 mg g^{-1} per week or between 2.5–11.2% of the original lichen biomass in one season (approximately 10 weeks). Similarly, Peck et al. (2000) showed that the arctic tumbleweed lichen *Masonhalea richardsonii* increased in biomass by about 10% per year in Alaska. These rates of growth are similar to those reported by Kärenlampi (1971). These lichens provide a large amount of the winter feed of reindeer, and in the island of Svalbard, may become severely depleted in biomass due to the intense grazing pressure, low rates of growth, and the indirect effect of reindeer trampling on lichen survival.

In temperate forest ecosystems, epiphytic lichens can form a significant proportion of the net primary production of the ecosystem. Using tethered arboreal lichens, Sillett et al. (2000) showed that the colonization of experimental branches was highest in clear-cut and old-growth Douglas fir forests and lowest in young (10-year-old, 1.5-m-tall) forests (Fig. 3.2). In general there was improved lichen colonization and growth on rough branches compared to smooth branches,

TABLE 3.3 Accumulation and Loss of N in Two Mat-Forming Lichen Species During 82 Days of Growth

	Stereocaulon paschale	*Cladonia stellaris*
Increment in total biomass N	758	95
Inorganic N in rainfall deposited	31	31
Inorganic N in rainfall retained	27	25
N lost as organic N	19	11
N fixation	669	0

Note: Values are expressed as mg N m^{-2} of pure lichen cover.
Source: Data from Crittenden (1989).

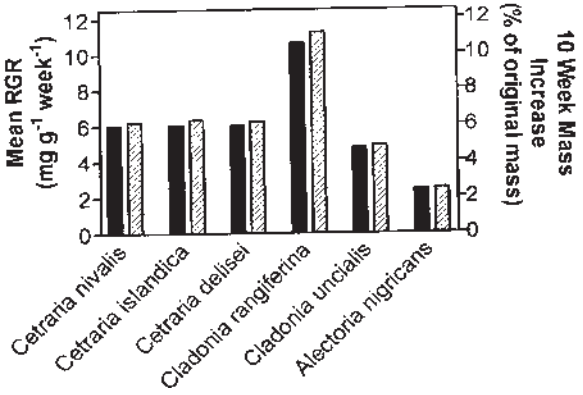

FIGURE 3.1 Relative growth rate of a range of lichen species from the article. Solid bars represent relative growth rate, hatched bars represents the relative growth rate over a 10 week interval. Data from Cooper and Wookey (2001).

but this preference was forest-dependent. For the lichen *Lobaria oregana* there was greater colonization of smooth bark in the clear-cuts, no difference between barks in the young forest, and a significance preference for rough bark in old-growth stands (Fig. 3.3). Differences in growth rate and colonization potential may be related to light levels. In a study of light use efficiency of five macrolichen species, Palmqvist and Sundberg (2000) showed that there was

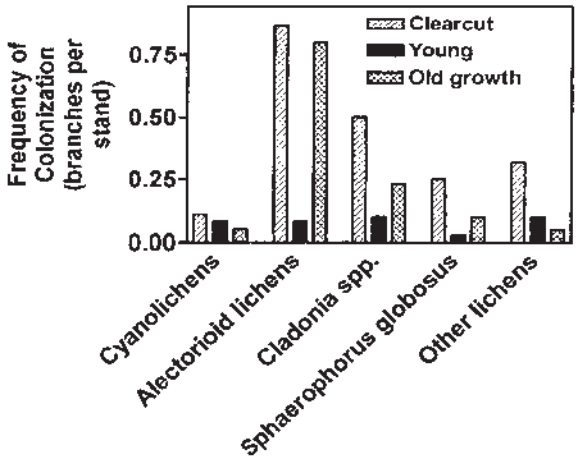

FIGURE 3.2 Frequency of occurrence of lichens on experimental brances located in clearout, young and old growth stands of Douglas fir forests. Data from Sillett et al. (2000).

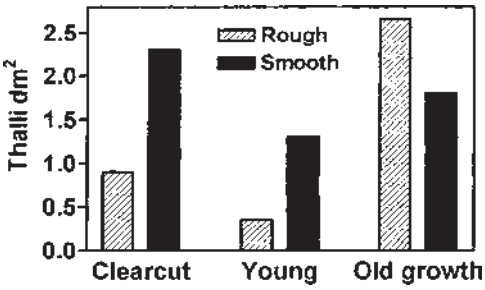

FIGURE 3. 3 Density of the lichen Lobaria oregana colonizing rough or smooth experimental branches located in clearcut, young and old growth Douglas fir forest stands. Data from Sillett et al. (2000).

a significant positive correlation between intercepted irradiance and growth when lichens were wet. They demonstrated that there was a range of between 0.5–2% of the light use efficiency per dry weight at a standard energy equivalent of light between lichens grown in low- and high-light regimes.

In tropical ecosystems, the production of lichen biomass is limited by the high rates of dark respiration, leading to a low net rate of carbon accumulation. Lange et al. (2000) determined that within the genus *Leptogium* between 47–88% of the carbon gained during photosynthesis was lost as respiration, thus limiting productivity (Table 3.4).

An important function of the fungal component of lichens is to support and protect the photosynthetic apparatus contained in the prokaryotic symbiont. Solhaug and Gauslaa (1996) showed that by extracting the lichen *Xanthoria parietina* with 100% acetone they were able to extract the compound parietin without damage to the lichen. At high light intensities, however, it was found that

TABLE 3.4 Carbon Budget of the Lichen *Leptogium* spp. in the Panamanian Tropics

Lichen species	Net photosynthetic gain (mg C (gC)$^{-1}$ d^{-1})	Respiratory carbon loss (mg C (gC)$^{-1}$ d^{-1})	Carbon loss as of carbon gain
Leptogium phyllocarpum adult	9.3	−7.2	77.4
Leptogium phyllocarpon juvenile	15.7	−7.4	47.1
Leptogium cyanescens	8.97	−5.4	60.2
Leptogium azureum	6.2	−5.5	88.7

Source: Data from Lange et al. (2000).

extracted lichens showed a reduction in photosynthetic oxygen production, evidencing damage to the photosynthetic apparatus in the absence of the blue light filtering chemical produced by the fungus, Both the physical support provided by the fungus and its ability to produce beneficial chemicals thus aid the process of primary production in lichens.

3.2 THE ROLE OF MYCORRHIZAE IN PLANT PRIMARY PRODUCTION

We saw in Chap. 2 how the saprotrophic fungal community in association with bacteria and soil fauna make mineral nutrients available for plant growth. Similar processes occur in both freshwater and marine ecosystems to provide nutrients for both pelagic and rooted vegetation. In both the terrestrial and, to a more limited extent, in freshwater and estuarine ecosystems, a symbiotic association between mycorrhizal fungi and plant roots influences the uptake of mineral nutrients from the substratum into plants for biomass production. This functional group of fungi have evolved along with their host plants and have a variety of ways in which they interact with both readily and poorly available nutrient resources to enhance plant growth. They are also important in protecting host plants against pathogens. In addition to these factors, these fungi may be more important than previously thought in influencing competition among component plant species of a plant community. This can occur by the fungal influence of host plant fitness and through the sharing of resources between plants of the same or different species within the plant community. The importance of mycorrhizal contribution to primary production in forested ecosystems was shown by Vogt et al. (1982). They showed that although the mycorrhizal fungi contributes only some 1% of total ecosystem biomass, the percentage of net primary production represented by mycorrhizal fungi was 14–15% (or 45% in young forest stands and 75% in mature stands) when combined with the fine root biomass supporting the mycorrhizal fungal tissue (Vogt et al., 1982). Pankow et al. (1991), however, suggest that the main role of mycorrhizal symbioses is not during the early, productive stages of plant succession in ecosystems, but rather in the protective stage, during which most resources are entrained in plant biomass. Here, they suggest, mycorrhizae control the cycling of nutrients from decomposing organic matter back into plants and reduce the likelihood of nutrient loss from the ecosystem.

3.2.1 The Mycorrhizal Habit

Mycorrhizae are symbiotic associations between fungi and plant roots. Their description and function have been detailed in many excellent texts, to which the reader is referred (Harley, 1969; Harley and Smith, 1983; Smith and Read,

1997). The ecology and role of mycorrhizae in ecosystems has also been explored in a variety of texts (Allen, 1991; Read et al., 1992; Varma and Hock, 1995; Mukerji, 1996). In this chapter we will try to take a wider view of the impact of mycorrhizae in the ecosystem without dwelling on the minutiae of physiological and biochemical processes involved in the physiology of the mycorrhizal association.

Approximately 95% of all vascular plants have a mycorrhizal association (Brundrett, 1991). Traditionally, mycorrhizal associations have been divided into a range of categories, based on the taxonomy of the fungal associate and the physical form of the interactions between the root and the fungus in the mycorrhizal structures that are produced in the symbiosis. A list of mycorrhizal forms, their plant associates, and the key features of the mycorrhizae is given in Table 3.5. Among the most common types of mycorrhizal association are the arbuscular mycorrhizal types, which are formed mainly by zygomycete fungal species. These fungi are mainly associated with herbaceous vegetation, grasses, and tropical trees, although a limited number of temperate woody plants may also associate with arbuscular mycorrhizae. The association is characterized by fungal penetration within the host root cortical cells and the development of a variously

TABLE 3.5 Outline of Some of the Features of Different Types of Mycorrhizal Associations

Mycorrhizal type	Host plant group	Characteristics	Fungal associate
Arbuscular mycorrhizae	Herbaceous plants, grasses; some trees	Formation of arbuscules within cortical cells of host root	
Ectomycorrhizae	Coniferous and deciduous trees	Formation of a sheath or mantle of fungal tissue around the root surface and a Hartig net of fungal penetration between the cortical cells to the endodermis	Basidiomycetes Ascomycetes
Ectendomycorrhizae			
Ericoid mycorrhizae	Ericaceaea	Hyphal coils within the host root cortical cells	
Arbutoid mycorrhizae	Arbutus	Hyphal coils within the host root cortical cells	
Orchidaceous mycorrhizae	Orchids	Fungal propagule carried in the seed of the plant	

developed, treelike branching of the hyphae between the host cell wall and plasmolemma called an arbuscule. It is here that the surface area of the interface between plant host and fungus is optimized for nutrient and carbohydrate exchange. In some instances, vesicles are formed in some cortical cells. These consist of a swollen hyphum occupying a large volume of the cell. This structure contains storage material, and its name gave rise to the vesicular-arbuscular mycorrhizal type. This name is now reserved for a limited number of associations, mainly with the fungal genus *Glomus* (Smith and Read, 1997). The arbuscular mycorrhizal association is formed with a large number of plant species and a relative small diversity of fungal species. Because these fungi do not produce large fruiting structures as in the Basidiomycotina, the identification of the fungal partner is by the anatomy of spores, which may be produced within or outside the host root.

The ectomycorrhizal habit consists of an association between, mainly, tree species and a range of fungal taxa consisting of basidiomycetes, ascomycetes and some zygomycetes. In this type, the fungus does not penetrate into the host cortical cells, but only between them, forming a Hartig net. The Hartig net exists outside the endodermis of the root. On the surface of the root, a sheath or covering of fungal material develops. This surface structure may be of varying degrees of complexity from a loose weft of hyphae to highly organized pseudoparenchymatous structures. It is the structure of the sheath, degree of branching, (induced by change in cytokinins), and nature of emanating hyphae or hyphal strands that allow morphological identification of these mycorrhizae (Agerer, 1987–1999; Ingleby et al., 1990: Goodman et al., 1996–2000). Ectomycorrhizal associations are formed between a limited number of plant species and a huge number of fungal species. In addition to ectomycorrhizae, ectendomycorrhizal associations also occur with tree species. These associations have both ectomycorrhizal and arbuscular mycorrhizal structural characteristics (Laiho & Mikola, 1964).

Ericoid mycorrhizae are similar in structure to arbuscular mycorrhizae, but are associated solely with members of the ericales (Ericaceae, Empetraceae, Epicaridaceae, Diapensiaceae and Prionotocaceae). All of these groups are sclerophyllous evergreens and reside in habitats where both nitrogen and phosphorus are sparsely available. The root systems of these plants consist of very fine roots containing a single layer of cortical cells, which the mycorrhizal fungi penetrate to form hyphal coils, rather than arbuscules (Read, 1996). The fungi associated with this type of symbiosis are still not completely identified, but consist of a relative few genera, including *Hymenoscyphus* and *Oidiodendron*. Closely associated with these mycorrhizae are the arbutoid mycorrhizae.
Orchidaceous mycorrhizae are unique in terms of the obligate nature of the association. The importance of the mycorrhizal association for seed germination and the initial establishment of the plant has been reviewed by Zettler and McInnes (1992) and Rasmussen and Wigham (1994). The fungal partner is usually ascribed

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to the genus *Rhizoctonia*, and there has been such evolution of the obligateness of the association that the fungus is transported in the seed of the plant.

Further details of the structure of all mycorrhizal associations can be found in Peterson and Farquhar (1994) and Smith and Read (1997). For the purposes of demonstrating the role in mycorrhizae in ecosystem processes, the following discussions will mainly be limited to the role of arbuscular-, ericoid-, and ectomycorrhizae.

3.2.2 The Basic Function of Mycorrhizae

In the previous chapter we saw how fungi are important in a variety of ways in developing the structure of soils and regulating soil fertility by the processes of decomposition and mineralization. The major ecosystem function of mycorrhizae is to assist host plants in the acquisition of mineral nutrients from soil. In the classic elementary texts of plant physiology, the function of nutrient uptake is ascribed to the root hairs, which increase the root surface area to provide the maximal root surface to soil pore-water interface. As we have seen, however, if approximately 95% of plants are mycorrhizal and these mycorrhizal associations alter root morphology, then this picture of nutrient uptake is too simplistic. The ability to assist the host plant in obtaining nutrients has been ascribed to the fact that during mycorrhizal development, root hair development is suppressed and the function of the root hair is replaced by fungal hyphae. These hyphae have two major benefits for sequestering nutrients. They are of smaller diameter than root hairs and can penetrate more easily and to a greater distance from the root into the soil, thus exploring a greater volume of soil and presenting a greater surface area for nutrient absorption than could the root–root hair system alone (Nye and Tinker, 1977; Clarkson, 1985; Hetrick, 1991; Marschner and Dell, 1994). The energetic efficiency results in a better balance between the investment of photosynthate to roots per unit nutrient absorbed (Vogt et al., 1982, Harley and Smith, 1983; Fitter, 1991). Rousseau et al. (1994) showed that for ectomycorrhizal pine seedlings the extraradical mycelium accounted for only 5% of the potential nutrient-absorbing system dry weight (fungi and roots), which represents a small investment in structural carbohydrate. The mycelium accounted for 75% of the potential absorbing area and over 99% of the absorbing length (Table 3.6), however. Similarly, Kabir et al. (1996) showed that mycelium of the arbuscular mycorrhizae colonizing roots of corn (*Zea mays*) and barley (*Hordeum vulgaris*) accounted for more than 83% of the soil fungal hyphae. The second benefit is that it is energetically more efficient to produce a long, thin hyphum than a root hair. The analysis of this cost-benefit equation for arbuscular mycorrhizae in natural conditions (Fitter, 1991), however, suggests that the nutritional benefit alone is not always worth the investment. Fitter (1991) suggests that the benefit is only realized at specific times in the life cycle of

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TABLE 3.6 Plant and Fungal Parameters for Pine Tree Seedlings Colonized by the Ectomycorrhizal Fungi *Pisolithus tinctorius* and *Cenococcum geophilum* Showing the Enhanced Nutrient Uptake Capacity of the Mycorrhizal Plants Due to Extraradical Hyphal Development

Plant/fungal parameter	*Pisolithus*	*Cenococcum*	*Nonmycorrhizal plant*
Mycorrhizal infection (%)	69.5	66.5	0
Fine root diameter (μm)	477	573	299
Root tip ratio	3.72	1.39	1.55
Fine root area (mm^2)	4.02	1.49	1.30
Hyphal area ($mm^2\,g^{-1}$ soil)	33.8	28.1	1.5
Rhizomorph area ($mm^2\,g^{-1}$ soil)	13.6	0	0
Total fungal area ($mm^2\,g^{-1}$ soil)	47.4	28.1	1.5
Hyphal length ($m\,g^{-1}$ soil)	6.42	2.8	0.28
Rhizomorph length ($m\,g^{-1}$ soil)	0.36	0	0
Total fungal length ($m\,g^{-1}$ soil)	6.78	2.8	0.28

Source: Data from Rousseau et al. (1994).

the plant in which nutrient (P) demand is greater than readily available supplies of the nutrient in soil; otherwise the cost of maintenance of the mycorrhizal symbiont is equivalent to the cost of root maintenance (Table 3.7).

The structural adaptations, physiology, and efficiencies of nutrient uptake by mycorrhizae are reviewed by S. E. Smith et al. (1994). The ability of mycorrhizal plants to access a larger pool of nutrients than nonmycorrhizal root systems was elegantly demonstrated by Nye and Tinker (1977) and Owusu-Bennoah and Wild (1979) using radiotracer phosphate to measure the depletion of phosphate in the soil around arbuscular mycorrhizal root systems. The distance that the depletion zone extended from the mycorrhizal root was shown to be greater than that from the nonmycorrhizal plant (Fig. 3.4), indicating that

TABLE 3.7 Cost of Plants of Maintenance of Arbuscular Mycorrhizal Infection

Biomass of mycorrhizal fungus	10–20% of root biomass
Cost of growth and maintenance of the fungus	1–10% of fungal biomass d^{-1}; i.e., 0.1–1% of root biomass d^{-1}
Root maintenance cost	ca. 1.5% of root biomass d^{-1}

Note: The cost of maintaining mycorrhizae ≡ root maintenance cost.
Source: Data from Fitter (1991).

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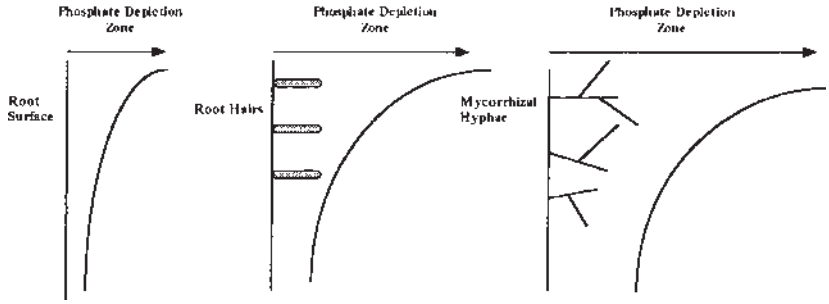

FIGURE 3.4 A model of increasing P depletion zones from a root surface created by the addition of root hairs and arbuscular mycorrhizae as protrusions from the root surface into the soil. Model derived from the data of Nye and Tinker (1977) and Owusu-Bennoah and Wild (1979).

the fungal hyphae were responsible for exploiting a larger soil volume than root hairs alone. Clark and Zeto (2000) have recently reviewed the literature on nutrient uptake by arbuscular mycorrhizae. They cite information from Li et al. (1991a, b), Jakobsen (1995), and Jakobsen et al.(1992a) that show that the depletion zone around the roots of clover are extended from 10 to 20 mm because of the presence of arbuscular mycorrhizae and that this distance can be extended up to 110 mm in some cases. The actual effect of the mycorrhizal association depends on the rate of growth of the extraradical hyphae of the fungal species, with *Acaulospora laevis* having hyphal extension rates of approximately 20 mm week^{-1}, but that of *Glomus* spp. less than 10 mm week^{-1}. In some cases in the ectomycorrhizal condition, the fungal partner has evolved not only individual extraradical hyphae, but may also develop mycelial structures called strands or rhizomorphs that have a distinct structure with conductive elements analogous to the vascular tissue of plants. These strands have been shown to be important in long-distance transport of nutrients and water (Duddridge et al., 1980), thus it is probable that in the ectomycorrhizal symbiosis the influence of the fungal partner can extend to great distances from the root surface. Indeed, we shall see in the next section that the distal parts of extraradical hyphal structures are capable of producing the enzymes that are usually associated with saprotrophic decomposer fungi. In addition to the development of adventitious hyphal structures to exploit soil for nutrients, arbuscular mycorrhizal fungi have been shown to alter the architecture of root systems. Berta et al. (1993) showed that the number of lateral roots produced by mycorrhizal plants was significantly greater than nonmycorrhizal plants, suggesting that there could be dual benefits of the mycorrhizal habit, one of increased root branching and the other of the fungal exploitation of soil for nutrients.

TABLE 3.8 Regression Analysis of the Variables Associated with Leek Response to Mycorrhizal Association with the Arbuscular Mycorrhizal Fungi *Glomus intraradices* and *G. versiforme* at Low Soil Phosphorus Availability ($<200\ \mu g\ g^{-1}$ soil)

Mycorrhizal species	Variable	Model R^2	P value
G. intraradicies	1–2 mm diam. aggregates	0.27	0.0003
G. versiforme	0.5–1 mm diam. aggregates	0.35	0.0001
	Total spore number	0.45	0.0077
	G. aggregatun spore number	0.51	0.0325

Source: Data from Hamel et al. (1997).

This simplistic model of the benefit of mycorrhizal associations of roots being able to exploit a larger volume of soil than the root alone has been shown to improve plant growth, leading to the "big plant-little plant" syndrome. Many investigators have shown the comparative growth and nutrient content of mycorrhizal an nonmycorrhizal plants (Michelsen, 1993; Repáč, 1996a,b; Jumpponen et al., 1998). The response to mycorrhizal infection may also be dependent upon other soil factors, however, Hamel et al. (1997) demonstrated positive correlations between growth enhancement by arbuscular mycorrhizae and the abundance of water-stable soil aggregates of the 0.5-to-2-mm-diameter class at low phosphate availability (Table 3.8). Similarly, Michelsen and Rosendahl (1990) showed that there was a synergistic benefit of mycorrhizal association of *Acacia* and *Leucaena* at low phosphate availability and droughting conditions (Fig. 3.5). Few investigators have, however, examined the temporal aspects of the effects of nutrient uptake during mycorrhizal development on

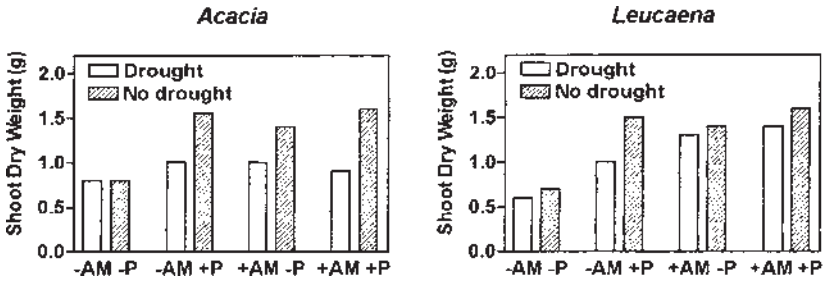

FIGURE 3.5 Shoot weight of seedling of *Acacia nilotica* and *Leucaena leucocephala* after 12 weeks in the presence or absence of arbuscular mycorrhizal inoculum (AM) or additional phosphorus (P) under drought or no drought stress. Data from Michelsen and Rosendahl (1990).

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TABLE 3.9 Regressional Relationships (r^2) Between Soil Factors and the Mycorrhizal Colonization of Seedlings of Birch and Sycamore When Taking into Account Structurally Mature and Immature Categories of Mycorrhizal Colonization

	Ectomycorrhizal birch			Arbuscular mycorrhizal sycamore
Soil property	Mature	Immature	Mature + immature	Mature + immature
PH	0	0.3*	0.29*	0.37*
Organic matter (%)	0.07	0.1	0.11	0.4*
Extractable N	0.01	0.19*	0.17*	0.22*
Total P	0.01	0.48*	0.51*	0.53*
Isotopically exchangeable P	0.01	0.3*	0.32*	0.43*
Water soluble P	0.02	0.22	0.23	0.55*

Note: Asterisk indicates significant regression.
Source: Data from Frankland and Harrison (1985).

roots. Most studies correlate nutrient uptake values to the number of morphologically developed mycorrhizal structures (root tips or infection units). Frankland and Harrison (1985) showed that the effects of mycorrhizae on host plant growth could be observed when there was little evidence of mycorrhizal structures in both ectomycorrhizal birch and arbuscular mycorrhizal sycamore (Table 3.9). The significance of these findings has not been fully explored, but it is possible that other effects of mycorrhizae may have gone unnoticed where the emphasis has been on the correlation of plant response to identifiable mycorrhizal structures. If we consider that most plant species have mycorrhizae, the enhancement of host plant growth per se cannot be the only benefit conferred upon the host plant. If all mycorrhizal associations acted with equal efficiency of operation, the mycorrhizal habit would not provide any differential benefit between plant species. What then would be the point of the evolution of the mycorrhizal habit when this is a carbohydrate drain to the host plant? Below we will explore some of the additional and differential benefits of the mycorrhizal habit for host plants.

3.2.3 The Distribution of Mycorrhizal Types in Relation to Nutrient Availability

The distribution of mycorrhizal types is dependent upon the geographic distribution of the host plant species and the nature of the soil. Read (1991a)

showed the geographical distribution of the main mycorrhizal types in the world, demonstrating that the arbuscular mycorrhizal habit was dominant in the temperate and tropical grasslands, tropical forests, and desert communities. Ectomycorrhizae were dominant in temperate and arctic forested ecosystems, and ericoid mycorrhizae were most common in the boreal heathland ecosystems. In order to place the distribution of the different types of mycorrhizae into some ecosystem framework, Read (1991a,b) put forward a hypothesis that the dominant type of mycorrhiza in an ecosystem was also related to the soil conditions and to the nature of the major form of nutrient from which the plant community derived its nutrition. He suggested that the world could be considered on a north–south gradient in mycorrhizal dominance, which could also be seen represented in an altitudinal transect down a mountain. He suggested that in condition in which the development of a soil is constrained by climatic conditions (extreme north and south latitudes or high altitudes), plant communities develop a high number and concentration of secondary metabolites (lignin, polyphenols, etc.) that make their litter recalcitrant to decomposition. In this scenario, organic matter accretes on the soil surface at a faster rate than it can be decomposed, leading to the accumulation of raw, undecomposed humic material. It is here that ericoid mycorrhizae dominate within a plant community of ericaceous species. At midlatitudes and at the midrange of altitude, coniferous and deciduous forest ecosystems dominate with their predominantly ectomycorrhizal fungal symbionts. Here a mixed range of organic plant litter resources provides a mixture of easily decomposed and recalcitrant resources, providing nutrients in both an inorganic and organic form. The ectomycorrhizae would be expected to have a range of physiological functions from efficient inorganic nutrient uptake to a high degree of enzyme activity for acquisition of nutrients that are poorly plant available. At low and equatorial latitudes, and low altitudes, and in certain ecosystems at midlatitudes (grasslands), arbuscular mycorrhizae dominate, as plant litter material is usually readily decomposed and soils contain a higher proportion of their nutrients in an inorganic form. The arbuscular mycorrhizae are therefore probably more adapted for efficiency of inorganic nutrient uptake and have lower abilities to access organic or poorly soluble forms of nutrients (Figs. 3.6 and 3.7). A summary of the functional roles of different mycorrhizal types can be found in Leake and Read (1997).

A. Mycorrhizal Ecosystem Services in Ericaceous Communities

The mycorrhizal fungi forming associations with ericaceous plant communities are capable of producing enzymes (protease and phosphatase) enabling the host plant to access organic forms of nutrients directly as a response to the low availability of inorganic nutrients, that are caused by the low rates of decomposition by the saprotrophic microbial community. The limitation in nutrient mineralization is often climatically regulated, as these ecosystems occur

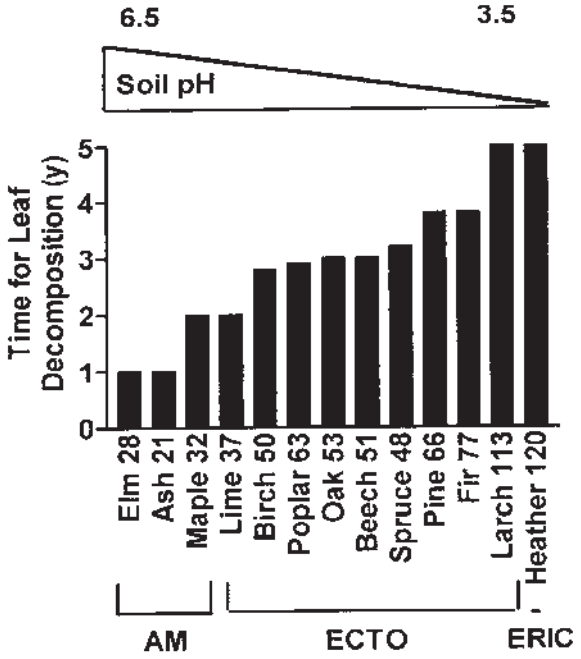

FIGURE 3.6 Ecological distribution of mycorrhizal types in relation to plant leaf litter resource quanty (represented as C:N ratios adjacent to tree name) of a selection of tree species and heather (*Calluna vulgaris*), the rate of decomposition of that plant litter and the pH of soil. (Redrawn from Read, 1991.)

at high altitudes or at high latitudes in which the annual heat sum is insufficient to maintain biological activity for considerable lengths of time during the year. The concept of a direct cycling system, whereby the mycorrhizal fungal community effects the decomposition of recalcitrant organic components, mineralization of nutrients, and direct uptake of those mineralized nutrients into the host plant, was proposed by Went and Stark (1968). It has been shown that these ecosystems tend to be most limited by nitrogen, and the production of mycorrhizal-generated enzymes affords the plant community with greater access to organic forms of nitrogen (Stribley and Read, 1980; Bajwa and Read, 1985; Leake and Read, 1989; 1990a,b). Indeed, Read and Kerley (1995) show that ericoid mycorrhizal plants derive most of their nitrogen from organic sources in highly organic soils (Table 3.10). Evidence for the use of organic nitrogen and phosphorus by ericoid mycorrhizae comes from a number of studies. Mitchell and Read (1981), Myers and Leake (1996), and Leake and Miles (1996) showed that *Vaccinum macrocarpon* could access phosphate from inositol hexaphosphate (a commonly

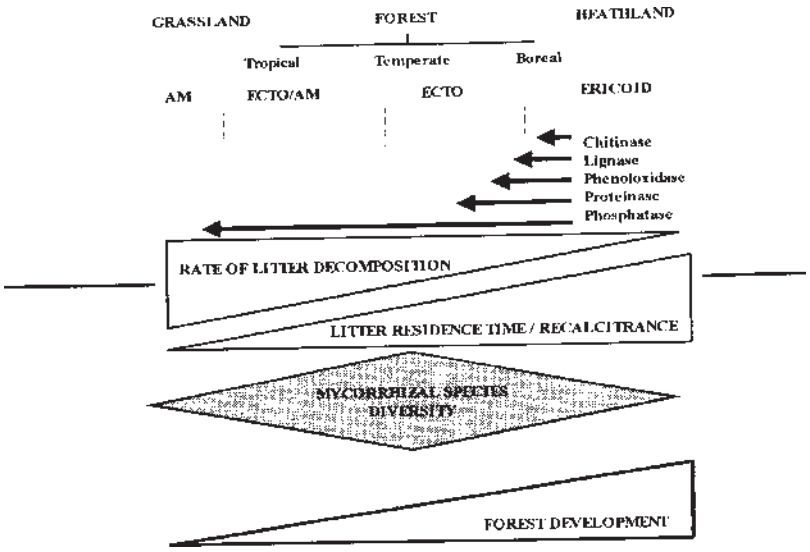

FIGURE 3.7 Relationship between the dominance of mycorrhizal type in ecosystems (above the line) and to forest development (below the line) to the changes in plant litter resources quality, its rate of decompositon and the enzxyme competence of the mycorrhizal community. (Modified from Read, 1991 and Dighton and Mason, 1985.)

occurring phosphorus compound in organic soils) and both P and N from phosphodiesters from nuclei (Fig. 3.8). Kerley and Read (1995) demonstrated the ability of the ericoid mycorrhizal fungus *Hymenoscyphus ericae* to decompose chitin and the ability of this fungus to effect transfer of some 40% of the nitrogen contained in N-acetylglucosamine to its host plants, *Vaccinium macrocarpon* and *Calluna vulgaris.* More recently, Xiao and Berch (1999) have shown that

TABLE 3.10 Proportion of Nitrogen Forms in the Soil Supporting the Growth of the Ericoid Mycorrhizal Plant *Calluna vulgaris*, Indicating the Central Role That the Mycorrhizal Fungi Play in the Acquisition of Nitrogen from Organic Sources

Nitrogen source	Proportion of sources of N in soil
Hydrolysable organic N	70
Humin and other recalcitrant N	26
Extractable NH_4–N	<1
Free amino acid N	1–4

Source: Data from Read and Kerley (1995).

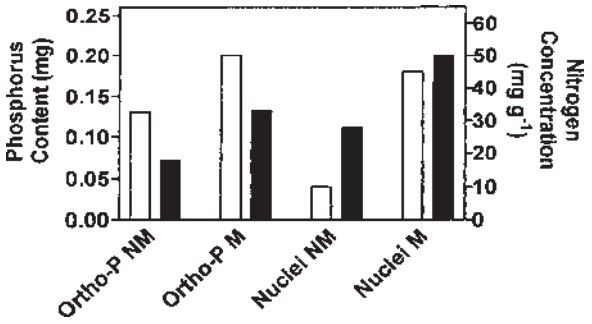

FIGURE 3.8 Shoot phosphorus content (open bars) and nitrogen concentration (solid bars) of the ericaceous plant *Vaccimium macrocarpon* in the presence (M) or absence (NM) of ericoid mycorrhizal inoculum when provided with orthophosphate (Ortho-P) or nutrients supplied in the form of nuclei. Data from Myers and Leake (1996).

the ericoid mycorrhizae (*Oidiodendron maius* and *Acremonium strictum*) of salal (*Gautheria shallon*) are able to utilize the amino acid, glutamine, the peptide, glutathione, and the protein, bovine serum albumin, as nitrogen sources. In the southern hemisphere, the Epicridaceae occupy a similar ecological niche to the Ericaceae of the northern hemisphere. Members of this family are also able to access organic forms of nutrients, as shown by the mycorrhizal endophytes of *Woollsia pungens*, which are able to degrade glutamine, argenine, and bovine serum albumin (Chen et al. 2000).

In soils in which most of the nutrients are in the form of organic compounds, nitrogen is not the only nutrient that becomes scarcely available for plant growth. In these soils, Phosphorus is also complexed within organic compounds and can be released through the action of a variety of phosphatase enzymes. Ericoid mycorrhizae are capable of producing phosphatase enzymes (Pearson and Read, 1975; Mitchell and Read, 1981; Straker and Mitchell 1985). In these low-pH soils, heavy metals are often more available than in other soils. Concentrations of iron and aluminum greater than $100\,\mathrm{mg\,l^{-1}}$ were shown to be inhibitory to phosphatase production by the ericoid mycorrhizal fungus *Hymenoscyphus ericae* (Shaw and Read, 1989). In low-pH soils, however, ericoid mycorrhizal associations have been said to "detoxify" the ecosystem by assimilation of phenolic and aliphatic acids (Leake and Read, 1991) and complexing toxic metal ions (Bradley et al., 1982). This ability allows the establishment of the host plant in extreme environmental conditions. (See Chap. 6.) The importance of ericoid mycorrhizae, their role in the acquisition of nutrients, and their tolerance of heavy metals may be of great importance to those ericaceous plant species that have been brought into cultivation. There is little

documented evidence of the role of ericoid mycorrhizae in these cultivated forms (Goulart et al., 1993), in which the extent of root colonization is much higher than expected, based on their survey of native and cultivated blueberry (*Vaccinium corymbosum*) in the United States.

B. Mycorrhizal Ecosystem Services in Forest Communities

At more temperate latitudes and at lower altitudes, the ericaceous-dominated plant communities give way to forest ecosystems. In these coniferous, deciduous and mixed forest biomes, the array of plant litter chemistry is diverse, with a mixture of readily degradable and recalcitrant materials. In these ecosystems, ectomycorrhizae dominate as soils develop a "mor" and "moder" type of humus over more base-rich parent material. In these ecosystems phosphorus as well as nitrogen can be limiting to plant growth. Again, the ability of mycorrhizal fungi to behave as saprotrophs to effect a "direct cycling" of nutrients from partially decomposed organic residues is a benefit to the plant community. In this context the ability of ectomycorrhize to produce a range of enzymes is a benefit, allowing the host plant to obtain both nitrogen and phosphate from organic resources and to compete against immobilization by the saprotrophic soil microbial community (Dighton, 1991). Ectomycorrhizae have been shown to produce nitrogen-degrading protease enzymes (Abuzinadah and Read, 1986a, b; 1989; Read et al., 1989; Leake and Read, 1990a, b; Zhu et al., 1994; Tibbett et al., 1999; Anderson et al., 2001), phosphate-solubilizing acid phosphatase enzymes (Bartlett and Lewis, 1973; Dighton, 1983; Antibus et al., 1992; 1997; Leake and Miles, 1996; Joner and Johansen, 2000), and other enzymes (Giltrap, 1982; Durall et al., 1994), enabling them to utilize forest floor carbon. Dighton (1991) has reviewed the abilities of mycorrhizal plants to utilize organic nutrients.

Abuzinadah and Read (1986a, b) demonstrated the use of peptides and proteins as nitrogen sources by ectomycorrhizae in culture and in symbiosis. Four tree species in mycorrhizal association with the fungus *Hebeloma crustuliniforme* were shown to be able to incorporate up to 53% of the total N contained in proteins or peptides, whereas nonmycorrhizal tree seedlings could access no nitrogen from these organic sources. Similarly, Wallander et al. (1997) showed that the uptake of nitrogen from alanine or ammonium was 10 times higher than from nitrate sources. In forested ecosystems, in which the decomposition rate and mineralization of nitrogen from plant residues is reduced because of low resource the quality (high C:N ratio) we have seen that heterotrophic microbial communities are capable of importing nitrogen (or other nutrients) from the surrounding environment (deeper soil horizons, patches of high rates of mineralization) into the low-quality resource in order to effect more rapid decomposition by lowering the C:N ratio. Similarly, in arctic regions, in which decomposition and nutrient mineralization is constrained by low temperatures, Tibbett et al. (1998a) suggest that there has been a pre adaptation of *Hebeloma*

species to utilize nitrogen in the form of proteins and glutamic acid, which are often released from organic matter during freezing. Indeed, they (Tibbett et al., 1998b, c) demonstrate that cold active phosphomonoesterase enzyme is only produced by *Hebeloma* when grown at 6°C. There is thus competition between the saprotrophic and mycorrhizal fungi for readily available nutrients (Kaye and Hart, 1997). This is particularly true if there is an abundance of nitrifying bacteria in the system, which utilize NH_4^+ as an energy source rather than carbon (Tate, 1995). These nitrifiers can consume considerable quantities of NH_4 (possibly up to 70% of the total available NH_4) and be in direct competition with plant roots and their mycorrhizae (Norton and Firestone, 1996; Kaye and Hart, 1997). Although Yamanaka (1999) showed that the ectomycorrhizal fungi *Laccaria bicolor*could utilize ammonium, nitrate, and urea as sources of nitrogen and *Hebeloma* spp. could also use bovine serum albumin, none of the mycorrhizal fungi could utilize nitrogen in the form of ethylenediamine or putrescine, suggesting that the ectomycorrhizal fungi could not compete with saprotrophic fungi for resources in decaying animal carcasses.

Bartlett and Lewis (1973) demonstrated the production of surface acid phosphatases by beech mycorrhizae and suggested their potential importance for phosphate acquisition by ectomycorrhizal plants from both complex inorganic and organic forms of phosphorus in the soil. As Häussling and Marschner (1989) determined that approximately 50% of the phosphorus in a Norway spruce forest was in the form of organic P, the benefit of the ability of ectomycorrhizal-associated forest trees to produce phosphatase enzymes was evident. They demonstrated that there was a two- to 2.5-fold increase in acid phosphatase activity in the rhizosphere as compared to the bulk soil. The ability to ectomycorrhizal fungi to access and incorporate phosphorus from complex organic forms of P, such as inositol hexaphosphate, has been demonstrated a number of times (Dighton, 1983; Mousain and Salsac, 1986; Antibus et al., 1992; 1997) and the regulation of the expression of this enzyme by external concentrations of orthophosphate has been shown by MacFall et al. (1991). Indeed, Antibus et al. (1992) showed that in some ectomycorrhizal fungi there was a greater uptake of phosphorus from organic supplies than from inorganic supplies because of the action of acid phosphatase and phytase enzymes (Table 3.11). In a mixed forest ecosystem, the benefit of ectomycorrhizal associations with tree species is shown to be an advantage in terms of the accession of P from both inorganic and organic sources, compared to an arbuscular mycorrhizal tree species (Antibus et al., 1997) (Fig. 3.9). In addition, there is evidence to show that ectomycorrhizae are able to access phosphorus from complex inorganic forms of phosphate (Lapeyrie et al., 1991). *Paxillus involutus* was able to solubilize calcium phosphate, but only in the presence of available ammonium or nitrate nitrogen. Other fungal species examined, however, could only solubilize this form of phosphate in the presence of

TABLE 3.11 Incorporation of ^{32}P Labeled Phosphorus (CPM mg dm^{-1} h^{-1}) into Ectomycorrhizal Fungal Mycelia from Either Inorganic (P_i) and Organic (P_o) Sources Due to the Activity of Mycelial Surface or Soluble Acid Phosphatase (*p*NPPase-*p*NPP release mg dm^{-1} h^{-1}) or Phytase (nmol P Released mg/(protein h) Enzyme Activity

Fungal species	P source	*p*NPPase		Phytase		^{32}P uptake
		Mycelium	Soluble	Mycelium	Soluble	
Amanita rubescens	P_i	1.8	60.0	55.2	0.7	17.0
	P_o	1.1	45.0	36.3	0.4	5.2
Entoloma sericeum	P_i	15.6	77.4	83.8	0.3	136.5
	P_o	18.3	41.4	60.0	0.3	4000
Hebeloma crustuliniforme	P_i	0.6	4.8	2.0	0.0	—
	P_o	0.6	11.0	2.7	Nd	—
Lactarius sp.	P_i	8.2	Nd	265.1	Nd	56.1
	P_o	6.3	Nd	198.4	Nd	148.4
Scleroderma citrinum	P_i	3.7	1.0	74.3	Nd	68.5
	P_o	4.7	1.0	2.3	Nd	93.3
Cenococcum geophilum	P_i	0.1	Nd	13.1	Nd	2.6
	P_o	0.7	Nd	23.2	Nd	457.9

Source: Data from Antibus et al. (1992).

ammonium N (Table 3.12). In all fungal species, the dissolution of the complex form of phosphate was enhanced in the absence of orthophosphate, suggesting a product suppression of the enzyme system (Kroehler et al., 1988). Kroehler et al. (1988) also showed that substrate hydrolysis yielded more inorganic phosphate than was taken up by the mycorrhizal fungi, indicating that the mycorrhizal

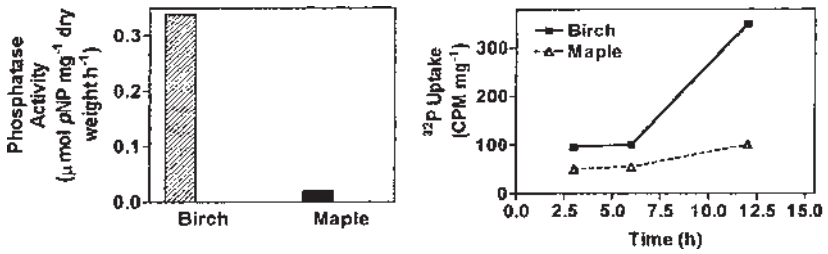

FIGURE 3.9 Acid phosphate activity of birch (ectomycorrhizal) and maple (arbuscular mycorrhizal) roots (left) and the uptake of radioactively labeled phosphorus from an organic P source (inositol polyphosphate), demonstrating the benefit of ectomycorrhizal associations in a mixed forest ecosystem for access to poorly available nutrient sources. Data from Antibus et al. (1997).

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TABLE 3.12 Solubilization of Complex Inorganic Forms of Phosphate by a Range of Ectomycorrhizal Fungal Species in the Presence (+P) or Absence (−P) of Soluble Orthophosphate and Available Nitrogen in the Form of Ammonium

	Ca phytate		$CaHPO_4$		$Ca_3(PO_4)_2$		$Ca_5(PO_4)_3OH$	
Fungal species	−P	+P	−P	+P	−P	+P	−P	+P
Paxillus involutus 1	150	100	100	80	80	80	100	80
Paxillus involutus 2	120	100	0	0	20	20	0	0
Laccaria laccata	150	150	100	100	50	50	100	50
Cenococcum geophilum	200	250	150	200	100	80	100	50
Hebeloma cylindrosporum	120	120	120	120	80	—	80	50
Pisolithus tinctorius 1	0	0	0	0	0	0	0	0
Pisolithus tinctorius 2	80	100	100	100	0	0	0	0
Hebeloma crustuliniforme 1	100	150	100	80	50	20	80	20
Hebeloma crustuliniforme 2	120	150	100	100	50	20	80	50
Laccaria bicolour	100	100	100	80	50	80	50	50

Source: Data from Lapeyrie et al. (1991).

activity may contribute to net nutrient mineralization. They and other authors have shown, however, that the availability of inorganic phosphorus in soil solution controls the rate of phosphates production by negative feedback mechanisms.

There is, however, variability among fungal species in their ability to produce enzymes (Dighton, 1983; 1991; Lapeyrie et al., 1991), and Read (1991b) suggests that species such as *Laccaria laccata* and *Pisolithus tinctorius* are poor enzyme producers, relying on enhancing nutrient uptake of mineral nutrients derived from breakdown of organic residues by the saprotrophic microbial community, whereas other species (*Paxillus involutus, Lactarius* spp., *Amanita* spp., and *Suillus* spp.) have a greater degree of enzyme competency. This idea is supported by the observations of Bending and Read (1996), who showed that the ectomycorrhizal fungi *Lactarius controversus, Paxillius involutus, Piloderma crocerum*, and *Pisolithus tinctorus* mycelia accumulated no more nitrogen from bovine serum albumin (BSA) as a nitrogen source than they did from a basal medium, whereas *Suillus bovinus* had greater access to the nitrogen in the BSA. A word of caution in the interpretation of enzyme studies in pure culture comes from the work of Anderson et al. (2001), who show that some of the variation in the ability of different isolates of *Pisolithus tinctorius* to utilize organic sources of nitrogen is due to the length of maintenance of the isolate on agar culture. Longer storage times appear to enhance organic nitrogen utilization potential.

Differences in the abilities of ectomycorrhizal fungi to produce enzymes has been linked to changes that occur within forest ecosystems over time. The changes in resources available to the decomposer community during ecosystem succession to a forested community (Heal and Dighton, 1986) and over the growth of a forest rotation (Cromack, 1981; Polglase et al., 1992; Hughes and Fahey, 1994) would imply that fungi occurring during the later stages of forest development or in more mature forests would benefit from greater enzyme competency than in early stages of forest development or young forests, in which litter inputs consist primarily of high resource quality substrates. Fleming et al. (1986) proposed the concept of mycorrhizal succession. They observed the occurrence of concentric bands of different ectomycorrhizal fungal species around the base of birch trees as they aged. The outermost ring consists of "early-stage" fungi, whereas those nearer the tree base were deemed "late-stage" fungi. Surveys of ectomycorrhizal fruit body production in Sitka spruce and lodgepole pine stands of different ages revealed a general pattern of succession of dominant mycorrhizae (Dighton et al., 1986) that was subsequently linked to possible changes in the nutrient resources available in the forest floor and the physiological function of the mycorrhizal fungi (Dighton and Mason, 1985, Last et al., 1987). The general pattern agrees somewhat with the knowledge of the dominance of mycorrhizae with higher enzyme competence in older forest stands in relation to a greater deposition of recalcitrant materials (Read, 1991a), although there is some debate over the suitability of using fruit bodies as an index of mycorrhizal abundance and dominance compared to actual measures of mycorrhizal root tip abundance (Termorshuizen and Schaffers, 1989; Egli et al., 1993; Yamada and Katsuya, 2001).

As we have seen in the decomposition of plant litter resources by saprotrophic fungi, there are successions of fungi that occur in relation to changes in available resources and the ability of the colonizing fungi to produce appropriate enzymes. Ponge (1990; 1991) showed that ectomycorrhizal invasion of pine leaves occurred during the latter stages of decomposition, in which the combination of saprotrophic fungal and faunal activity rendered the matrix more penetrable by roots and mycorrhizal fungi and nutrients became more available in an inorganic form. These fungal successions vary, depending upon the nature of the initial resource. An example of the local changes in fungal flora during the exploitation of nutrient patches comes from the studies of Sagara (1995), in which patches of nutrients arise from localized additions to the soil from urine, feces, and dead animal bodies. He identified clear successions of mycorrhizal fungi fruit bodies over a time course in which later successions favor the appearance of *Laccaria bicolor* and *Hebeloma* spp., which have an affinity for high ammonium content in soil (Table 3.13). Additionally, he cites evidence for the exploitation of subterranean mole middens by the ectomycorrhizal fungus *Hebeloma radicosum*, which under these conditions is able to "defend" its site of

TABLE 3.13 Fungal Fruitbody Appearance and Successions on Two Localized Substrates and an Ammonium-Treated Control Site (500 g m^{-2} N) in a Pine Forest in Japan

	Time (days)							
Species	0	100	200	300	400	500	600	1700
Human feces								
Ascobolus hansenii	+							
Peziza sp.	+							
Laccaria laccata		+				+		
Dead cat								
Ascobolous denudatus	+							
Tephrocybe tesquorum	+							
Hebeloma spoliatum		+	+					
Lactarius chrysorrheus							+	+
Mitrulia sp.							+	
Aqueous ammonia								
Ascobolous denudatus	+	+						
Amblyosporium botrytis	+	+						
Pseudombryophila deerata		+						
Tephrocybe tesquorum		+	+					
Coprinus echinosporum		+	+					
Peziza spp.			+					
Tephrocybe ambusta			+					
Laccaria bicolor						+	+	+
Hebeloma sp.						+	+	

Source: Data from Sagara (1995).

occupancy against the more common *H. spoliatum.* It is assumed that the change in competitiveness is due to the exploitation of local environmental variables, such as available nutrients. This argument may explain some of the changes in the phenology of fruiting of ectomycorrhizal fungal species, in which there is both a spatial and temporal element to the appearance of different mushroom species in *Abies firma* forests of Japan (Matsuda and Hijii, 1998).

Adding to the evidence to support the idea that some ectomycorrhizal fungi are involved in the direct cycling of nutrients from organic matter to the plant is the fact that in temperate forested ecosystems much of the fine root system and its associated mycorrhizae occur in the upper organic humic soil horizons. In a laboratory study, Repáč (1996) showed that ectomycorrhizal colonization of tree roots increased in the presence of organic matter. It is juxtaposition of roots, fungal hyphae, and the nutrient-rich organic material that provides the best option for mineralization and direct uptake of nutrients by the roots, minimizing

the chance for leakage loss to drainage water. In addition, Newberry et al. (1997) suggest that the activity of ectomycorrhizal fungal communities on the roots of some tropical legume tree species allows exploitation of phosphorus in deeper soil layers than are being colonized by surface feeder roots. In this way, the authors suggest, mycorrhizae are able to keep phosphorus cycling in the biotic components of the forest (Fig. 3.10). They suggest that there is a strong interaction among the phosphate acquisition capacity of the mycorrhizae, the environmental controls of phosphate release, and the seasonal demands form P by the trees, especially during mast years. They refer to this as a phenological and climatic ectomycorrhizal response (PACER), which optimizes phosphate utilization and minimizes phosphate leaching loss.

Many of the ectomycorrhizal fungal species exhibiting enzyme activity have rapid hyphal growth and large mycelial networks, many of which are aggregated into cords or rhizomorphs (Read (1991a). These rhizomorphs allow translocation of nutrients from distal parts of the extraradical mycelial network to the root in an analogous way to mycelial cord systems of wood-rotting fungi (Rayner et al., 1985; Wells and Boddy, 1990; 1995; Cairney, 1992; Boddy, 1999). The mycorrhizal mycelium can, in fact, be so dense in these humic soil horizons that they have been termed "mats" (Griffiths et al., 1990). They may form almost 10–20% of the top 10 cm of soil in a temperate forest ecosystem (Cromack et al., 1988), and account for 45–55% of the total soil biomass (Cromack et al., 1979). Aguilera et al. (1993) showed that these mat-forming ectomycorrhizal communities in Douglas fir forests are important in increasingly removing organic nitrogen from the soil pool and immobilizing it into high C:N

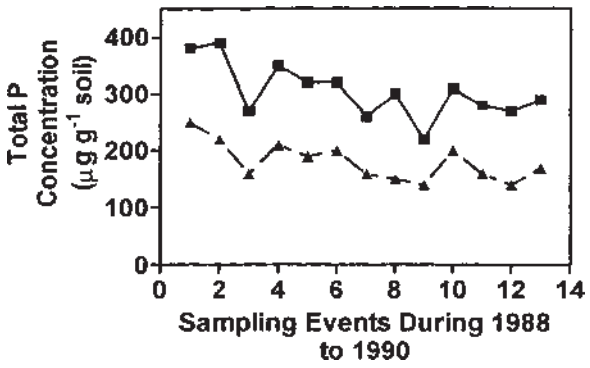

FIGURE 3.10 Total phosphorus concentration of soil in the root layer of high density (squares) and low density (trianges) of tropical cesalps, indicating the effect of ectomycorrhizal fungi in maintaining high levels of phosphorous in the rooting zone of these leguminous trees. Data from Newbery et al. (1997).

ratio fungal tissue as forest growth progresses. Although the forest soil thus becomes enriched with organic nitrogen as the forest matures, this N becomes increasingly less available to plant growth. The patchy existence of nutrients or accessible resources for mycorrhizal utilization in soil would indicate that these fungi would be adapt to be able to exploit a variety of resources as and when they become available. Indeed, Tibbett (2000) indicates that in both ericoid and ectomycorrhizal symbioses the extraradical hyphae exhibit significant morphological and physiological plasticity (Bending and Read, 1995a, b; Cairney and Burke, 1996), which makes them ideally suited for the exploitation of patchily distributed nutrient resources. Then density of hyphae of ectomycorrhizal has also been shown to alter in response to both the concentration and nature of nitrogen resources offered. Dickie and Koide (1998) showed that the hyphal foraging was increased by the production of less dense hyphal growth at low concentrations of nitrogen in either an inorganic or organic form. It is suggested that this response, which is similar to that seen for saprotrophs (Ritz, 1995; Rayner, 1991; Rayner et al., 1994), affords they mycelia greater abilities to exploit patchily distributed resources.

In a plant species that is able to associate with either arbuscular-or ectomycorrhizal partners, van der Heijden (2001) showed that there was different functional significance between the arbuscular mycorrhizal and ectomycorrhizal associate of willow (*Salix repens*). The arbuscular mycorrhizal fungus *Glomus mosseae,* had a low rate of root colonization, but showed significant short-term effects on shoot growth and root length. The ecotomycorrhizal fungus *Hebeloma leucosarx*, however, had high levels of root colonization and improved host plant growth over a longer term. Arbuscular mycorrhizal colonization resulted in higher shoot P uptake, shoot growth, root growth, and response duration in plants collected in December than for those collected in March, whereas the ectomycorrhizal and nonmycorrhizal treatment showed no difference among cuttings collected on different dates. The differential effects of the two mycorrhizal types could be related to the availability of nutrients at different times of the year and the differences in function of the two types of mycorrhizae.

Vogt et al. (1991) reviewed the role of ectomycorrhizae in forest ecosystem function. They suggested that four areas of research should be prioritized: (1) the cost-benefit analyses of maintaining mycorrhizal associations, (2) the role of mycorrhizae in nutrient and carbon storage, (3) the significance of mycorrhizal linkages between host plants, and (4) the role of mycorrhizae in the acquisition of nutrients from organic sources. As we have seen, some efforts have been made to address these questions in recent years. In particularly, the role of fungi in interconnecting host plant species has altered our view of plant community structure and function from a competition interaction to a combination of competition and synergism. (See Sec. 3.2.6.) The image of a forest ecosystem permeated by fungal mycelia, which act as a plumbing system to convey carbon

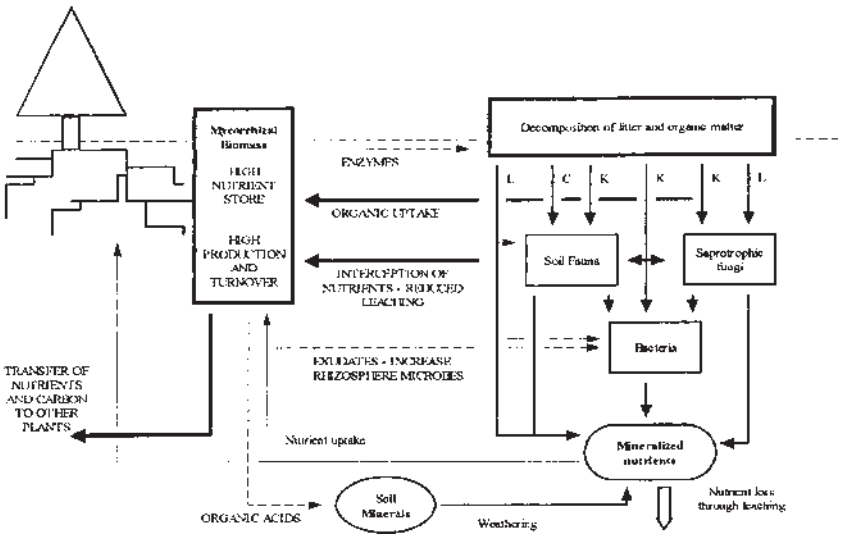

FIGURE 3.11 Diagram showing the 'traditional' approach to decomposition and plant nutrient uptake, driven by the saprotrophic fungal community (thin arrows). The affect of mycorrhizae are shown by thick arrows and the dotted arrows showing mycorrhizal enzyme activity, exudation of carbohydrates to stimulate synergistic activities with bacteria (PGPBs and helper bacteria) and the secretion of rock dissolving organic acids. L, C and K represent leaching, comminution and catabolism, respectively. Redrawn from Vogt et al. (1991).

and nutrients among ecosystem elements, has been painted by Rayner (1998). Our perception of the role of fungi in nutrient cycling as being a process of decomposition and nutrient mineralization by saprotrophs followed by plant uptake aided by mycorrhizae has changed, however. We now appreciate a much closer association of the mycorrhizal fungi with the decomposition process with synergistic interactions between the saprotrophic and mycorrhizal communities (Fig. 3.11). We are still a long way, however, from answering all the questions concerning the intricacies of these interactions and functions.

C. Mycorrhizal Ecosystem Services in Herbaceous Communities

In warmer, moist environments, in which nutrient cycling occurs at a more rapid pace, the major forms of nutrients in soil are in the inorganic phase in soil water. Arbuscular mycorrhizae dominate under these conditions in temperate grasslands and in tropical forests and grasslands. In these ecosystems of herbaceous-dominated plant communities, decomposition is rapid and organic matter rapidly becomes incorporated into the soil mineral matrix. The nutrient supply for plants is mainly through inorganic nutrients, mineralized by saprotrophic activity on

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the high resource quality plant residues. Phosphorus tends to be a limiting nutrient in these systems (Read, 1991b), and the arbuscular mycorrhizal associations of these plants appears to confer a greater efficiency in effecting plant acquisition of mineral nutrients (Hetrick, 1989). Jeffries and Barea (1994) reviewed the role of arbuscular mycorrhizal fungi in biogeochemical cycling and the maintenance of sustainable plant-soil interactions. Arbuscular mycorrhizae are of particular importance in agriculture (Gianinazzi and Schüepp, 1994), but discussion of these ecosystems is out of the scope of this book, except when specific principles relative to natural ecosystems are discussed. Jeffries and Barea (1994) discuss the influence of arbuscular mycorrhizae on biogeochemical cycling and sustainability by improving plant nutrition, preventing root pathogens, and improving soil structure by binding soil particles together with mycelia. As a consequence of the relatively high availability of inorganic to organic sources of nutrient in these soils, these mycorrhizal types have only limited enzyme expression. It has, however, been shown that they are capable of producing phosphatase enzymes to solubilize poorly available phosphates in soil (Azcón et al., 1976; Singh and Kapoor, 1998). Indeed, Jayachandran et al. (1992) recorded the ability of nonmycorrhizal big bluestem grass (*Andropogon gerardii*) to access phosphorus from glycerophosphate and adenosine monophosphate, but not from phytic acid, RNA, ATP, or CMP (cytidine 2′-and 3′ monophosphate). In the presence of the arbuscular mycorrhizal fungus *Glomus etunicatum* plants were able at access all forms of organic phosphorus, and uptake into the plant was 500- to 600-fold higher in the mycorrhizal plants than in the nonmycorrhizal plants (Fig. 3.12). Bolan (1991) suggests that the arbuscular

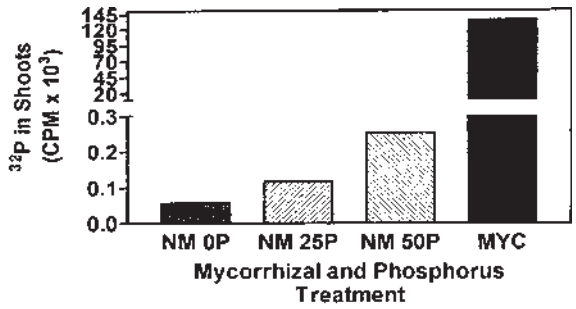

FIGURE 3.12 Incorporation of radioactive phosphorus into shoots of big bluestem (*Agropyron genardii*) from an organic phosphorous source (cytidine diphosphate) when in symbiotic association with the arbuscular mucorrhizal fungus (*Glomus etunicatum*) (MYC) in comparison with phosphorus incorporation in the presence of 0, 25 or 50 mg P kg^{-1} of the organic phosphate in the absence of mycorrhizae. Data from Jayachandran et al. (1992).

mycorrhizal benefit for phosphate uptake into plants is due to three factors: (1) exploitation of a larger soil volume, (2) faster movement of phosphate into the root via fungal hyphae, and (3) the ability to solubilize complex inorganic forms of phosphate. He suggests that mycorrhizal fungi may help to overcome the three rate-limiting steps of phosphate uptake by increasing the rate of diffusion into plant roots, the phosphate concentration at the root surface, and the rate of phosphate dissociation from the surface of soil particles (Fig. 3.13). The ability of arbuscular mycorrhizae to solubilize phosphate may be an important factor in permitting plants to grow in calcareous soils in which phosphate is limited because of complexing with heavy metal ions. Tyler (1994) shows that the inability of the calcifuge plant species *Carex pilulifera, Deschampsia flexuosa, Holcus mollis, Luzula pilosa, Nardus stricta*, and *Veronica officinalis* to grow on limestone is because of their inability to decouple the iron-phosphate complexes to derive both elements essential to their growth. Calcicole species, however, appear to have developed mechanisms of acquiring both P and Fe from these soils by the production of organic acids in the rhizosphere (Ström, 1997; Lee, 1999) (Table 3.14). Part of this ability may be linked to the arbuscular mycorrhizal

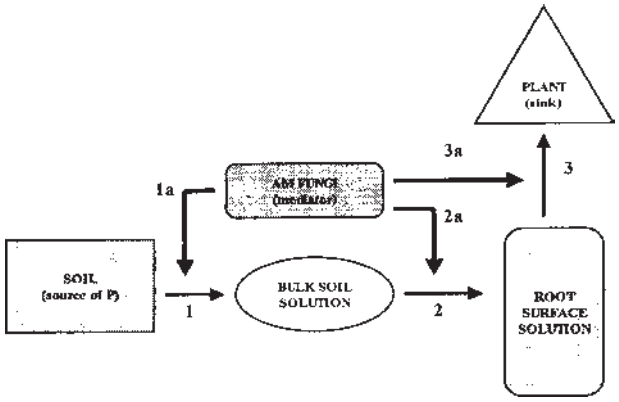

FIGURE 3.13 Rate-limiting processes in the uptake of phosphorus by plants and the role of arbusculr mycorrhizae in overcoming these limitations. Thin arrows represent flows in the non-mycorrhizal condition, 1 being release of P from soil particles, 2 diffusion to the root surface, and 3 uptake by the plant. Thick arrows indicate the influence of the mucorrhizae, with 1a being chemical modification of the P release mechanism by enzyme or organic acid production, 2a decreasing the diffusion distance by the exploitation of soil by extraradical hyphae, and 3a reducing the threshold concentration of P required to permit transfer of P across the plant cell membrane. Adapted from Bolan (1991) with kind permission of kluwer Academic Publishers.

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TABLE 3.14 Production of Organic Acids in the Rhizosphere of Calcifuge and Calcicole Plant Species Showing the Adaptation of Calcicoles in Order to Solubilize Phosphate and Essential Heavy Metals

		Organic acid production (m mol m^{-3} soil solution) where root weights are equivalent										
		Monocarboxylic				Dicarboxylic			Tricarboxylic			
Plant strategy	Species	Lactic + Acetic	Proprionic	Formic	Pyruvic	Malic + Succinic	Tartaric	Oxalic	Citric	Isocitric	Aconitic	SUM
Calcifuge	*Deschampsia*	8.9	0.4	4.8	0.4	0.3	0.2	1.7	1.0	0.2	0.2	17.3
	Viscaria	7.9	0.3	5.1	0.3	1.4	0.2	3.1	0.5	0.2	0.2	11.7
Calcicole	*Gypsophila*	8.0	0.3	4.3	0.4	3.7	13.4	6.2	4.5	0.2	0.2	40.8
	Sanguisorba	11.9	0.3	5.9	0.4	1.3	0.2	7.9	3.8	0.2	0.9	32.6

Note: The role of mycorrhizal fungi is not implied, but it is probable that they could be involved in increasing the function of organic acid production.
Source: Data from Ström (1997).

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associations of the calcicoles, although Lee (1999) points out that we know little of the role of mycorrhizae in the process of adaptating calcicolous plants, but there is evidence suggesting that fungi can produce organic acids (Azcón et al., 1976; Bolan, 1991; Singh and Kapoor, 1998). Goh et al. (1997) showed that the colonization of wheat roots by arbuscular mycorrhizae in calcareous soil significantly increased the availability of both phosphorus and zinc (Fig. 3.14), although the effect of the mycorrhiza was not seen in plant growth. Clark and Zeto (2000), however, point out that arbuscular mycorrhizae are not only limited to enhancing phosphorus uptake into the host plant; enhanced nitrogen uptake has also been observed, but may be more generally related to the induced demand by achieving greater plant size due to the mycorrhizal effect of overcoming phosphate limitations. In particular, the interaction among mycorrhizae and nitrogen-fixing leguminous plants is of importance in assisting the delivery of phosphate to plants to maximize nitrogen fixation in root nodules (Azcón-Aguilar et al., 1979; Peoples and Craswell, 1992; Herrera et al., 1993). Additionally, there is some evidence of arbuscular mycorrhizae being able to utilize organic forms of nitrogen (Ames et al., 1983). As we saw in the previous chapter, arbuscular mycorrhizal fungi may play an important role in the maintenance of soil fertility by increasing the organic matter content with chemicals that can assist in the development of soil aggregates, help to maintain aggregate stability, and hence retain soil fertility (Wright and Upadhyaya, 1998).

The differences among the physiological activities of ericoid, ecto-, and arbuscular mycorrhizae suggest a reason for the differences in the range of fungal species forming a mycorrhizal association with the different plant groups. In the ericoid situation, there appears to be an overwhelming need to be able to mobilize nitrogen in soils in which a large percentage of nitrogen is stored in a

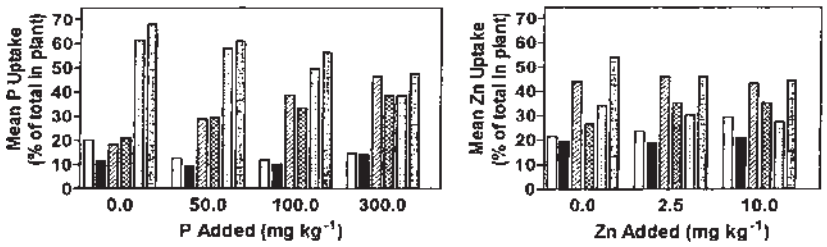

FIGURE 3.14 Incorporation of phosphorus (left) and zinc (right) into wheat plants grown in calcareous soil at various levels of P and Zn supply in the soil. Each pair of columns in each graph represents non-mycorrhizal (left) and mycorrhizal (right) condition and element incorporation into the plant root, straw and grain, respectively from left to right. (Data from Goh et al., 1997).

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plant-inaccessible organic form. It is therefore possible that only a limited number of fungal species have evolved the abilities both to form mycorrhizal associations with ericaceous plants and to produce the required protease enzymes required in the adverse environmental conditions that limit the distribution of these plant species. In the ecosystems in which ectomycorrhizae dominate, the diversity of plant litter resources available to provide nutrients for plant growth is more varied and consists of both readily decomposable and recalcitrant forms. Soils in these systems have a tendency to be either nitrogen- or phosphorus-limited, or not nutrient-limited at all. There is the opportunity in this situation for multiple lines of evolution of the mycorrhizal habit within a number of fungal taxa, allowing for optimization of inorganic nutrient uptake and/or the production of protease, phosphatase, or other enzymes. Koide et al. (2000) showed that the role of arbuscular mycorrhizae was probably not directly an effect on plant growth but indirectly by a change in the rate of uptake of phosphorus and phosphorus use efficiency by plants. The effect of mycorrhizal colonization of roots of *Lactuca* and *Abutilon* spp. increased the rate of phosphrus uptake (phosphorus efficiency index) by 23% and 32%, respectively, but had no effect on the nonmycorrhizal plant *Beta* sp. The mycorrhizal association significantly reduced the phosphorus use efficiency of *Lactuca*, however, but did not alter that of *Abutilon* or *Beta*, leading to a slight increase in growth of *Lactuca*, a significant increase in growth of *Abutilon*, and no effect on *Beta*. This indicates that the effect of mycorrhizal colonization of roots of different plant species has different effects and that the resulting outcome may influence more than the growth of the host plant, including its relative fitness within the plant community.

Fitter (1985) suggested that we knew relatively little about the ecological significance and ecosystem functioning of arbuscular mycorrhizae in field conditions. Most information regarding the function and physiology of these mycorrhizae came from either laboratory or greenhouse studies of the studies of mycorrhizae in an agricultural context. He cites work in natural ecosystems, such as that of Rangeley et al. (1982), on the growth of clover in acid grassland ecosystems in which plant growth was severely limited in the absence of added phosphorus, but in which the effect of mycorrhizal inoculation without added fertilizer had no effect on plant growth. In contrast, growth of clover on brown earth soil of higher pH and fertility responded positively to the addition of one of the two arbuscular mycorrhizae in the second year, showing an improvement in yield. Fitter suggested that in comparison with laboratory experiments, the difference in response in the field could be due to the interconnectedness of plants via mycorrhizae, the effects of faunal grazing reducing the function of mycorrhizae, or differences in the longevity of roots compared to artificial systems. Some of these concepts have been explored more recently. Very little influence of mycorrhizal association of natural grasses could be seen in the uptake of phosphorus and a variety of heavy metals (Sanders and Fitter, 1992a,b), although

the authors suggest that a benefit of the association occurs seasonally, during times in which phosphorus availability is low and plant demand is high. This is possibly a reason for the maintenance of the mycorrhizal association in the community.

In a study of the carbon and phosphorus balance of bluebell, Merryweather and Fitter (1995a) closely document changes in the allocation of phosphorus and carbon between the soil and plant parts. They suggest that bluebell is obligately mycorrhizal. They were not able to fully demonstrate the benefit of the mycorrhizal association, but were able to incorporate its existence into the nutrient and carbon budget. In a companion paper (Merryweather and Fitter, 1995b), however, they suggest that the role of arbuscular mycorrhizal association of roots of bluebell increases with age. During the ageing process, bluebell bulbs descend further into the soil to zones in which phosphorus becomes increasingly depleted. As they do so, the roots become increasingly more colonized by mycorrhizae, and the enhanced phosphorus gained by this association allows the fecundity (measured as bulb diameter) to be maintained (Fig. 3.15).

In a continuation of this study, Merryweather and Fitter (1996) showed that an application of benomyl to soil in the field reduced the arbuscular mycorrhizal association of bluebells and demonstrated that the although concentrations of phosphorus in the vegetative parts of the plant were reduced, preferential allocation of phosphorus to flowers and seeds was maintained, despite the reduced function of the mycorrhizae (Fig. 3.16). This information suggests that there is some control of the plant's fitness by the presence of the mycorrhizal symbiosis.

The large diversity of fungal species involved in ectomycorrhizal associations would be expected to have a diversified role and to be able to respond to changes in the environment by altering species composition on root

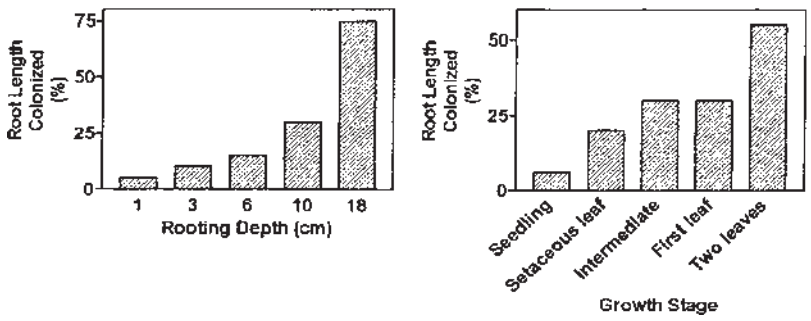

FIGURE 3.15 The effect of rooting depth (left) and stage of plant development (right) on the arbuscular mycorrhizal development of roots of the bluebell (*Hyacinthoides non-scripta*) collected in the wild. Data from Merryweather and Fitter (1995).

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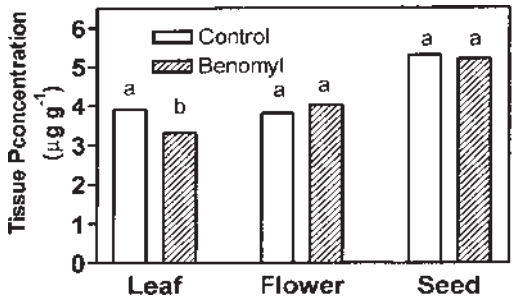

FIGURE 3.16 Tissue phosphorus concentrations of blueball leaves (in March) and flowers and seeds at the end of the growing season for control plants (open bars) and plants treated with a soil application of benomyl (hatched bars) to reduce the arbusculr mycorrhizal colonization of the roots. Pairs of bars sharing the same letter are not significantly different from each other. Data from Merryweather and Fitter (1996).

systems to optimize the nutrients available. Inorganic nutrients are frequently more available in arbuscular mycorrhizal-dominated environments. In this situation there does not seem to be the need for diversification of function, hence the low number of fungal taxa that have evolved the mycorrhizal habit. There may be more differences among fungal species within the arbuscular mycorrhizal community than initially appears evident, however. Dodd (1994) cites the work of Jakobsen et al. (1992a,b) that shows greater soil volume exploitation by the mycorrhizal fungus *Acaulaospora laevis* than *Glomus* sp. and thus the ability of the former species to obtain phosphorus from a greater distance from the root surface. The role of mycorrhizal diversity, particularly in ectomycorrhizae, will be discussed in the following section. It may be that in the arbuscular mycorrhizal symbiosis the host plant plays a more important role in determining the nature of the function of the mycorrhizal effect, where it may be growth, phosphorus content, or plant fitness, a subject that will be discussed in more depth in Chap. 5.

Faunal grazing on arbuscular mycorrhizal fungal extraradical hyphae has been shown to reduce the efficiency of the mycorrhizae in acquiring nutrients, particularly phosphorous, for the plant. Warnock et al. (1982) showed that there was a strong interaction between collembolan density and the growth of the host plant. The effect of this grazing is likely to be more important in agroecosystems, in which the diversity of soil fauna is reduced and high densities of collembola can occur in the absence of predators. In addition it has been shown that nematode feeding on mycorrhizal fungal hyphae can also reduce the effectiveness of the mycorrhizal association and has the effect of altering a plant's competitive fitness (Brussard et al., 2001).

3.2.4 Edaphic Relations, Biodiversity, and Function

Evidence to demonstrate the differences in activity among ectomycorrhizal fungal species is plentiful within the literature. In many papers that compare the plant response to a variety of ectomycorrhizal associates, there are differences in plant response (Villeneuve et al., 1991a). Most of these studies are conducted in the laboratory or greenhouse, however, in somewhat artificial conditions. Field observation of the advantage of inoculation of tree seedlings with a variety of mycorrhizal species frequently shows that there are differences in growth rates of the host plant with different mycorrhizal fungal symbionts, that mycorrhizal plants perform better than nonmycorrhizal plants (especially in disturbed situations), and that the inoculated mycorrhizal species are frequently replaced by native mycorrhizal flora (Villeneuve et al., 1991b).

Demonstrations of the effect of different ectomycorrhizae in the field are more difficult to obtain (Miller, 1995). Jones et al. (1990) showed that soil type influenced the performance of ectomycorrhizae, but demonstrated that in general *Laccaria proxima* induced a higher level of tissue phosphorus content in willow (*Salix viminalis*) than did *Thelephora terrestris*. In field-grown birch, Dighton et al. (1990) injected radioactive inorganic phosphorus into soil in zones around birch trees whose mycorrhizal community was known to be dominated by different ectomycorrhizal species based on the appearance of fruit bodies. They measured the incorporation of ^{32}P into the leaves of trees in which the radiotracer was injected into different mycorrhizal zones. Despite the complexities of isotopic dilution, nonuniform translocation within the tree canopy, and the fact that the actual mycorrhizal community on roots did not always entirely match what was anticipated from fruit body appearance, they showed that the influx of phosphorus into leaves was higher when influenced by mycorrhizal communities dominated by *Hebeloma* spp. than by communities dominated by either *Laccaria* spp. or *Lactarius* spp. (Fig. 3.17). Evidence from the evaluation of enzyme production by mycorrhizal fungi also suggests that there are significant differences in the ability of different fungal species to produce the enzyme (Dighton, 1983; Antibus et al., 1992; 1997; Leake and Read, 1990b) and that the availability of the inorganic form of the nutrient in soil has a negative feedback on enzyme production (Sinsabaugh and Liptak, 1997). Given these facts and the information that the root system of individual forest trees can maintain a community of many ectomycorrhizal fungal species at the same time (Zak and Marx, 1964; Gibson and Deacon, 1988; Palmer et al., 1994; Allen et al., 1995; Shaw et al., 1995), it is therefore possible that the ectomycorrhizal community on root systems is functionally plastic and able to be changed locally at a spatially and temporal scale to optimize resource utilization as the local environmental conditions change. Tibbett (2000) indicates that in both ericoid and ectomycorrhizal symbioses the extraradical hyphae exhibit significant

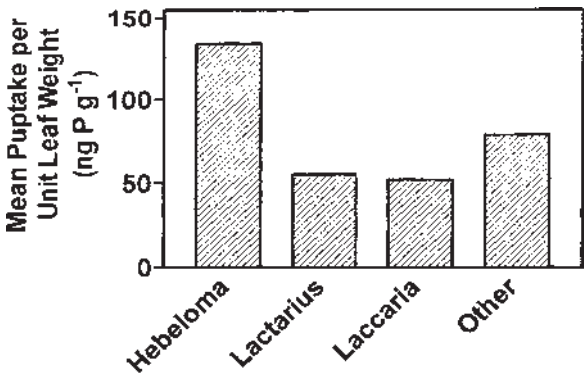

FIGURE 3.17 Uptake of inorganic phosphorus supplied to the upper 5 cm of soil in areas dominated by different ectomycorrhizal species under birch trees in the field. Data from Dighton et al. (1990).

morphological and physiological plasticity (Bending and Read, 1995a,b; Cairney and Burke, 1996), which makes them ideally suited for the exploitation of patchily distributed nutrient resources.

Large-scale influences on the environmental conditions that can alter mycorrhizal species composition on plant root systems are explored in Chap. 6, in which the effects of acidifying pollutants, heavy metals, and radionuclides on fungi are considered. We may consider here more subtle changes in environmental conditions that are brought about in an ecosystem by "natural" processes, however. We have already identified the process of forest succession and forest growth and its influence on the resources available to the decomposer fungal community and the mycorrhizal community. For example, the function of mycorrhizae appears to have a more dramatic effect on plant growth in oligotrophic systems than in fertile systems. In localized areas of nutrient-poor soils, such as volcanic fields and glacial outwash (Gehring and Whitham, 1994; Jumpponen et al., 1998, respectively), growth of pinyon pine on cinder soils was doubled by the addition of ectomycorrhizae compared to the effect of mycorrhizae on adjacent loam soil. This fact was attributed to the multiple effects of the mycorrhizae in the cinder soil to overcome multiple stresses of cinder soil having half the moisture, one-third of the available phosphorus, and no mineralizable nitrogen compared to the loam. Growth of lodgepole pine on glacier outwash soil was enhanced by the dark, septate mycorrhizal fungus *Phialocephala fortinii* because of its ability to enhance phosphate acquisition in this nutrient-poor ecosystem.

Within forested ecosystems, fire is often a natural event that maintains both plant and fungal diversity. There are many examples of changes in ectomycorrhizal species' composition of the fungal community resulting from

forest fire (Visser, 1995; Jonsson et al., 1999a). These changes suggest that there is a succession of mycorrhizal fungi during the re-establishment of a mature forest (Frankland, 1992; 1998; Boerner et al., 1996). The nature of the ectomycorrhizal community establishing on the next rotation of forest trees is dependent upon the degree of damage to the former mycorrhizal community, however. Where the effects of fire on the soil-surface organic matter and soil is minimal, there will be a residual ectomycorrhizal community on the dying roots of the former forest trees. If re-establishment of the forest is rapid, these dying roots will act as a source of mycorrhizal inoculum, thus maintaining a species diversity in the new forest similar to what existed in the old (Baar et al., 1999; Jonsson et al., 1999b). The forest can thus maintain some degree of continuity and stability. As nutrient conditions, however, (influenced by the degree of nutrient mineralization from the fire and/or loss of organic matter) together with changes in physical characteristics of the soil (increased heating due to solar radiation absorbance by a dark soil surface) may affect the relative survival of the mycorrhizal species and their physiological function. In dry sclerophyllous shrub communities in Australia, the effect of fire on arbuscular mycorrhizal colonization of roots appears to be more closely related to the density of host plants than a direct influence of fire on the mycorrhizae (Torpy et al., 1999).

In addition to the improvement of plant nutrition, mycorrhizal associations have a significant impact on plant–water relations and can help to alleviate drought stress (Sánches-Díaz and Honrubia, 1994). This benefit can arise from direct water flow through fungal hyphae, improvement in the plant phosphate nutrition, and altered hormonal balance. Fitter (1985) suggested that because of the observed lack of nutritional benefit of mycorrhizal association afforded to plants in natural ecosystems, it is likely that other benefits, such as drought tolerance, are more likely to be the rationale for the existence of mycorrhizae. Augé (2001) reviewed the effects of arbuscular mycorrhizal colonization of roots in relation to drought. His review of the current literature suggested that root colonization by arbuscular mycorrhizal fungi increased water relations of plants under both drought conditions and during periods of adequate water supply. The effect of arbuscular mycorrhizal infection of the tropical trees *Acacia nilotica* and *Leucaena leucocephala* benefited *Leucaena* most in the presence of droughty conditions. The addition of phosphorus to soil improved the growth of both plant species and the addition of mycorrhizae mirrored the effect of adding P, but the effect of mycorrhizae was greater than the effect of P addition in *Leucaena* under drought stress (Michelsen and Rosendahl, 1990) (Fig. 3.18). Cruz et al. (2000) showed the effect of mycorrhizae on drought protection in papaya, in which the decrease in leaf water potential was less in arbuscular mycorrhizal plants during drought than in nonmycorrhizal plants. Protection against drought is not restricted to mycorrhizal endophytic fungal species. Indeed, leaf endophytes of grasses have been shown to confer drought tolerance by the production of loline

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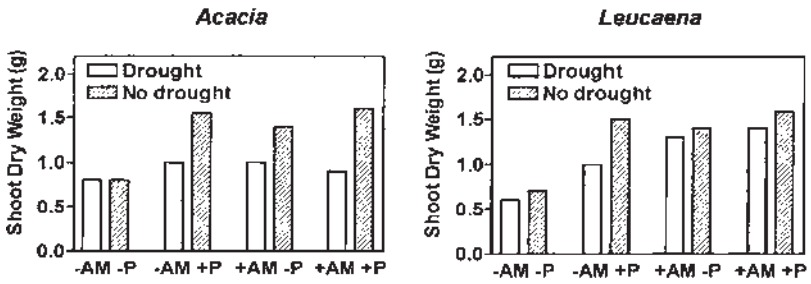

FIGURE 3.18 Effects of arbuscular mycorrhizal inoculum and added phosphorus on the growth of *Acacia* and *Leucaena* in the presence or absence of drought. Data from Michelsen and Rosendahl (1990) with kind permission of Kluwer Academic Publishers.

alkaloids, which act as osmoregulators (Belesky and Malinowski, 2000). Cheplick et al. (2000), however, found no benefit of endophytes in *Lolium perenne* for drought tolerance; in fact, growth under both droughty and normal conditions was lower in the presence of the endophyte than in its absence. It is thus possible that the effect of fungal endophytes is dependent upon a variety of environmental conditions. The influence of fungi on drought tolerance of trees is not limited to fungal endophytes. Inoculation of seed or seedlings of a Nigerian pulp wood tree, *Gmelina arborea*, with the saprotrophic fungus, *Chaetomium bostrychoides*, not only increases seed germination, but also increases the tolerance of the plant to desiccating conditions (Osonubi et al., 1990) (Table 3.15).

TABLE 3.15 Plant Biomass (g Dry Weight) of Gmelina Seedlings Inoculated in the Seed or at the Seedlings Stage with the Saprotrophic Fungus *Chaetomium bostrychoides* Before and After a Drought Event

Time	Plant part	Inoculum onto	Droughted	Undroughted
Before drought	Shoot	Seed	1.35	0.99
		Seedling	0.83	0.79
	Root	Seed	0.72	0.48
		Seedling	0.22	0.35
After drought	Shoot	Seed	9.36	5.89
		Seedling	6.92	5.67
	Root	Seed	4.47	2.65
		Seedling	4.22	2.58

Source: Data from Osonubi et al. (1990).

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Where irrigation plays a big part in the management of agroecosystems the evaporation of water often leaves localized increases in soil salinity. Juniper and Abbott (1993) demonstrated that this increase in soil salinity can reduce the germination of arbuscular mycorrhizal spores and reduce extraradical hyphal growth. Plants growing in these saline soils thus, have a reduced mycorrhizal component, which is probably detrimental to their growth and survival. The impact of salinity on mycorrhizal colonization of plants is, however, a matter of degree. Some degree of tolerance of arbuscular mycorrhizae to salinity has been observed (Sengupta and Chaudhuri, 1990), although reductions in their development have been shown to occur with increasing salinity (Semones and Young, 1995; Baker et al., 1995; Johnson-Green et al., 2001). Johnson-Green et al. (2001), however, suggest that although mycorrhizal function is reduced in these highly saline soils, mycorrhizae could still be of benefit in the revegetation of salt-degraded soils.

Other small-scale changes in environmental conditions can also significantly affect the community and therefore probably the functions of mycorrhizal communities. Patchilly-distributed leaf litter resources exist whose influence may change the community structure of the mycorrhizae and the response of the mycorrhizal community to optimize nutrient retention and stability within the ecosystem. Repeated harvesting of forest floor leaf litter in a Swedish spruce forest has been shown to reduce the abundance of ectomycorrhizae on roots, but not the number of species (Mahmood et al., 1999), although Baar and de Vries (1995) showed that complete removal of the leaf litter on a Scots pine forest floor in The Netherlands increased the diversity of mycorrhizal fungal species, whereas doubling the leaf litter reduced diversity below that of control plots in which leaf litter was left unmanipulated. In experiments investigating the effects of leaf litter extracts on the growth of ectomycorrhizae in culture, Baar et al. (1994) showed extracts of pine leaf litter reduced the growth of *Laccaria proxima* and *Rhizopogon luteolus* and only affected the growth of *Paxillus involutus* and *Xercomus badius* at high concentrations. Extracts of the grass *Deschampsia flexuosa* inhibited growth of *L. proxima*, *P. involutus*, and *R. luteolus*, however, but enhanced the growth of *Laccaria bicolor*. Koide et al. (1998) showed that the polyphenols catechin and epicatechin gallate act similarly to pine leaf litter water extracts in stimulating the growth of *Suillus intermedius* and reducing the growth of *Amanita rubescens* (Fig. 3.19), but that the volatile compounds α- and β- pinene had differential effects on a range of ectomycorrhizal fungi. This study suggests that the phenolic content and composition of leaf litter can exert a significant control of the ectomycorrhizal communities developing within the vicinity of the litter.

In a mixed forest ecosystem in the New Jersey pine barrens, Dighton et al. (2000) showed that there were localized patches of leaf litter occupying the forest floor. These patches were large, small, or nonexistent. Dighton et al. established by both measurement of existing leaf litter patches and by experimentation that

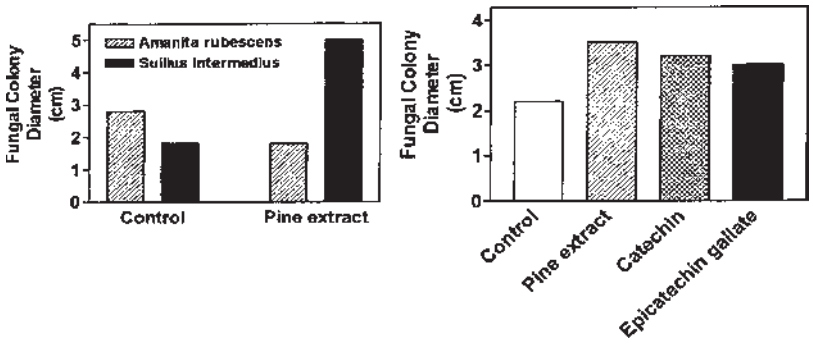

FIGURE 3.19 The effects of pine leaf liter water extraction on the growth of the two ectomycorrhizal fungi, *Amanita rubescens* and *Suillus intermedius* (left), and the effect of pine leaf extract, or two pehnolic compounds on the growth of *S. intermedius* in culture. Data from Koide et al. (1998).

the size of the litter patch that accumulated was dictated by the density of stems of the ericaceous understory vegetation (huckleberry and blueberry), which acted as a leaf litter dam. Large litter patches had different leaf species composition than the small patches, and the influence of the leaf species composition and the physical effects of leaf litter accumulation altered both soil chemistry and physical conditions in such a way that different ectomycorrhizal communities developed on the pine and oak roots invading those leaf litter patches (Fig. 3.20).

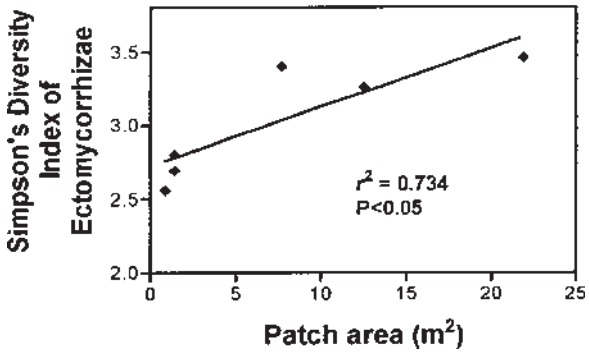

FIGURE 3.20 Changes in the diversity of ectomycorrhizal fungal species occupying leaf litter patches of increasing size in the New Jersey pine barrens. Larger leaf patches contain a higher proportion of oak leaves than pine leaves, thus altering the resource quality of leaf litter and soil chemistry due to leachates from the litter. Data from Dighton et al. (2000).

The probable influence of leaf litter species on both the mycorrhizal composition and function of the ectomycorrhizal community was evaluated by Conn and Dighton (2000). Using both laboratory studies and leaf litterbag experiments in the field, they showed that roots of pitch pine seedlings favored a mixed leaf litter community of oak and pine over either of the leaf litter species alone. The ectomycorrhizal fungal community developing on roots in each of the leaf litter types was also different. During the decomposition of oak leaves, phosphorus was immobilized into the decomposing leaf litter, whereas nitrogen was immobilized in pine. By determining the phosphatase activity of each of the mycorrhizal types found on the roots and relating the enzyme production with the percentage contribution of the mycorrhizal type to the whole community, Conn and Dighton (2000) showed that the mycorrhizal communities on roots exploiting oak and oak/pine mixed leaf litters had a higher proportion of phosphatase-producing mycorrhizae than on pine (Fig. 3.21). They attribute this to the lack of available phosphorus in oak-containing litters, in which phosphorus is being immobilized during the initial stages of decomposition. There thus appears to be some positive interaction between the local environmental conditions and the development of ectomycorrhizal communities in relation to the ability of the mycorrhizae to utilize the resources available.

Another example of the influence of plants and plant litter on the community structure of ectomycorrhizae comes from evidence that shows that *Rhododendron maximum* (an ericaceous shrub) severely reduces regeneration of hardwood and coniferous seedlings in the southern Appalachians. Walker et al. (1999) showed that litter manipulations within these forests did not affect total mycorrhizal colonization of tree roots, but altered the distribution of *Cenococcum geophilum* mycorrhizae. It was noticed after the first year, however, that hemlock seedlings regenerating in rhododendron thickets had significantly less

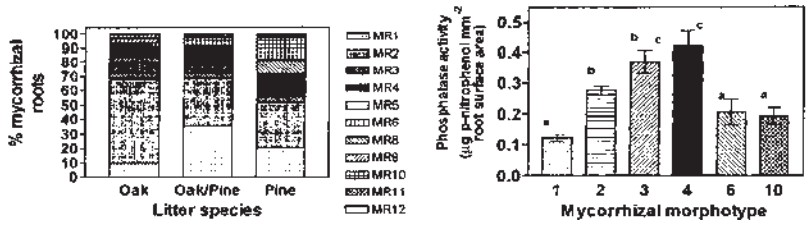

FIGURE 3.21 The effect of pine and oak leaf litter and their mixture on the ectomycorrhizal species development and phosphatase activity of pine roots invading the litter. The graph on the left shows the proportional contribution of mycorrhizal types to the community in each leaf litter type. The graph on the right shows that mycorrhizal types found more frequently in the oak litter produce more phosphatase enzyme as this litter type immobilizes P in the initial stages of decomposition. Data from Conn and Dighton (2000).

ectomycorrhizal colonization of their roots (19%) than trees outside the thickets (62%). Within the ectomycorrhizal community, root colonization of 1-year-old hemlocks by *C. geophilum* was significantly higher in the presence of rhododendron (10.4%) than without (4.6%), although this difference was lost after 2 years of growth. The effect of the difference in mycorrhizal colonization of roots within and outside rhododendron thickets resulted in a 50% reduction in seedling shoot biomass in the second year (Fig. 3.22).

The relationship among biotic diversity, or biodiversity, in ecosystems, the function of that diversity, and the stability of ecosystems has been a matter of debate in the ecological world for many years (McCann, 2000; Schwartz et al., 2000). Recent attention has been focused on the role of diversity in function, and a number of manipulative experiments have been performed in which the outcome of altered plant species' diversity on ecosystem functions have been measured (Tilman, 1993; 1997; 1999; Tilman et al., 1996). We know that there is considerable diversity in soil biota, and recently questions have been asked about the soil micro-organisms' function (Ritz et al., 1994), as much of the previous research had concentrated on measuring biomass rather than function. In the concluding chapter of this volume (Coleman et al., 1994) the need to explore the role of diversity and function in soil biota is reiterated. It is only recently that mycorrhizal ecologists have risen to that challenge and investigated the functional interactions of mycorrhizal communities on the same plant (Perry et al., 1989; Parladé and Alvarez, 1993; Reddy and Natarajan, 1997; van der Heijden et al., 1998a, b; Jonsson et al., 2001; Baxter and Dighton, 2001). Chu-Chou and Grace (1985) showed that radiata pine seedlings performed better in the presence of three ectomycorrhizal symbionts than with one. Similarly, two ectomycorrhizal species were found to produce larger host plants than one (Parladé and Alvarez, 1993; Reddy and Natarajan, 1997). The yield of competing Douglas fir seedlings was enhanced as the number of ectomycorrhizal partners was increased (Perry et al., 1989). Under low fertility situations in Sweden,

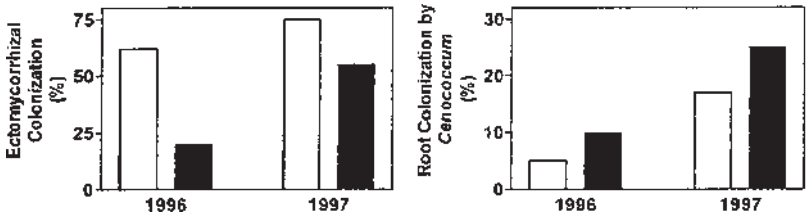

FIGURE 3.22 The effect of *Rhododendron* thickets (black bars) on the development of ectomycorrhizal colonization of hemlock tree roots (left) and the effect of the presence of *Rhododendron* on the abundance of *Cenococcum* mycorrhizae in (right). Data from Walker et al. (1999).

Jonsson et al. (2001) showed that the growth of birch trees was higher when they were associated with eight ectomycorrhizal species than comparable plants associated with single fungal species.

The efficiencies of different ectomycorrhizae to access nutrients from the soil were shown in the field by Dighton et al. (1990). Using radiotracer phosphorus, they were able to show that the uptake of phosphorus into the canopy of birch trees was significantly higher in the root zone colonized mainly by *Hebeloma* mycorrhizae, compared to *Lactarius* or *Laccaria*. (Table 3.16). By manipulating both the actual diversity and species composition of ectomycorrhizae on birch seedlings, Baxter and Dighton (2001) were able to demonstrate that changes in plant performance were related to the diversity per se of the ectomycorrhizal community they supported rather than the actual species composition of that mycorrhizal community. As the community of mycorrhizae increased, the proportional representation of each species declined, but the total number of mycorrhizal root tips per plant increased. In response to the increased mycorrhizal diversity, plant shoot biomass declined, but root biomass increased (Fig. 3.23). Using a stepwise multiple regression analysis, they showed, however, that changes in plant biomass (root and shoot) and plant phosphate content were significantly correlated with ectomycorrhizal diversity rather than the level of root colonization (Table 3.17). This suggests that there is some function to mycorrhizal diversity in that the interaction of ectomycorrhizal fungi on the same root system has an influence on plant performance rather than either the total level of mycorrhizal infection or the species composition of the mycorrhizal community. The study by Jonsson et al. (2001), however, suggests that the effects of mycorrhizal fungal diversity may depend on the context in which they exist. The community structure may be beneficial, detrimental, or neutral, depending on the nutritional conditions of the soil, plant age, or other factors, hence, Fitter (1985; 1991) says that it is not always obvious what the function of mycorrhizae is in a natural ecosystem but that

TABLE 3.16 Mean Phosphorus Uptake into the Canopy of Field-Grown Birch Trees in Relation to the Dominant Ectomycorrhizal Fungal Species Colonizing the Root into Whose Sphere of Influence Radiophosphorus Was Placed

Dominant mycorrhizal species	Phosphorus uptake per unit leaf weight ($ng\,P\,g^{-1}$)
Hebeloma	134
Lactarius	55
Laccaria	52
Other	79

Source: Data from Dighton et al. (1990).

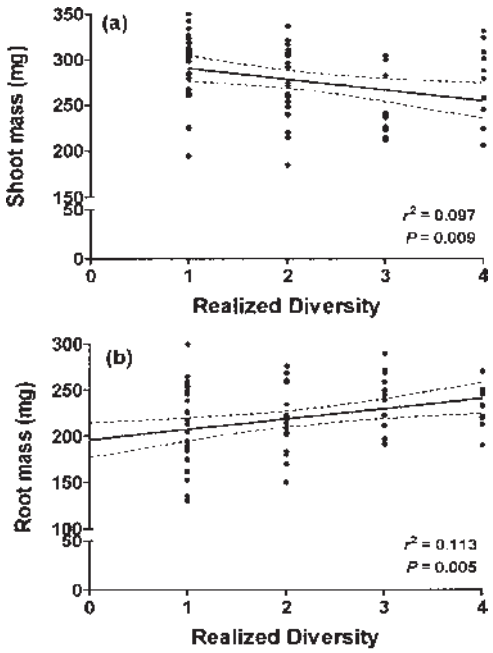

FIGURE 3.23 Effect of ectomycorrhizal species diversity on shoot and root growth of birch seedlings when inoculated with a random mixture of mycorrhizal fungal species, selected from a species pool. Data from Baxter and Dighton (2001).

a clear nutritional benefit accrues in an agricultural context. In his commentary on this work, Leake (2001) correctly points out that the study of Baxter and Dighton (2001) was conducted under laboratory conditions and that plant and fungal responses may be different in a more realistic field situation. These results, however, show how little we really understand of the complexities of fungal interactions and the role of diversity in the mycorrhizal community.

Cairney (1999) discussed the range of ectomycorrhizal species and their varied physiological functions, suggesting that we know relatively little about variation in the physiology of the few fungi that we have studied extensively in the laboratory, let alone the myriad of other species about which we know very little and especially of those fungi that we have yet to encourage to grow in culture. In addition, in their review article, Cairney and Burke (1996) cite examples of heterogeneity of the function of mycelia of the same ectomycorrhizal fungus as it exploits pockets of different resources in the soil. They suggest that this heterogeneity of function drives both the ability of

TABLE 3.17 Relationship Between Plant Growth Parameters and Either Ectomycorrhizal Fungal Diversity or Degree of Root Colonization by Ectomycorrhizal Fungi, Irrespective of Species, as Determined by Stepwise Multiple Regression Analysis

	Dependent variable	Step variable	R^2	P
Growth	Total mass	NS	—	—
	Shoot mass	Diversity	0.129	0.002
	Root mass	Diversity	0.156	<0.001
	Root: shoot	Diversity	0.224	<0.001
	Root length	Colonization	0.243	<0.001
Nutrients	Total N (mg)	NS	—	—
	Total N ($mg\,g^{-1}$)	Colonization	0.037	0.109
	Shoot N (mg)	NS	—	—
	Shoot N ($mg\,g^{-1}$)	Diversity	0.112	0.005
	Root N (mg)	NS	—	—
	Root N ($mg\,g^{-1}$)	Diversity	0.037	0.110
	Total P (mg)	Diversity	0.179	<0.001
	Total P ($mg\,g^{-1}$)	Diversity	0.177	<0.001
	Shoot P (mg)	Diversity	0.081	0.017
	Shoot P ($mg\,g^{-1}$)	Diversity	0.150	<0.001
	Root P (mg)	Colonization	0.115	0.004
	Root P ($mg\,g^{-1}$)	Colonization	0.074	0.023

Note: NS = step variable did not meet the 0.15 significance level for incorporation into the model.
Source: Data from Baxter and Dighton (2001).

ectomycorrhizae to exploit resources and enzyme expression, nutrient uptake, and translocation within the mycorrhizal system (Cairney, 1992).

Changes in the availability of photosynthate can also influence the mycorrhizal community and its function on the roots of host plants. Cullings et al. (2001) showed that the effect of defoliation of a mixed *Pinus contorta* (lodgepole pine)/*Picea engelmannii* (Engelmann spruce) forest in Yellowstone National Park was to alter the ectomycorrhizal species composition on the tree roots (Fig. 3.24). Lodgepole pine trees were defoliated to 50%, while Engelmann spruce were left untreated. There were no significant effects of defoliation on either ectomycorrhizal colonization (142.0 mycorrhizal tips/core in both defoliated and control plots) or species richness (5.0 species/core in controls and 4.5 in treatments). The ecosystem-dominant ectomycorrhizal species, *Inocybe* sp., however, was rare in defoliation plots, whereas both Agaricoid and Suilloid species were dominant in both the defoliated plots and the control plots. Ectomycorrhizal fungal species associating with both lodgepole pine and

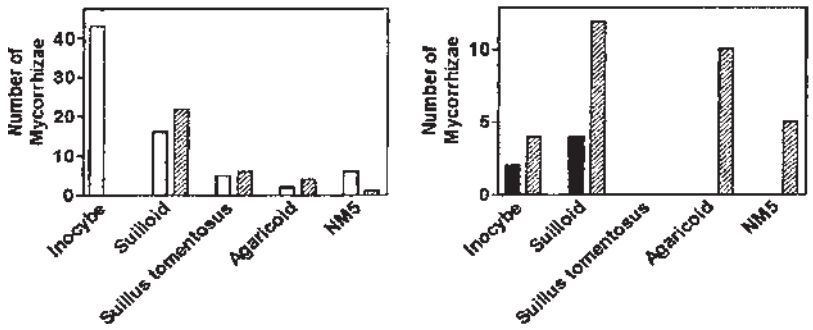

FIGURE 3.24 The effect of faunal defoliation (right column of each pair of bars) on the ectomycorrhizal community structure of lodgepole pine (*Pinus controrta*) [left] and Englemann spruce (*Picea engelmannii*) [right]. Data from Cullings et al. (2001).

Engelmann spruce were affected by defoliation, which suggests that changing the photosynthetic capacity of one species can affect the mycorrhizal associations of neighboring trees of a different species. A study of the effects of winter browsing of willow by elk (Peinetti et al., 2001) showed that browsing induces higher shoot biomass production but similar leaf biomass and leaf area per plant, a lower number but larger shoots, a lower number and bigger leaves, and flower inhibition. In addition to the changes in aboveground plant parts, they inferred that browsing induces lower allocation of resources belowground, resulting in higher soil N uptake. Although they did not discuss the effects of grazing on the mycorrhizal condition of the trees, it is apparent that the changes in resource allocation within the plant would place different demands on a mycorrhizal community colonizing the roots. Reduced carbohydrate allocation belowground would reduce the ability of the trees to support mycorrhizae, but the increase demand for nitrogen would require the presence of an active mycorrhizal flora. We know little about the influence of aboveground herbivory on the mycorrhizal status and activity of plants.

As we stated earlier, fungi do not exist alone in the environment. Especially in soil, mycorrhizal fungi are in close juxtaposition with a range of other fungi, bacteria, and fauna. The effect of fungi may thus be considerably affected by their interactions with these other organisms. The interaction between mycorrhizae and saprotrophs in litter decomposition is one example of an interaction that may alter the rates of decomposition, nutrient mineralization, and the ultimate fate of the nutrients released during the decomposition process. We have seen that many ectomycorrhizae have the capacity to act as decomposers. Gadgil and Gadgil (1971; 1975) first suggested that there could be strong interaction between mycorrhizal tree roots and the saprotrophic community in soil, in which

the presence of roots can suppress the rate of decomposition of leaf litter (Table 3.18). Berg and Lindberg (1980) repeated Gadgil and Gadgil's experiment in a northern coniferous forest and found the opposite effect—that the presence of tree roots did not influence the rate of leaf litter decomposition. In a laboratory study of controlled mycorrhizal inoculation of trees in the presence and absence of saprotrophic fungi, Dighton et al. (1987) showed that the presence of the saprotrophic fungus *Mycena galopus* reduced the decomposition potential of the ectomycorrhizal fungi *Suillus luteus* and *Hebeloma crustuliniforme*, which are associated with seedling pine roots. More recently, Zhu and Ehrenfeld (1996) revisited this argument in an oligotrophic forest system to show that the presence of roots increased the activities of saprotrophic fungi and soil fauna to increase the rate of leaf litter decomposition and nutrient mineralization. The nematode faunal population of rooted chambers was significantly enhanced. The difference in results among studies is probably related to the overall fertility of the soil and the relative dependence of the system on readily available or unavailable sources of nutrients. The balance between the relative abilities of the saprotrophic fungal community and the ectomycorrhizal community to effect leaf litter decomposition is also dependent upon the species composition of the two groups of fungi. Colpaert and van Tichelen (1996) showed that the decomposition of beech leaf litter is much less in the presence of Scots pine tree seedlings colonized by the ectomycorrhizal species *Thelephora terrestris, Suillus bovinus*, or *Paxillus involutus* than in the presence of the saprotroph *Lepista nuda* (Table 3.19). Indeed, nitrogen mineralization only occurred in the presence of *Lepista*. The authors suggest that ectomycorrhizal fungi are capable of effecting leaf litter decomposition (Durall et al., 1994) in the absence of a competing saprotroph, but that saprotrophic fungi are superior competitors for the organic resources and suppress the decomposing abilities of the ectomycorrhizal fungi. Lindahl et al. (1999) showed that the interaction between the ectomycorrhizal fungi *Suillius luteus* and *Paxillus involutus* and the wood decomposing saprotroph *Hypholoma*

TABLE 3.18 Effect of Combinations of Ectomycorrhizal Tree Seedlings and Saprotrophic Fungi on the Decomposition of Leaf Litter

Treatment	Dry weight of litter after 6 months (g)
Mycorrhizal plant + litter + saprotrophs	8.23
Nonmycorrhizal plant + litter + saprotrophs	7.60
No plant: + litter + saprotrophs	7.68
Mycorrhizal plant + litter	9.57
Nonmycorrhizal plant + litter	8.58

Source: Data from Gadgil and Gadgil (1975).

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TABLE 3.19 Weight of Beech Leaf Litter Remaining and Respiration per Unit Leaf Litter Weight After the Decomposition of 2 g Leaf Material in 26 Days in the Presence of Scots Pine Seedlings in the Absence (Control) or Presence of Ectomycorrhizal Associates *Thelephora terrestris* or *Suillius bovinus* or in the Presence of the Saprotrophic Basidiomycete *Lepista nuda*

Fungus	Litter dry weight (g)	Decomposition constant (k)	Litter respiration ($mg\,CO_2\,d^{-1}\,g^{-1}$)
Control	1.51	0.12	2.0
Thelephora terrestris	1.48	0.15	4.5
Suillius bovinus	1.39	0.22	11.0
Lepista nuda	0.92	1.00	14.0

Source: Data from Colpaert and Van Tichelen (1996).

fasciculare resulted in a net transfer of phosphorus from the saprotroph to the mycorrhizal fungi. This suggests a positive synergistic activity of the mycorrhizae, which can more readily absorb and translocate away mineral nutrients derived from the activity of a saprotroph than the saprotroph itself can (Table 3.20). The authors show that up to 25% of the P present in the mycelium of the saprotroph is captured by the mycorrhizal fungi and translocated to the host tree within 30 days, whereas the reciprocal transfer of phosphorus was three orders of magnitude lower. The interaction between these different functional groups of fungi is still far from clear, however. As Singer and da Silva Araujo (1979) state, the differences in the dependence of tropical forest trees on

TABLE 3.20 Partitioning of Radiophosphorus Label Applied Either to Wood That Was Being Decomposed by *Hypholoma fasciculare* or to Scots Pine Seedlings Colonized by Either *Paxillus involutus* or *Suillus variegates* Mycorrhizae.

		Partitioning of ^{32}P	
Application of label	Site of label measured	*Paxillus*	*Suillus*
Hypholoma labeled	Fraction outside wood block	8	7
	Fraction in plant	12	14
	Fraction in plant shoot	29	15
Mycorrhiza labeled	Fraction outside plant	24	22
	Fraction in wood	0.09	0.15

Note: The data show greater transfer of phosphorus from the decomposing wood to the plant than from the plant to the wood.
Source: Data from Lindahl et al. (1999).

ectomycorrhizae rather than arbuscular mycorrhizae may be linked to the ability of the ectomycorrhizal associates to effect leaf litter decomposition. They showed that in a white podsol campinarana soil trees were obligatorily ectomycorrhizal where there were large accumulations of raw humus and low rates of leaf litter decomposition. In contrast, in trees in a latisol-terra-firma soil, in which the rate of leaf litter breakdown and mineral nutrient availability are much higher, the fungal community is dominated by saprotrophs, and the trees are primarily associated with arbuscular mycorrhizae.

Evidence from natural abundance isotopic ratios, however, suggests that there may not be much direct competition between saprotrophic and ectomycorrhizal fungi for either nitrogen or carbohydrates (Hobbie et al., 1999). By analyzing the $\delta^{15}N$ and $\delta^{13}C$ values of fruit bodies of mycorrhizal and saprotrophic fungi, vegetation, and soils from both young, deciduous-dominated and older, coniferous-dominated forest sites, they showed that mycorrhizal fungi had consistently higher N values and consistently lower C values than saprotrophic fungi. Foliar $\delta^{13}C$ values were always isotopically depleted relative to both fungal types (Table 3.21). It is suggested that isotopic fractionation by mycorrhizal fungi during the transfer of nitrogen to plants may be due to enzymatic reactions in the fungi that produce isotopically depleted amino acids, which are passed on to the host plant. The authors thus maintain that the mycorrhizal associations of the trees maintain a higher level of $\delta^{15}N$ enrichment in the plant because of the changes exerted by the mycorrhizal fungus. Enriched carbon signatures of mycorrhizal fungi compared to those of foliage may be due to the fungal use of such isotopically enriched photosynthates as simple sugars, in contrast to the mixture of compounds present in decomposing leaves.

TABLE 3.21 Variation in the Nitrogen and Carbon Stable Isotope Signatures of Various Component Parts of a Mixed Forest Ecosystem Showing the Differences in Signatures Between Ectomycorrhizal and Saprotrophic Fungi

		$\delta^{15}N$ (λ)	$\delta^{13}C$ (λ)
Fungi	Mycorrhizae	4.2	−25.6
	Saprotrophs	−1.3	−22.6
Plant parts	Alder leaves	−1.3	−29.7
	Spruce leaves	−3.7	−28.8
	Fine roots	−2.0	−27.5
Soil an soil nitrogen	Mineral soil	6.0	−25.6
	Organic soil	0.6	−27.5
	Ammonium–N	−0.7	
	Nitrate–N	−0.1	

Source: Data from Hobbie et al. (1999).

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These methods provide interesting information on the rates of transfers of nutrients and carbon within the ecosystem, but the details of the transfers (sources and sinks) and transfer rates (source and sink strengths) are currently a major focus of research.

In addition to interactions among ectomycorrhizal fungi and saprotrophic fungi in soil, there has been shown to be close associations of these mycorrhizal fungi and bacteria within the rhizosphere. In his reviews, Garbaye (1991; 1994) discusses that importance of these so-called helper bacteria (Garbaye and Bowen, 1987; 1989; Duponnois and Garbaye, 1990; 1991; Fitter and Garbaye, 1994). It is suggested that these bacteria assist in the fungal/plant recognition system (Duponnis, 1992), receptivity of the host root to the mycorrhizal fungus and enhancement of the mycorrhizal fungal mycelial growth (Duponnois and Garbaye, 1990; Garbaye and Duponnois, 1992) prior to root colonization, alteration of the rhizospheric soil by altering pH, production of ion-complexing compounds (siderphores) and the nutrient balance (Wallander and Nylund, 1991), and germination of fungal propagules (Ali and Jackson, 1989), which is probably most important in arbuscular mycorrhizae (von Alten et al., 1993). The main ecological implication of these helper bacteria, however, is to enhance the rate of root colonization, assist in the acquisition of nutrients by the production of enzymes, and to complex ions that help to detoxify soil for plant growth. In addition, there are synergistic interactions among mycorrhizae and other bacteria in soil, particularly root nodulating and free-living, nitrogen-fixing bacteria (Barea et al., 1997). These associations are particularly important in agroecosystems, in which the sustainability of soil fertility is of prime importance. The actual variation in the species composition of bacteria around ectomycorrhizal roots in the field, however, is largely unknown. New methods for the identification of these communities (Mogge et al., 2000), together with more information about the physiological attributes of these bacteria, such as phosphate solubilization (Berthelin and Leyval, 1982; Leyval and Berthelin, 1983; Singh and Kapoor, 1998), will allow us a greater understanding of the ecological and ecosystem processes that accrue from these close associations among mycorrhizae and bacteria.

Although there is a large body of information showing that different species of trees associate with different communities of ectomycorrhizae, there is less information on the host plant/arbuscular mycorrhizal species specificity. It is generally thought that there is low specificity; however, Eom et al. (2000) showed that after 4 months of growth there were significantly different arbuscular mycorrhizal communities developing under different component plant species from a tallgrass prairie (Fig. 3.25).

Barni and Siniscalco (2000) investigated the changes in arbuscular mycorrhizal colonization of roots of plants in a vegetation succession following agricultural disturbance. They compared the mycorrhizal associations of

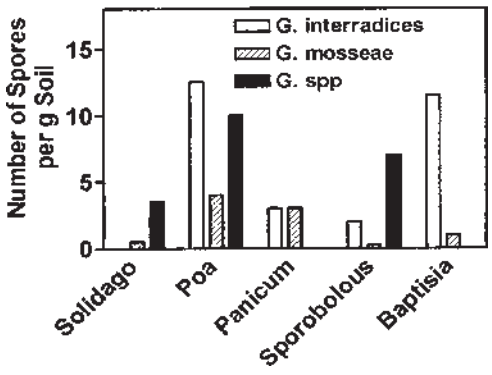

FIGURE 3.25 Mean spore densities of arbuscular mycorrhizal fungi *Glomus interradices*, *G. mosseae* and *Glomus* spp. indicating differences in the mycorrhizal community structure on roots of five plant species (*Solidago missouriensis*, *Poa pratense*, *Panicum virginiatum*, *Sporobolus heterolepis* and *Baptisia bracteata*). Data from Eom et al. (2000).

the component plant species in an agricultural field with fields abandoned for up to 3 years, supporting ruderal vegetation, a grassland, shrubland, and early successional and late successional woodlands. They showed that shortly after agricultural field abandonment, the ruderal vegetation was composed primarily of annual species, which were largely nonmycorrhizal. After 2 to 3 years more perennials were recruited into the community and most plant species had arbuscular mycorrhizal symbionts as droughting became more of a problem and available nutrients in soil were reduced. It was only at the later stages of woodland establishment that the arbuscular mycorrhizae were displaced by ectomycorrhizae, where both a change in plant host species and accumulation of organic plant residues in the woodland phase, led to a dominance of ectomycorrhizae, which have the ability to utilize organic forms of nutrients.

3.2.5 Mycorrhizae in Aquatic and Estuarine Ecosystems

Fungi are essentially aerobic organisms, and their physiological functions are inhibited by inundation with water. Waterlogged soils are generally anoxic except at the water–soil interface at the soil surface. In these conditions, iron, sulfur, and manganese compounds may be produced by the anaerobic bacterial communities, and together with the reduction in oxygen availability, reduce root and mycorrhizal growth (Khan and Belik, 1995). Gadgil (1972) demonstrated that a short period of inundation (7 weeks) reduced the phosphate uptake by radiata pine and Douglas fir, but that both P uptake and succinic dehydrogenase

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activity of the mycorrhizae was negligible after 14 to 16 weeks of waterlogging conditions. Khan (1993) showed that as one moved from plants growing in water up the stream bank, roots of the tree *Casuarina cunninhamiana* became increasingly colonized by arbuscular and ectomycorrhizae. It can thus be inferred that the physiological function of mycorrhizae on trees is reduced under waterlogging conditions as mycorrhizal colonization of the root system is impaired.

Mycorrhizal fungi, however, are able to survive and successfully colonize plants growing in aquatic and salt marsh ecosystems. Both Khan and Belik (1995) and Cooke and Lefor (1998) report that approximately 50–100% of plants found in aquatic or developing shorelines (respectively) shared arbuscular mycorrhizal colonization of their root systems. Miller (2000) showed that semiaquatic grasses had reduced root colonization by arbuscular mycorrhizal fungi as water depth increased, but that some level of mycorrhizal infection was present in most of the samples, even at the highest levels of inundation. Water depth was the major controlling factor of the mycorrhizal colonization of the two grass species studied (*Panicum hemitomon* and *Leersia hexandra*), compared with the difference among plant species and the water depth-plant species interaction. White and Charvat (1999) investigated the phosphorus interactions in an emergent aquatic plant (*Lythrum salicaria*) and mycorrhizal colonization of roots. Arbuscular mycorrhizal colonization of the roots increased significantly with increasing phosphate levels in water until a threshold of 1000 μg PO_4 l^{-1} was exceeded, after which mycorrhizae did not form (Fig. 3.26). It is interesting that mycorrhizal infection did not have a positive effect on total plant biomass at low levels of P availability, but significantly reduced plant growth at the highest level of phosphate addition (47.5 mg PO_4 l^{-1}, at which no mycorrhizae were seen to develop. At intermediate levels of P availability, however, mycorrhizal

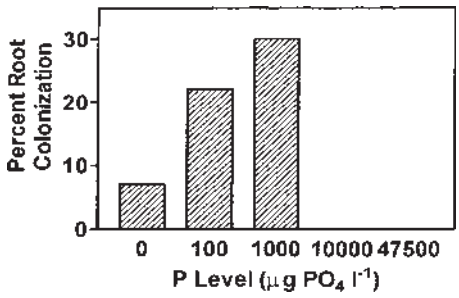

FIGURE 3.26 Arbuscular mycorrhizal colonization of roots of the emergent aquatic plant *Lythrum salicarina* in hydroponic sand culture at different levels of P supply. Data from White and Charvat (1999).

colonization increased the rate of root growth over that of shoot biomass, thus increasing the root:shoot ratio (Fig. 3.27).

Mycorrhizae are known to exist in salt marshes around the globe (Rozema et al., 1986; van Duin et al., 1989; Sengupta and Chaudhuri, 1990; Hildebrandt et al., 2001, including marshes along the East Coast of the United States (Cooke et al., 1993; Hoefnagels et al., 1993). Within salt marsh plant communities, the colonization of roots by arbuscular mycorrhizae appears to be species-dependent. Consistent reports indicate that species such as *Spartina alterniflora* are nonmycorrhizal, whereas *S. cynosuroides* is frequently mycorrhizal (Hoefnagels et al., 1993; Cooke and Lefor, 1998). *Spartina alterniflora* and *S. cynosuroides* are similar in growth form and both grow in intertidal marsh elevations on the East Coast. *Spartina alterniflora* is a dominant grass in high-salinity marshes, while *S. cynosuroides* is a dominant grass in brackish marshes (Smith and Read, 1997), but they do overlap in their tolerance of brackish water (Parrondo et al., 1978; Stribling, 1998). A variety of factors affect the degree of root colonization by these fungi. Using ergosterol as an indicator of fungal colonization in roots, fungi in living roots of *Spartina* spp. were confirmed in both North Carolina (Padgett and Celio, 1990) and New Brunswick, Canada (Mansfield and Bärlocher, 1993). Both studies found that the greatest fungal biomass coincided with periods of active root growth. The degree of mycorrhizal colonization in salt marshes is known to vary with season. van Duin et al. (1989) showed that the greatest level of colonization occurred during the summer months when plants were growing maximally. Mansfield and Bärlocher (1993) suggested that fungal activity may depend to some extent on the availability of young feeder roots for colonization by mycorrhizal fungi and influence both in intensity and formation of specific fungal structures (Cooke et al., 1993; Brown and Bledsoe, 1996; Hildebrandt et al., 2001). This variation in

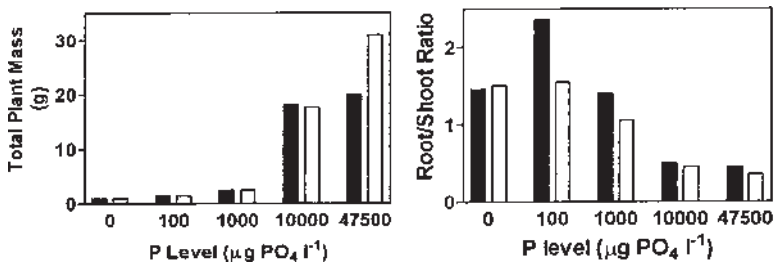

FIGURE 3.27 Total plant mass (left) and root:shoot ratio (right) of the emergent aquatic plant *Lythrum salicarina* with (solid bars) and without (open bars) arbuscular mycorrhizal inoculum grown in hydroponic sand culture at different levels of P supply. Data from White and Charvat (1999).

degree of mycorrhizal colonization could be the cause of reports of nonmycotrophy in *S. alterniflora* and other species. Also, this increase in root colonization during times of maximal plant growth suggests a link between the depletion of readily available nutrients and the development of mycorrhizae in an effort to increase efficiency of scavenging for scarce resources. Cooke and Lefor (1990) showed that the establishment of vegetation on a disturbed salt marsh was negligible in the absence of mycorrhizal inoculation, suggesting that disturbance factors remove residual inoculum from the sediments.

There appears to be little information on the role of arbuscular mycorrhizal association with salt marsh plants, however. In a waterlogged pioneer zone, Brown and Bledsoe (1996) found that mycorrhizal colonization of *Jaumea carnosa* roots was significantly reduced at a higher elevation than in the channels or marine sites, but that the degree of colonization was not related to redox potential. The degree of root colonization appeared to be related to the higher levels of nitrogen in the sediments of the channels and creeks, however, in which faunal activity increased sediment aeration and plant litter decomposition. In agricultural soils, Juniper and Abbott (1993) found that soil salinity reduces the germination of arbuscular mycorrhizal spores and reduces hyphal growth, but there is no reason to suspect that this will not be the case in salt marsh ecosystems.

The benefits and costs to plant and fungal partners and the biological and edaphic factors controlling the functioning of salt marsh mycorrhizae are poorly understood (Brown and Bledsoe, 1996). In many salt marsh ecosystems, it is phosphorus rather than nitrogen that is generally recognized as the primary limiting nutrient (Valiela and Teal, 1974). This provides a possible explanation for the evolution of a close association of salt marsh plants and arbuscular mycorrhizae for the purpose of enhancing P acquisition. In conducting a nitrogen- and phosphorus-enrichment experiment in Louisiana, Buresh et al. (1980) found that plants fertilized with phosphorus had increased phosphorus content. The enhanced plant phosphorus content was considered "luxuriant," as no growth increase was observed, but perhaps the increased phosphorus benefited other aspects of plant fitness. In the same study it was determined that only a limited amount of phosphorus was apparently available to *S. alterniflora*, because in nitrogen-enriched areas increased growth successively led to decreased phosphorus content in plants. Other studies have reported initial increases in mycorrhizal colonization as phosphorus availability increased and then subsequent decreases in colonization as phosphorus concentrations continued to increase (Johnson, 1998; White and Charvat, 1999). In a recent study in the greenhouse under different periods of artificial tidal inundation, high and low salinity, the addition of phosphorus, and the presence and absence of mycorrhizal inoculum, McHugh (2001) showed that mycorrhizal colonization of *Spartina alterniflora* was much less than in *S. cynosuroides*. The hyphal

colonization of root of *S. alterniflora* was reduced in higher saline conditions, but a similar decrease was not found in the abundance or arbuscules of *S. cynosuroides* in this study or in another study involving a mycorrhizal halophyte (Allen and Cunningham, 1983). There were few differences in the level of mycorrhizal colonization of roots with effective depth (duration of inundation) for either species, but although Cooke et al. (1993) found vesicles in roots of salt marsh species *Spartina patens* and *Distichlis spicata* down to 42 cm in depth, arbuscules were only found to a depth of 37 cm, with a significant reduction in abundance below 25 cm. McHugh and Dighton also found no effect of mycorrhizal inoculum on the shoot biomass or P content of either plant species; however, mycorrhizal colonization of the roots of *S. cynosuroides* increased the total amount of nitrogen assimilated by the plant (Fig. 3.28). In both species, however, inoculation resulted in more shoots per pot, or increased tillering. Increased tillering resulting from mycorrhizal colonization has been observed in dune grass (Gemma and Koske, 1997) and wetland rice (Solaiman and Hirata, 1998) and could serve a useful function of significantly enhancing rates of lateral spread in field plantings and subsequently affect rates of soil stabilization in restoration projects. Jasper (1994) suggests that mycorrhizae are important in revegetation projects by (1) enhancing plant establishment through improved nutrition, (2) maintaining diversity and altering plant competitive fitness, (3) contributing to the recycling of resources and increasing ecosystem stability, and (4) stabilizing soil.

Hyde et al. (1998) suggest that there is some evidence that the presence of mycorrhizae enhances oxygen uptake by the host plant and thus improves its

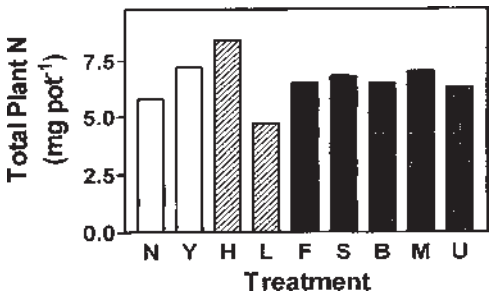

FIGURE 3.28 Effect of arbuscular mycorrhizal infection on shoot nitrogen content of plants of ***Spartina cynosuroides***. Experimental conditions were: mycorrhizal infection (clear bars; **N** = un-inoculated, **Y** = inoculated) added phosphorus (hatched bars; **H** = 3.10 mg PO_4-P/l, **L** = 0.31 mg PO_4-P/l) water salinity (solid bars; **F** = no salt added, **S** = 7 ppt salt) tidal inundation (stippled bars; **B** = bottom level, **M** = middle level, **U** = upper level). Data from McHugh and Dighton (unpublished).

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resistance to salt. This evidence is supported by the work of Rozema et al. (1986). They showed that the sodium concentration of shoots of mycorrhizal *Aster tripolium* was lower than nonmycorrhizal plants when grown in 300 mm NaCl. In their study, however, there was a positive effect of mycorrhizal colonization of host plant growth, so the reduction in sodium content could have been due to dilution in the increased plant biomass.

3.2.6 Interplant Linkages: Competition Vs. Synergism

In the 1960s Bjorkman (1960) discovered that by injecting radioactive carbon into the stem of a pine tree he could detect the isotope in an adjacent *Monotropa* plant. *Monotropa* is an achlorophyllous plant that was thought to be parasitic on the roots of trees, as it could not manufacture its own carbohydrates by photosynthesis. He also noted that there were ectomycorrhizal associations of the roots of both the *Monotropa* plant and the tree. He therefore suggested that there could be a carbohydrate exchange between plants by the mycorrhizal connection between them. The concept of interconnectedness of plants within the ecosystem by mycorrhizal bridges has been a subject of research that has been dotted with examples of inconclusive results and skepticism. More recently however there have been a number of good research projects that have shown the presence of interplant transfer of both carbon and nutrients between plants connected by mycorrhizal "bridges". Subsequent to Bjorkman's work, Read et al. (1985) demonstrated that the ^{14}C label applied to pine tree seedlings was preferentially transferred to neighboring unlabeled pine trees seedlings rather than to neighboring plant species associated with arbuscular mycorrhizae. From this finding, they suggested that there was strong evidence that there was movement of carbon between the donor plant (labeled with the ^{14}C isotope) and the recipient plants that shared the same ectomycorrhizal associations. The study of Finlay and Read (1986a, b, c) showed unidirectional transfer of phosphorus from the ectomycorrhizal mycelium into the host tree, but no translocation from a radio-labeled host tree into adjacent unlabeled trees. This suggests that the interplant transfer of nutrients may depend upon the strengths of sources and sinks of nutrients in the whole system. In the experimental chambers used for this study, it was assumed that there was little difference in source and sink strengths among neighboring plants but a general demand for phosphorus by all plants growing within the chambers.

At around the same time, interest was raised regarding the possibility of plants exchanging nutrients in the same way—via mycorrhizal bridges. Heap and Newman (1980a, b) provided evidence that there could be transfer of phosphorus among plants of the same species, in cases in which their roots were interconnected

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by the same arbuscular mycorrhizal fungus. They also showed that there could be transfer among different plant species (*Lolium* and *Plantago*) by the same mechanism. In their study of radiocarbon movement between longleaf pine (*Pinus palustris*) trees and the understory species of spiderwort (*Tradescantia hirsutiflora*), however, Taber and Taber (1984) suggested that it was the very close juxtaposition between the roots of both plant species that allowed rapid transfer of carbon from the pine tree to the spiderwort rather than a mycorrhizal mechanism. Newman and Eason (1989) continued with the idea of transfer of nutrients among plants, suggesting that this transfer might be more ecologically meaningful if there was a physiological reason to induce the transfer. They suggested that the transfer would be greater if one of the plants in the pair were undergoing senescence and, in order to conserve resources elicited a net transfer of nutrients from the dying plant root system to adjacent roots of live plants through mycorrhizal connections. This is analogous to the idea of differences in source and sink strengths outlined above. The dying roots act as a source of nutrients and carbon, while the growing plants act as nutrient and carbon sinks. Indeed, the results of Newman and Eason (1989) demonstrated a net flux of phosphorus from dying roots of *Lolium perenne* to living roots of *Plantago lanceolata*, which both have the ability to form arbuscular mycorrhizal associations. There was no net transfer of phosphorus to cabbage (*Brassica oleracea*), however, which does not form mycorrhizae (Fig. 3.29). In a similar series of experimental studies, Eason et al. (1991) showed that there was greater transfer of phosphorus among plants associated with the same mycorrhizal type (arbuscular mycorrhiza to arbuscular mycorrhiza) than there was among mycorrhizal types (arbuscular mycorrhiza to ectomycorrhiza), although the magnitude of this effect was species-specific.

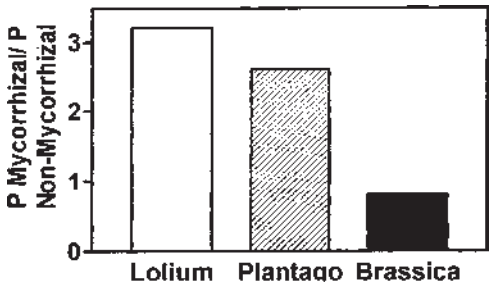

FIGURE 3.29 Ratio between ^{32}P in mycorrhizal plants over ^{32}P in non-mycorrhizal plants in experimental situations where ^{32}P has been applied to a dying plant in a pair of plants that could be connected by arbuscular mycorrhizal fungi. The data show significant interplant transfer of phosphorus for both *Lolium* and *Plantago*, that form mycorrhizae, but not to *Brassica*, which is a non-mycorrhizal plant species. Data from Newman and Eason (1989) with kind permission of Kluwer Academic Publishers.

Similarly, Carleton and Read (1990) showed that there could be transfer of phosphorus and carbon between pine trees and feather moss (*Pleurozium schreberi*) communities in the understory over distances of several centimeters, because of the interconnecting ectomycorrhizal fungi.

The significance of interplant transfers of carbon and nutrients have been explored in the review articles of Amaranthus and Perry (1994), Read (1998), and Rayner (1998). Amaranthus and Perry (1989) showed that when Douglas fir was planted into partially cleared sites (containing remnant ectomycorrhizal plant hosts) the survival of the planted trees was around 90%. Where trees were planted into totally cleared areas (no remnant ectomycorrhizal plant hosts) plated tree survival after 2 years was only 50%. They attributed the reduction in survival to the lack of a viable, communal ectomycorrhizal network into which the new trees could connect. They suggested that this network provided greater stability of the system, allowing carbon and nutrient exchange to take place among connected plants, and especially allowing new recruits to be able to access a larger pool of nutrients and carbon than they would be able to on their own. This synergistic activity among surviving mature plants and recruits into the ecosystem would allow both greater ecosystem stability and greater continuity of the species composition of the ecosystem following disturbance. It has only been recently, however, that the direct net transfer of carbon or nutrients has actually been demonstrated in the field rather than in laboratory or greenhouse conditions. To that end, Simard et al. (1997a,b,c) were able to show transfer of carbon from paper birch (*Betula papyrifera*) to Douglas fir (*Pseudotsuga menziesii*) in both partial and deep shade (Fig. 3.30). They showed that the amount of carbon transferred

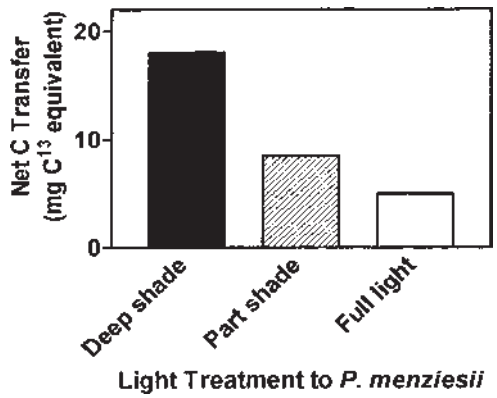

FIGURE 3.30 Carbon transfer from birch to Douglas-fir seedlings through ectomycorrhizal connections in the field, where the fir trees were subjected to various degrees of shading. Data from Simard et al. (1997).

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between plants could form a significant proportion of the carbon contained in the shoots (13% for *P. menziesii* and 45% for *B. papyrifera*), which they suggest could considerably supplement photosythetically derived carbon in the plant. Indeed, Wu et al. (2002) have shown that some 24% of ^{14}C label occurring in the underground parts of pine seedlings was allocated to the extraradical hyphal component of their ectomycorrhizal association. Also, the trenching experiments of Simard et al. (1997a) show the importance of maintaining an intact community of mycorrhizae in the forest for seedling trees to connect to. In their trenched plots, Douglas fir seedlings planted into a birch-dominated community had approximately half the diversity of mycorrhizal fungi associated with their roots than counterparts planted into untrenched plots in the same forest. The increased mycorrhizal diversity in untrenched plots significantly increased the photosynthetic capacity of the Douglas fir seedlings compared to that of seedlings in trenched plots, although no significant increase in biomass was evident.

Within arbuscular mycorrhizal communities, there is information suggesting that these interplant connections may be important in determining the coexistence of plants in the community. Walter et al. (1996) demonstrated interplant transfer of phosphorus in tallgrass prairie communities. They showed that the amount of phosphorus transferred from donor to recipient plant was species-dependent and decreased with increasing distance among neighboring plants. The transfer among plants was greater within forbs and cool season C_3 grasses than in C_4 grasses (Fig. 3.31), suggesting that there is some selectivity in the process of interplant transfer. This difference between plant groups may

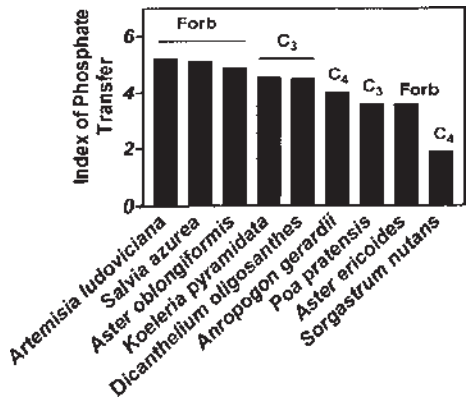

FIGURE 3.31 Index of phosphorus transfer from radioisotopically labeled donor plant (*Andropogon gerardii*) to the shoots of neighboring plant species in a tallgrass prairie community. Data from Walter et al. (1996).

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confer an advantage to those plants that are capable of greater interplant transfers than plants with lesser abilities. Although the authors included a benomyl treatment to reduce the degree of mycorrhizal infection, the effect of this fungicide did not alter rates of transfer of phosphorus. No measures of mycorrhizal infection were made, however, except to say that mycorrhizae were seen even in the presence of benomyl, so it is suggested that the close juxtaposition of roots may be the mechanism for interplant nutrient transfer as much as mycorrhizal bridges. Ronsheim and Anderson (2001) examined the influence specificity of the plant–arbuscular mycorrhizal association on intraspecific interactions in *Allium vineale*. By surrounding a target plant with genetically identical neighbors, neighbors from the same population, or neighbors from a different population, they could evaluate the effect of the presence or absence of a soil fungal community. Overall, the presence of a soil fungal community dominated by mycorrhizal fungi was beneficial for plant growth, especially if the neighbors were genetically identical or from the same population as the target plant. There is thus specificity in the interaction between *A. vineale* plants and the soil fungal community at the population level. Such specificity favors intraspecific interactions among plants from the same population. These findings lend support to the hypothesis that plants from the same population are able to share a more efficient hyphal network than if the individual plants were to stand alone. In contrast, Ikram et al. (1994) found no transfer of nitrogen or phosphorus among the arbuscular mycorrhizal legume, *Pueraria phaseoloides*, and the rubber tree *Hevea brasiliensis*. They suggest that the improvement in growth of the plant mixtures probably results from an increase in the rate of decomposition and mineralization of legume plant residues rather than from any direct link between the roots of the legume and rubber trees.

We therefore have some information suggesting that plants can exchange both carbon and nutrients via mycorrhizal bridges connecting the root systems of adjacent individual plants. The ecological significance of this is that there is a greater likelihood that the community structure and existence will be maintained during periods of stress or disturbance—an example of ecosystem homeostasis. The ability of mature trees in a forest to act as nurse trees for seedling recruitment by the passage of photosynthate, and possibly nutrients to young trees growing in suboptimal light conditions, suggests a mechanism for maintaining forest cover in the event of death of the mature canopy trees. Given that many temperate forest ecosystems are dominated by ectomycorrhizal fungi and that tree growth is highly dependent upon the rate of mineralization of nutrients from a largely organic pool of nutrients, the interconnectedness of the forest through mycorrhizal bridges will optimize nutrient retention within the plant community and maximize the nutrient capture through decomposition or organic residues by ectomycorrhizal fungi or their interaction with saprotrophs (Lindahl et al., 1999). F. A. Smith and S. E. Smith (1996) look upon the carbon drain from the host plant

to the mycorrhizal fungus as a complex phenomenon in which the degree of carbon exchange may exceed the value of the fungal association to the host plant. They refer to the mycorrhizal fungus as being a "cheater" in cases in which the carbon drain is increased to the fungal partner under conditions of stress or under high levels of nutrient (P) availability, the hyphal growth appears to be out of the control of the root, and the fungus tends to show signs of pathogenicity. They also discuss the link among plants by mycorrhizal bridges as being a form of "cheating," but this can be interpreted differently as supporting cooperative links among plants, and improving overall fitness of the species. It is obvious that this is an area in which we know little of the spatiotemporal distribution of source-sink strengths for carbon and nutrients in complex ecosystems, where at one point in space and time the mycorrhizal symbiosis may be of great economic benefit to the host plant and at another the exact same interaction may have a different function, possibly even a parasitic one. In a grassland/forb ecosystem, the interplant transfer of nutrients may be species-specific. This condition may be an evolutionary strategy to defend the community against invasion by alien species, which cannot readily form interspecific plant linkage with the native community. The ecological and ecosystem consequences of these interplant connections have not been fully explored and much of the hypotheses suggested here are mere speculation. Evidence is nevertheless accumulating to prove that the transfer of nutrients and carbon can occur between plants of different species, suggesting that we must rethink our concepts of plant competition being the driving force determining plant community composition.

To further complicate understanding of the interconnectedness of plant root systems by mycorrhizal fungi, we can explore the discreteness of the categories of mycorrhizal types that exist. Recently there have been suggestions that plants of different taxonomic groups may not have distinct mycorrhizal symbionts, but that they may indeed, share mycorrhizae. For example, Lodge and Wentworth (1990) cite the reports of Read et al. (1977) and Chilvers et al. (1987), in which there is displacement of arbuscular mycorrhizae by ectomycorrhizae on *Alnus, Heliathemum*, and *Eucalyptus* with increasing age of tree. In their own work, Lodge and Wentworth (1990) showed that ectomycorrhizae displaced arbuscular mycorrhizae on *Populus* and *Salix* with increasing soil moisture content. Largent et al. (1980), Dighton and Coleman (1992), and J. E. Smith et al. (1995) have indicated that different mycorrhizal types may occur of the same plant species. The studies demonstrated that *Rhododendron* spp. (members of the Ericales) can support both ericoid- and ectomycorrhizal symbioses. If this is more widespread in forested systems, in which the ericaceous community form an understory shrub community in coniferous and mixed forests, there is a greater chance of not only interconnectedness among plants of the same species, but also among plants of different species and functional groups. With the information we have outlined above, regarding the potential role of ericoid mycorrhizae mineralizing nitrogen

from organic resources on the forest floor and the wider role of ectomycorrhizae in mineralizing phosphate as well as nitrogen and having a greater diversity of functional groups to optimize mineral nutrient resources, the ability of these plants to translocate nutrients and carbon among these functional groups of plants could alter the way in which we conceive competition among plants in a forest community. As the ericaceous plants form an understory community, they grow in shaded conditions. It may be that at certain times their photosynthesis is unable to keep pace with their demand and benefit may be derived from carbon translocated from adjacent canopy tree species through mycorrhizal connections. Such a time could be conceived to occur after a ground fire, where the aboveground component of the ericaceous community is temporarily damaged and resprouting is dependent upon belowground carbon reserves. It could thus be envisioned that the plant community evolved as a whole rather than by competition among its component parts. J. E. Smith et al. (1998) showed that *Pseudotsuga menziesii* seedlings could develop arbuscular mycorrhizal associations with *Glomus intraradices* when grown in conjunction with the grass *Calamagrostis rubescens*. Growth of *A. menziesii* and nutrient content, however, was significantly reduced when grown with the grass, but this was partly compensated for by the development of arbuscular mycorrhizae in the roots of the tree seedlings. This suggests that the interaction among mycorrhizal types on the same host is dependent upon the environmental conditions and the balance among competitive and synergistic interactions. There appears to be no simple interpretation of the limited data on these interactions; it is only by continued study of the functional ecology of the plant/mycorrhizal system that the large-scale functional aspects of the role of fungi in the ecosystem will be elucidated.

3.3 THE ROLE OF FUNGAL PATHOGENS IN PLANT PRIMARY PRODUCTION

The degree of impact of a fungal pathogen on its host plant depends on the fungal species and the environmental conditions in which the plant is grown. In many cases the intensity effect is increased when plants are grown in suboptimal conditions and are already under some stress. Burdon (1993) categorizes plant pathogens as (1) ***castrators***, who have a highly significant effect on plant fecundity by affecting flowers and seed development but little effect on vegetative growth; (2) ***killers***, who cause wilting and damping off of seedlings, and (3) ***debilitators***, who cause lesions or chronic infections. In terms of reducing primary production, all forms of pathogens can be significant, but their mode of effect is different and the occurrence of each type may depend upon the phenology of the host plant.

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The most classic examples of significant reduction in plant performance due to fungal pathogen attack have been seen in the devastating potato blight in Ireland during the 1840s (Austin Bourke, 1964), oak decline in Europe (Brasier, 1996), and chestnut decline in North America (Anangostakis, 1987). Most of these fungal diseases were either introduced or infected exotic plant species, however. The movement of plant and fungal species throughout the world is posing a serious threat to natural ecosystems (Rossman, 2001; Brasier, 2001). The problem of discerning the effects of fungal pathogens in natural ecosystems and plant communities is much more difficult and is similar to the problem outlined above for the function of mycorrhizal fungi. The effects of these pathogens may be small or only occur at specific times of the year, making the effects of these fungi much less obvious than the introduced pathogens, pathogens on exotic plant species, and particularly those pathogens that attack our monospecific plantations of crop plants. The literature on the effects of fungal pathogens on crop plant species is immense and beyond the scope of this book. I will refer the reader to the journals that specialize in reporting these data, such as *Phytopathology*, *European Journal of Pathology*, and *Plant Disease*.

The reduction in plant performance as a result of fungal pathogen attack can be shown by the work of Alexander and Mihail (2000). Here the forage plant *Kummerowia stipulacea*, which has become naturalized in parts of the United States was grown in soil, microwave sterilized soil, and sterilized soil inoculated with the damping-off fungus *Pythium* spp. Both plant density and plant biomass were significantly reduced by the presence of the fungal pathogen (Fig. 3.32).

One effect of foliar pathogens is to reduce the photosynthetic capacity of the host plant. Given that mycorrhizal fungi are dependent on a carbon supply

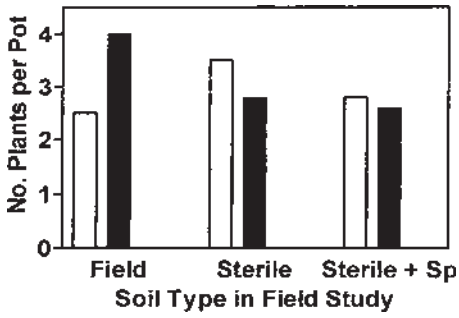

FIGURE 3.32 Number of plants and plant biomass of *Kummerowia stipulacea* in the presence and absence of the plant pathogen *Pythium* in field soil, soil sterilized by microwaving and sterile soil amended with fungal pathogen spores (Sp). Data from Alexander and Mihail (2000).

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from the host to maintain their biomass, loss of photosynthetic capacity could result in impaired mycorrhizal function. Cullings et al. (2001) showed that partial defoliation of Englemann fir reduced the total abundance of ectomycorrhizal fungi on roots and altered the species composition. *Inocybe* spp. were removed from the mycorrhizal community by defoliation, but Suilloid and Agaricoid mycorrhizae dominated under conditions of reduced carbon supply.

The incidence of fungal plant pathogens on grasses has been shown to increase with increasing latitude (Clay, 1997) . It is assumed that this is related to the increased stresses imposed on plants by adverse climatic conditions, which make them more susceptible to pathogen attack. Much of the data underpinning this statement comes from agroecosystems, however, and Clay (1997) states that the number of pathogens per host plant is significantly lower in noncrop plant species than in crop species (Fig. 3.33).

Interactions among phylloplane pathogenic fungi and leaf surface bacterial and saprotrophic fungal communities are important in determining the ability of the pathogen to develop pathological symptoms on the host plant (Seddon et al., 1997). The effect of these leaf surface biocontrol agents is dependent upon the phenology of the plant and the infectiveness of the pathogen in relation to that phenology. If the pathogen is present in the host plant prior to leaf expansion or arrives at the time of leaf expansion before a saprotrophic community can develop, the effect of the saprotrophic community to exclude the pathogen is limited. Much effort has been put into the development of both bacterial and fungal biocontrol agents in the phylloplane for agriculture. Some of these are discussed in Chap. 5. It has been shown however, that environmental conditions can significantly alter the phylloplane fungal community. In their study, Magan and Baxter (1996) showed that atmospheric SO_2 and elevated CO_2 can alter the community structure of both saprotrophic and pathogenic fungi on wheat flag leaves.

Simulation models predict significantly enhanced risks of fungal pathogen outbreaks and increased severity of these outbreaks on crop plants with predicted

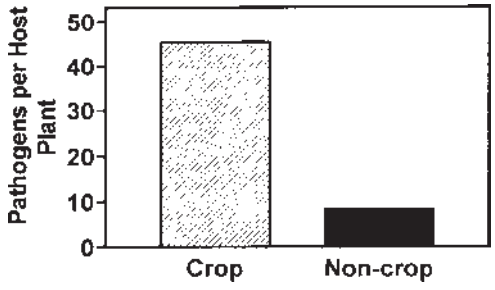

FIGURE 3.33 Mean number of fungal pathogens per host graminoid plant in relation to the agricultural status of the plant species. Data from Clay (1997).

TABLE 3.22 Emerging Plant Pathogens for Which Solutions Are Being Sought by Genetic Manipulation of Plant Species to Increases Disease Resistance

Disease		Hosts	Geographic distribution
Fungal	Late blight	Potato, tomato	Spreading worldwide
	Downy mildew	Corn, sorghum	Spreading out of Southeast Asia
	Rust	Soybean	Spreading from Southeast Asia and Russia
	Karnal bunt	Wheat	Pakistan, India, Nepal, Mexico, United States
	Monilia pod rot	Cocoa	South America
	Rust	Sugarcane	The Americas
	Blast	Rice	Asia
Viral	African mosaic	Cassava	Africa
	Streak disease	Maize, wheat, sugarcane	Africa
	Hoja blanka	Rice	The Americas
	Bunchy top	Bananas	Asia, Australia, Egypt, Pacific Islands
	Tungro	Rice	Southeast Asia
	Golden mosaic	Bean	Caribbean Basin, Florida, Central America
	Plum pox virus	Stone fruits	Europe, India, Syria, Egypt, Chile
	High plains virus	Cereals	Great Plains, United States
Bacterial	Leaf blight	Rice	Japan, India
	Wilt	Banana	The Americas

Source: Data from Moffat (2001) reprinted with permission from Science 2001: American Association for the Advancement of Science.

increases in temperature and reduced rainfall (Jahn et al., 1996; Luo et al., 1995). Similarly it is predicted that *Phytophthora*-induced decline of oaks in Europe would also increase due to climate change (Brasier, 1996). The race thus begins to promote more disease resistance into our crop plants, both by selecting naturally evolving resistance (Hines and Marx, 2001) and by artificially altering resistance by manipulating genes in order to combat some of the emerging plant pathogens (Moffat, 2001) (Table 3.22).

3.4 INTERACTIONS AMONG MYCORRHIZAE AND PLANT PATHOGENS

A number of plant pathogenic fungi attack their host plant via roots. It is at the soil–root interface that these pathogens encounter the elevated populations of fungi and bacteria that are encouraged to grow in the rhizosphere by the presence

of readily available carbohydrates in the form of root exudates and dead root cells. In particular, the mycorrhizal fungal community associated with a plant's roots can have special significance in terms of creating a defense mechanism against root pathogenic fungi (Marx and Davey, 1969a,b, Sylvia and Sinclair, 1983; Chakravarty et al., 1991; Quarles, 1999). If we consider the ectomycorrhizal condition, we can have both a fungal/fungal interaction due to chemical (antibiotic) interference of pathogen growth (Fravel, 1988; Chakravarty and Hwang, 1991; Duchesne, 1994) and a physical defense by virtue of the presence of a fungal sheath that envelops the short roots that are colonized by the mycorrhizal fungus (Marx, 1973). The implications of ectomycorrhizae as biocontrol agents for root pathogens of economically important trees is reviewed by Quarles (1999). In the arbuscular mycorrhizal condition, there is probably little physical protections, as less mycorrhizal fungal tissue exists at the root surface. Additionally, root-feeding pathogenic nematodes are of economic importance in agricultural systems. It has been shown that mycorrhizal fungi can impede nematode invasion of roots.

In natural ecosystems we know relatively little about the effect of mycorrhizae in the protection of host plants against root fungal pathogens. Most of the documented proof we have of the protective effect comes from agricultural ecosystems, in which the host plant species composition is of low diversity (usually a monospecific crop) or from the forest nursery industry, in which again a monospecific crop is being grown. It is of interest to note, however, that mycorrhizae have the ability to protect host plants from pathogens even if we cannot yet put this knowledge into the context of understanding plant community dynamics in natural ecosystems.

3.4.1 Interactions with Arbuscular Mycorrhizae

In a recent review of the role of arbuscular mycorrhizae in plant disease prevention, Borowicz (2001) came to the conclusion that of the published studies on this subject between 1970 and early 1998, her meta-analysis revealed that most studies were performed on economically important plant species (agricultural crop plants) in low phosphate soil conditions in greenhouse or microplot experiments. She concludes that a much wider set of studies must be carried out before we can extrapolate the information gained to agricultural ecosystems in general, let alone to natural ecosystems. From her analyses, we can see that in general, 50% of the studies showed that arbuscular mycorrhizae afforded some degree of protection to their host plant against plant pathogenic fungi and nematodes. The effect of the pathogenic fungi was usually to reduce the growth of the arbuscular mycorrhizal fungus, but this effect was not seen as frequently for nematodes. The interaction between the two fungal functional

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groups resulted in a reduction of growth of both competing fungi in only 16% of the reported cases.

The effect of arbuscular mycorrhizae is probably to improve the nutrition of the host plant or alter its physiology in such a way that the plant is better able to defend itself against the pathogen (Dehne, 1982; G. S. Smith, 1988; Volpin et al., 1994) rather than by direct competition between the mycorrhizal fungal and the pathogenic fungus or nematode. The effect of arbuscual mycorrhizae on plant parasitic nematodes includes reduction in fertility and egg production of the nematode, reduced penetrability of the root, and enhanced phosphorus content of the plant, affording improved growth (Roncadori, 1997).

Abdalla and Abdel-Fattah (2000) showed that there was a significant protective effect of arbuscular mycorrhizal fungus *Glomus mosseae* against the two pod rot pathogens *Fusarium solani* and *Rhizoctonia solani* (Table 3.23). The mycorrhizal effect increased peanut plant growth and yield. At plant maturity, inoculation with *F. solani* and/or *R. solani* significantly reduced the shoot and root dry weights, pod number, and seed weight of peanut plants, but growth and biomass of peanut plants inoculated with *G. mosseae* was significantly higher than that of nonmycorrhizal plants, both in the presence and absence of the pathogens. Although the presence of the pathogens reduced root colonization by the mycorrhizal fungus, propagule numbers of each pathogen isolated from a variety of plant parts were significantly lower in mycorrhizal compared to nonmycorrhizal plants, thus not only did *G. mosseae* protect peanut plants from infection by pod rot fungal pathogens, it reduced the fecundity of the fungal pathogen.

In culture conditions, Elsen et al. (2001) demonstrated that the presence of the arbuscular mycorrhizal fungus *Glomus intraradices* significantly reduced the reproductive capacity of the burrowing nematode *Radopholus similis* on carrot

TABLE 3.23 Interactions Between Two Root Pathogenic Fungi (*Fusarium solani* 1, *Rhizoctonia solani* 2) and an Arbuscular Mycorrhiza (*Glomus mosseae*) on Plant Growth and Fecundity of Peanut Plants, Showing Alleviation of the Detrimental Effects of the Pathogen by the Mycorrhizae

Treatment	Shoot weight (g)	Root weight (g)	Pods per plant	Pod weight (g)	Seed weight (mg)
Control	9.28	1.12	9.7	191	64.5
Mycorrhiza	13.02	1.91	12.3	232	72.5
Pathogen 1	6.66	0.85	8.0	144	45.9
Pathogen 2	6.89	1.22	7.0	125	39.8
M + pathogen 1	8.79	1.18	10.6	189	66.0
M + pathogen 2	9.08	1.13	8.7	190	60.5

Source: Data from Abdalla and Abdel-Fattah (2000).

root tissue. The mycorrhizal fungus suppressed the *R. similis* population by almost 50% (Table 3.24) and thus increased protection of the root against the nematode.

In contrast to the interactions among mycorrhizae and fungal pathogens, Salonen et al. (2001) investigated the effect of arbuscular mycorrhizae on a plant parasite of clover and a grass. In greenhouse experiments, the grass *Poa annua* or clover (*Trifolium pratense*) was grown in the presence or absence of an arbuscular mycorrhizal fungus and in the presence or absence of the root hemiparasitic plants *Odontites vulgaris* (for *Poa*) and *Rhinanthus serotinus* (for clover). Mycorrhizal colonization of roots of *P. annua* had little effect on plant growth, whereas the hemiparasite infection caused a significant reduction in host biomass. The mycorrhizal status of *P. annua* did not affect the biomass or the number of flowers produced by the parasitic *O. vulgaris* plants. In contrast, root colonization by arbuscular mycorrhizae of clover greatly increased the host plant biomass, but the hemiparasite infection had no effect. The effect of the mycorrhizae on the hemiparasitic *R. serotinus* plants attached to clover was to increase the parasitic plant biomass and induce the production of more flowers than plants growing with nonmycorrhizal hosts. Salonen et al. (2001) caution, however, that improvement of the performance of the parasitic plant when attached to a mycorrhizal host depends on the degree of growth promotion afforded to the host plant by the mycorrhizae.

There appears to be a fine balance between the beneficial effects of a mycorrhizal fungus and the detrimental effects of a plant pathogenic fungus. In an experimental manipulation of the fungal communities associated with the annual grass *Vulpia ciliata* by the application of two fungicides, Newsham et al. (1994) showed that there was an interaction among the pathogenic and mycorrhizal fungal associates of the target plant. The fungicide perchloraz did not affect the abundance of arbuscular mycorrhizae on the plant, nor did it affect

TABLE 3.24 The Influence of Arbuscular Mycorrhizal Colonization of Carrot Root Tissue on the Invasion of Roots by the Parasitic Nematode *Radopholus similes* and Number of Nematodes in the Growth Medium

	Nematodes in roots			Nematodes in soil			Total
Mycorrhiza	Juvenile	Female	Male	Juvenile	Female	Male	nematodes
Present	1662	609	117	1238	776	305	4707
Absent	2950	1739	384	1439	2372	589	9472

Note: The reduction in nematode numbers is statistically significant for males and females in the root tissue and females in the medium. The data show a significant protection effect of the arbuscular mycorrhiza.
Source: Data from Elsen et al. (2001).

plant performance. Benomyl, however, significantly reduced mycorrhizal colonization of roots, but this did not significantly lower plant growth or phosphorus inflow. However, benomyl did increase plant fecundity, measured by seed number. In one instance, the authors suggested that the effect of the fungicide benomyl was to reduce the abundance of root pathogenic fungi as well as mycorrhizal fungi. The lack of mycorrhizal response (reduced growth with reduced colonization) was thus offset by the improvement in growth of the plant when relieved of the stress of such root-inhabiting weak pathogens as *Fusarium oxysporum* and *Embellisia chlamydospora.* Much more work needs to be done to understand the role of both plant pathogens and mycorrhizae and the interaction between the two in instances such as this, in which no pathological symptoms were observed. It is possible that the balance achieved between the mycorrhizae and the pathogens could alter with phenology of the plant or changes in the edaphic and environmental conditions, leading to enhanced growth on one hand and significantly reduced growth on the other. How is the balance maintained? Has this been an evolutionary pathway to maintain a balance between two different functional groups of fungi? How much do these interactions play in the determination of plant fitness and express themselves in the community composition of plant assemblages?

3.4.2 Interactions with Ectomycorrhizae

The effect of ectomycorrhizal fungi on the prevention of pathological symptoms of pine tree root pathogenic fungi has been shown, particularly in nursery conditions (Marx, 1969; 1980; Marx and Davey, 1969a,b). Similarly, Sylvia and Sinclair (1983) showed that the ectomycorrhizal fungus *Laccaria laccata* suppressed *Fusarium oxysporum* on Douglas fir seedlings. The same mycorrhizal fungus was also found to protect *Pinus banksiana* seedlings from *Fusarium* (Chakravarty and Hwang, 1991). Branzanti et al. (1999) showed the protective effect of four ectomycorrhizal fungi, *Laccaria laccata, Hebeloma crustuliniforme, H. sinapizans,* and *Paxillus involutus,* on pathogens of chestnut seedlings. At the end of the first growing season, half of the mycorrhizal and nonmycorrhizal seedlings were challenged with *Phytophthora cambivora* or *P. cinnamomi* spores. Five months later, mycorrhizal plants infected with pathogenic fungi showed no sign of infection. The ectomycorrhizal fungi increased seedling growth and biomass in the presence of the pathogen.

Interest in the interaction between these two functional groups of fungi has led to the use of mycorrhizal fungi as biocontrol agents (Duchesne, 1994; Quarles, 1999). The role of fungi in this regard, however, appears only to have been observed on seedling trees and in the artificial confines of nurseries. The potential role of these interactions in the maintenance of plant communities in natural ecosystems has only been speculated (Rayner, 1993). As was suggested

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above in the discussion on interactions among arbuscular mycorrhizae and pathogenic fungi, we still know relatively little about the interaction among these groups of fungi in natural ecosystems. The same questions that were posed above are equally pertinent to ectomycorrhizal plant communities.

3.5 SYNOPSIS AND OUTLOOK

From the above discussion, we can see that fungi are important in many ways in moderating the rate of primary production by plants in the ecosystem. As an essential partner in the lichen symbiosis, fungi regulate the water and nutrient supply for photosynthesis. In much the same way, fungi are important for vascular plants as mycorrhizae. The literature is far from replete with references to net primary production figures from a wide variety of ecosystems. Most information has come from the arctic and boreal ecosystems, in which lichens are important food sources for animals, particularly during periods of the year in which other plants are unavailable. As lichens are sensitive to land use change and pollution, it would be useful to have a greater understanding on the relative importance of lichen primary production in relation to that of plants. How much does total net primary production of an ecosystem drop if the lichen community is reduced? What would be the consequences of lichen removal from an ecosystem on organisms higher up the food web?

It is obvious that the effect of mycorrhizae on plant growth is not limited to nutrient uptake. Certainly not all mycorrhizal types function in the same way, nor do species within the same mycorrhizal functional group work at the same efficiency; they differ in terms of their relative abilities to access inorganic and organic nutrient sources. Their responses to environmental stimuli are also different, leading to the dominance of one mycorrhizal type over another, depending on the environmental conditions and the plant species supported there. How do these different mycorrhizal types respond to changes in environment (e.g., climate change, pollutants)? These are important questions that are being addressed and that have ecosystemwide consequences.

The existence of linkages among plants by mycorrhizal fungal hyphae in natural ecosystems has recently been conclusively proved (Simard et al., 1997a, b). The sharing of nutrients not only among plants of the same species, but more important, among plants of different species, has started to alter our concepts of how plant species interact in the community. How much sharing of resources among plant species actually occurs in natural ecosystems? Is this sharing only occurring if the supply and demand of resources is asymmetric between the two plants? How much does this sharing of resources increase the stability and resilience of the ecosystem? How much functional redundancy occurs if the occurrence of linkages among plants is high and the mycorrhizal diversity is also high? Do all mycorrhizal species produce these linkages?

Our categorizing of mycorrhizal associations has not allowed us to consider plant species sharing different types of mycorrhizae. Evidence exists, however, that some tree species change their dominant mycorrhizal associates from arbuscular mycorrhizae to ectomycorrhize as the trees age. What is the functional significance of these changes in symbiotic partners? In a similar way there is evidence to suggest that some ericaceous plants can support ericoid, ecto-, and possibly arbuscular mycorrhizae (Dighton and Coleman, 1992; J. E. Smith et al., 1995). Why should a plant need to associate with a variety of mycorrhizal types and does this have ecosystem consequences?

Pathogens have a negative effect on plant growth by reducing photosynthesis and the general health of the host plant. Much of the evidence of negative effects of fungal pathogens comes either from the agricultural literature or from studies of exotic fungi on plants or fungi on exotic plants. How important are fungal pathogens in natural ecosystems? Have our current ecosystems evolved with a balance among plants and fungi with a degree of resistance to fungal pathogens in such a way that only damaged or weak individuals are significantly impacted by the fungal pathogens?

It is clear from our discussions that fungi play a role in plant production, but the subtleties of their interactions and the global consequences of the interactions among plants and fungi are still incompletely understood. As efforts continue to control the fungal pests of economically important crops and to find the beneficial effects of manipulating mycorrhizae on plant roots, the long-term effects of such manipulation on the functioning of natural ecosystems has to be considered. Have the components of ecosystems coevolved to produce a fine balance among the components, including fungi, which could be damaged if the fungal community alone is altered significantly?

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4

Fungi, Secondary Productivity, and Other Fungal–Faunal Interactions

Fungi are an important component of the food supply to many grazing animals. How many of us have picked a mushroom in the woods only to find it riddled with holes and full of fly larvae and other invertebrates? In many European countries, wild mushrooms are an important component of human's diet. In recent times, however, the cultivation of mushrooms by commercial growers has become more important than personal fungal forays, especially as the commercial production of mushrooms is independent of season. Indeed, the value of mushrooms as a food source for humans runs to a sale of approximately 426,625 Mg of *Agaricus* and specialty mushrooms in the United States at a sales value of $863 million (data for the year 2000–2001, National Agricultural Statistics Service, USDA).

It is therefore not surprising that a number of vertebrate and invertebrate animals consume mushrooms as part of their diet (Cave, 1997). Not only is the survival and growth of these organisms dependent upon fungi, but the animals have effects on the fungi by the dispersal of spores or reduction in the fecundity of the fungi. In addition to consumption by vertebrates, the unseen grazing of fungal mycelia by soil fauna is often equally important. Many soil animals are dependent upon fungi as food or as modifiers of the plant resources, making them more palatable. We saw earlier that leaf litter in aquatic ecosystems became more palatable to the "shredder" community as a result of prior colonization and activity of saprotrophic fungi (Suberkropp, 1992; Graca et al., 1993; Gessner et al., 1997). It is the fungi that support the populations of many groups of collembola, mites, and nematodes in soil (Anderson, 2000; Edwards, 2000; Moore and de Ruiter, 2000; Ruess et al., 2000). In response, these animals exert their influence on the fungal biomass and community composition. This grazing

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effect can be significant in regulating the function of the fungal community in terms of modifying rates of leaf litter decomposition, affecting competition among fungi for resources, and reducing the efficiency of mycorrhizae to effect nutrient uptake into host plants.

In the same way that fungi can have both beneficial and detrimental effects on plants, so too some groups of fungi are pathogens of invertebrates and vertebrates. Many diseases of fish and humans are fungal, and the role of fungi as pathogens of invertebrates has been utilized as biocontrol of insect, mite, and nematode pests of agricultural crops (Larsen et al., 1997; Bird et al., 1998; Manueli et al., 1999). Recently there has been concern regarding the impact of fungal pathogens on the populations of tropical frogs (Reed et al., 2000; Warkentin et al., 2001; Fellers et al., 2001).

In a number of specific instances there have evolved close associations between animals and fungi. Leaf-cutting ants and termites rely on fungi as a food source to such a degree that they maintain cultures of specific fungal species, exclude others, and tend to the growth of their food supply as if it were an agricultural crop. In other examples, the close association between bark beetles and the fungi that they transport with them is an essential relationship that permits the larvae of the beetle to obtain sufficient nitrogen from the tree that they invade (Ayres et al., 2000). It is thus not possible just to discuss the effects of fungi as food on the maintenance of animal growth and population size. We must also consider some of the complex interactions and feedback effects of grazing on the fungi themselves, as such feedback influences ecosystem processes. The interactions discussed in this chapter are shown in boldface type in Table 4.1.

4.1 FUNGI AS FOOD FOR SECONDARY PRODUCERS: POSITIVE IMPACTS ON FAUNAL PRODUCTIVITY

Fungi are rich in important nutrients, particularly nitrogen, phosphorus, minerals, and vitamins (Fogel, 1976; Grönwall and Pehrson, 1984) (Table 4.2). Clinton et al. (1999) measured the nutrient content of fungal fruit bodies (mushrooms of both mycorrhizal and saprotrophic basidiomycetes) of a *Nothofagus* forest floor and showed that all elements other than calcium are more concentrated in fungal tissue than the forest floor material. This suggests that fungi would be preferred food resources for many animals. Much of the nitrogen they contain is in complex forms, however, such as indigestible cell walls (Cork and Kenagy, 1989a), thus for animals to effectively utilize the nutrients in fungi, they are required to have a complex community of gut symbionts to assist in the breakdown of these compounds. Indeed, experiments conducted by Cork and Kenagy (1989b) showed that the weight of ground squirrels declined when fed entirely upon fruit

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TABLE 4.1 Ecosystem Services Provided by Fungi

Ecosystem service		Fungal functional group
Soil formation	Rock dissolution	Lichens
		Saprotrophs
		Mycorrhizae
	Particle binding	Saprotrophs
		Mycorrhizae
Providing fertility for primary production	Decomposition or organic residues	Saprotrophs (Ericoid and ectomycorrhizae)
	Nutrient mineralization	Saprotrophs (Ericoid and ectomycorrhizae)
		Saprotrophs
	Soil stability (aggregates)	Arbuscular mycorrhizae
Primary production	Direct production	Lichens
		Mycorrhizae
	Nutrient accessibility	Mycorrhizae
	Plant yield	Pathogens
		Mycorrhizae
	Defense against pathogens	Endophytes
		Saprotrophs
	Defense against herbivory	Endophytes
		Mycorrhizae Pathogens
Plant community structure	Plant–plant interactions	
Secondary production	**As a food source**	**Saprotrophs**
		Mycorrhizae
	Population/biomass regulation	**Pathogens**
Modification of pollutants		Saprotrophs
		Mycorrhizae
Carbon sequestration and storage		Mycorrhizae (Saprotrophs)

Note: The services that will be discussed in this chapter are in bold face type. Fungal groups in parentheses are regarded as of lesser importance in that function.

bodies of the hypogeous ectomycorrhizal fungus *Elaphomyces granulatus*, as more than 80% of the nitrogen was locked up in complex forms and could not be made available in the digestive tract of these animals. Fogel and Trappe (1978) showed that fungi consist of a large amount of water (70–94%) and contain fewer

TABLE 4.2 Protein and Mineral Content of a Range of Fungal Species Used as Food by the Red Squirrel (*Sciurus vulgaris*)

Fungal species	Protein	P	Ca	Mg	K	Na
Amanita muscaria	25	0.48	0.13	0.04	7.9	0.02
Pholiota sqaurrosa	35	0.96	0.05	0.1	3.1	0.02
Cortinarius delibutus	17	0.55	0.09	0.07	5.4	0.02
C. armillatus	18	0.68	0.11	0.12	6.4	0.02
Gomphidius glutinosus	18	0.56	0.08	0.11	3.8	0.02
Lactarius sp.	16	0.67	0.06	0.12	4.9	0.02
L. torminosus	17	0.46	0.12	0.09	3.0	0.02
L. uvidus	22	0.52	0.06	0.07	3.5	0.03
L. deliciosus	30	0.60	0.06	0.1	2.5	0.02
Russula flava	18	0.29	0.06	0.07	3.9	0.02
Boletus sp.	15	0.53	0.09	0.05	2.2	0.02
B. edulis	30	0.62	0.10	0.12	4.1	0.02
Hydnum repandum	26	0.52	0.16	0.06	4.1	0.03
Elaphomyces granulatus	17	0.21	0.08	0.12	0.6	0.10

Source: Data from Grönwall and Pehrson (1984).

calories per unit weight than nuts, eggs, and meat. Kinnear et al. (1979) provides figures of fungi having around 40% (by weight) of lipids and 8–10% of proteins. Despite these shortcomings of fungi as high-quality food supplies, however, they are consumed by a number of vertebrate and invertebrate animals to a greater or lesser degree.

Some invertebrate animals are entirely fungiverous, whereas others ingest fungi inadvertently along with plant remains or soil. For a number of vertebrates, fungi or fungal-based food serves as a primary or temporary food source for times of the year when little other food is available. For example, the reindeer herds of Fennoscandia rely heavily on lichens as a food source during the winter months, without which the populations could not be sustained (Cooper and Wookey, 2001). Mathiesen et al. (2000) showed that more than 25% of the gut contents of Norwegian reindeer consist of lichens during March. The energy value of this diet is regarded as good, despite the fact that the structural carbohydrates differ significantly from plant carbohydrates. The hemicellulose in lichens contains xylan and lichen starch in β-1-4 and β-1-3 glucoside linkages. It is this factor that Mathiesen et al. (2000) suggest induces increased bacterial fermentation in the gut, which results in an increase in the development of food-absorptive papillae on the gut wall in reindeer fed exclusively with a lichen diet.

4.1.1 Fungi in the Diet of Vertebrates

Claridge and May (1994) reviewed mycophagy in Australian mammals. They identified 37 species of native and fair species of feral mammals as exhibiting mycophagy of some sort. The degree of dependency of each animal species on fungi as a staple or essential part of the diet is difficult to establish. It is estimated, however, that fungi comprise more than 25% (by volume) of the diet of brush-tailed potoroo (*Potorus longipes*) at all times of the year. Fungi occurred in the feces of these animals 90% or more at the time during most months and never fell below 80%. Other animals, such as the smoky mouse (*Pseudomus femeus*), relied on a diet of seeds and moths during the summer months, when fungal fruiting bodies were unavailable. During the winter, however, the smoky mouse, along with bush rats (*Rattus fuscipes*), relied heavily on fungi. The fungi consumed are from a wide variety of taxa. Lichenized fungi, however, have rarely been reported to be consumed by the Australian megafuanal population. Potoroos consume the most varied fungal diet of any animal (36 fungal taxa), and most of the fungi are of hypogeal fungi. It would appear that body size limits the diversity of fungal species eaten, with rats and mice (<150 g body weight) feeding mainly on arbuscular mycorrhizal spores of the Endogonaceae (Cheal, 1987). Large animals, however, such as the feral pig, eat a wide variety of fungal species.

On the island of Svalbard in the Barents Sea, areas that had been free of reindeer for a number of years now support large herds. As these animals rely on lichens for a major part of their diet, two aspects of their foraging are posing severe threats to the lichen community and the sustainability of a viable food reserve (Cooper and Wookey, 2001). Because of the relatively slow growth of lichens in this high arctic region, calculated as 2.5 to 10.6 mg g^{-1} wk^{-1} relative growth rate, the density of reindeer and their grazing activity is likely to outpace lichen growth. Studies in Finland by Kumpula (2001) show that reindeer consumed up to 2.6 kg lichens per day during the most intensive digging period when snow covers the ground. With the assumption that a reindeer grazes an area of approximately 30 m^2 per day during the period of snow cover and calculating the energy requirements of a reindeer, Kumpula (2001) estimated that each reindeer requires some 1000 kg ha^{-1} dry weight of lichens to sustain it during the winter. In addition to the grazing pressure per se, trampling of lichens by the reindeer herds is an important reason for the decline in both species diversity and biomass of lichens in areas in which reindeer herd density is high. As Crittenden (2000) points out, however, there are too few data on the rates of the growth of lichens to be able to predict large mammal-carrying capacity based on the reliance of these animals on a predominantly lichen diet. It is interesting to note that although grazing reduces lichen biomass, the presence of reindeer significantly increases the lichen nitrogen content from 0.43–0.91% but no similar increase in N concentration of Scots pine or *Empetrum* shrubs, which are

the dominant vegetation of the area (Stark et al., 2000). These authors also noted an increase in the abundance of bacteria and fungal-feeding nematodes in reindeer-grazed areas, suggesting a more general increase, in microbial activity induced by the presence of the reindeer herd.

The abundance of particularly hypogeous (subterranean fruiting) fungi in forests can be considerable. Fogel (1976) estimated that there could be between 11,052 to 16,753 fruiting bodies produced per ha per year in old-growth Douglas fir forests in western Oregon. Fruiting accounts for some 2.3 to 5.4 kg ha^{-1} dry mass of fungus. These fungi have a higher content of nitrogen, phosphorus, potassium, and micronutrients than epigeous fungi (fungi fruiting above ground), making them a higher-quality food resource for mammals (Fogel and Trappe, 1978; Trappe, 1988). In comparison with available plant parts, many fungi have similar food value but less fat content for herbiverous small mammals (Fogel and Trappe, 1978) (Table 4.3). Fungi thus form a significant proportion of the diet of these animals (Fig. 4.1).

4.1.2 Fungi in the Diet of Invertebrates

In their reviews of fungivory, both Shaw (1992) and McGonigle (1997) concentrate on invertebrate consumption of fungi. An older review of the interactions between fungi and insects by Wilding et al. (1989) describes a wide variety of interactions with a range of fungal taxa and functional groups. There are a number of groups of invertebrates that inhabit the mushroom-fruiting

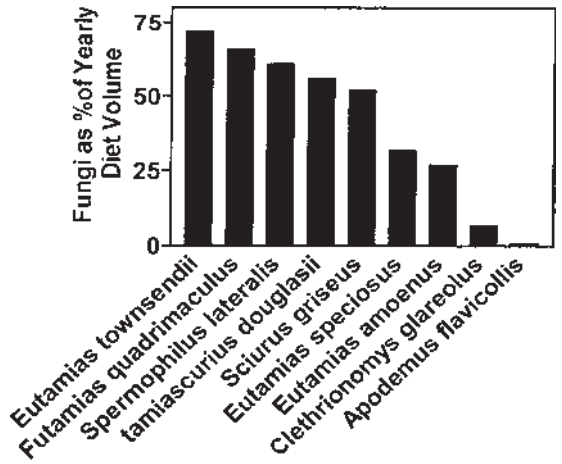

FIGURE 4.1 Percentage contribution of fungi to the annual diet of nine small mammal species in the Pacific Northwest. *Source*: Data from Fogel and Trappe (1978).

TABLE 4.3 Chemical Composition of Fungi in Comparison with Plant Parts and Meat

		Protein	Fat	Carbohydrate	Ash
Fungi	*Agaricus bisporus*	50	1.2	—	7
	Boletus edulis	33	5	58	7
	Clavaria flava	1927	2	47	5
	Lactarius deliciosus	19	7	28	6
	Lentinus edodes	40	5	54	3
	Marasmius oreades	35	3	34	10
	Morchella esculenta	12	2	46	10
	Saccharomyces cerevisiae	14	1	21	—
	Suillus granulatus	21	2	70	6
	Suillus gervillei	20	2	64	6
	Suillus luteus	17	4	53	6
	Trichoderma favovirens	25	—	75	9
	Tuber malnosporum	11	2	42	8
Nuts	Chestnuts	11	7	72	2
	Butternut	28	61	3	3
	Black walnut	30	57	6	2
	Pecan	10	72	10	2
	Hickory nuts	15	68	7	2
	Filbert nuts	16	64	12	2
	Beech nuts	22	52	19	3
Meat	Chipped beef	30	6	1	—

Source: Data from Fogel and Trappe (1978).

structures of basidiomycete fungi. Large, fleshy mushrooms are often heavily invaded by dipteran larvae. Studies of fly larvae that consume mushrooms have shown that there is little correlation between the fungi considered poisonous to humans and those consumed by invertebrates. Indeed, Jaenike et al. (1983) found that many species of the fly *Drosophila* were tolerant of the toxic component of *Amanatia* spp., α-amanitn. High densities of collembola can often be found grazing the surface and spores of less fleshy species, such as *Laccaria* spp. Hanski (1989) reviewed the interactions between fungi and insects, considering fungi as insect food. He suggests that the spatial distribution of fungal fruiting bodies can influence the feeding activities of above-ground fungiverous insects. In the same way, he suggests that the seasonal appearance of particularly basidiomycete fruit bodies can influence the growth and development of insect larvae and consequently the fecundity of the adult insect. This may be a determining factor in why most fungal-feeding insects are polyphagous rather than monophagous; they have a greater chance of finding at least one fungal species fruiting at any time (Table 4.4).

TABLE 4.4 The Degree of Polyphagy in Diptera Breeding in Nine Genera of the Agaricales

Fungal genus	Number of species used as food by Diptera larvae
Amanita	6
Hygrophorus	4
Cortinarius	5
Russula	17
Boletus	5
Tricholoma	6
Lactarius	14
Suillius	5
Leccinum	5
Small genera	37

Source: Data from Hanski (1989).

It has been shown that not all fungi are equal in either their ability to provide the necessary nutrients for adequate growth, and also that the specific secondary metabolites produced by certain fungal species act as deterrents to animal grazers, thus not all fungi are equally palatable to specific animals. From the limited evidence in the literature on fungal selection by a variety of faunal groups, it would appear that there is no consistent pattern in preference of specific species and avoidance of others throughout all faunal groups. The preferred fungal species thus varies among animal groups and even among genera and species within the same faunal taxon. Soil microfaunal feeding preferences have been determined by numerous feeding trials in the laboratory. Reddy and Das (1983) provided evidence to suggest that mites showed little food selection when offered single or mixed cultures of *Trichoderma*, *Cladosporium*, and *Pythium*, whereas collembola preferred a mixed microfungal diet. In addition, they demonstrated that the different fungi had different food values, resulting in differences in the total numbers of animals at the end of a 9-week experiment. Compared to the control food (agar medium alone), this showed that some fungi were more beneficial for population growth and others were detrimental (Table 4.5).

Many animals have distinct preferences for certain species of fungi and dislikes for other species. Their selection must, however, be based upon other characteristics of the fungi than the poisons that affect humans. Parkinson et al. (1979) demonstrated that the collembolan *Onichiurus amatus* actively avoided a particular basidiomycete fungus that caused its death, even without the fungus being ingested. Shaw (1988) compared the palatability of a range of ectomycorrhizal and saprotrophic fungi to the same collembolan species and

TABLE 4.5 The Influence of Three Microfungi on the Numbers of Soil Arthropods Remaining in Culture After Nine Weeks Compared to Control Systems Containing Agar Medium Alone

Microarthropod	*Trichoderma*	*Cladosporium*	*Pythium*	*Control*
Mesostigmata	2	3	530	250
Prostigmata	90	25	70	18
Cryptosigmata	3	6	18	5
Total mites	95	34	618	273
Isotomidae	5	5	4	45
Entomobryidae	1	1	—	5
Total collembola	6	6	4	50

Source: Data from Reddy and Das (1983).

concluded that there was a consistent hierarchy of preferences (Table 4.6). Thimm and Larink (1995) showed that four collembolan species (*Folsomia candida*, *Onychiurus fimatus*, *Sinella coeca*, and *Proisotoma minuta*) out of the five tested each had a preference for a different species of arbuscular mycorrhizal fungus. *Xenylla grisea*, however, did not show a fungal-feeding preference, but was observed feeding mainly on nonmycorrhizal root tissue.

TABLE 4.6 Hierarchy of Feeding Preferences of the Collembolan *Onichiurus amatus* When Offered a Range of Fungal Species Grown in Agar Culture

Fungal species	Mean percentage of fungal colony area consumed	Mean fecal count per culture vessel
Marasmius androsaceus	72.2	74.8
Laccaria proxima	41.4	70.8
Lactarius rufus	55.7	64.5
Suillus luteus	50.7	48.9
Mycena galopus	68.2	19.2
Suillus bovinus	18.2	16.6
Rhizpogon roseolus	20.7	13.8
Paxillus involutus	21.3	13.1
Mycena epiterygia	24.2	10.6
Piolithus tinctorius	0.2	2.1
Clitocybe sp.	1.2	1.1
Hebeloma crustuliniforme	1.7	1.0

Source: Data from Shaw (1988).

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Nematodes are ubiquitous in soils. Fungiverous nematodes may feed on a variety of fungal species, and the selection of fungi to eat may be linked to both the palatability and nutritional value of the fungi. Sutherland and Fortin (1968) provided a choice of seven ectomycorrhizal fungi to the nematode *Aphelenchus avenae* and found that *Amanita rubescens* provided the best resource for nematode reproduction. Three species of *Suillus*, *Cenococcum geophilum*, and *Russula emetica* provided similar nutritional value, but *Rhizopogon roseolus* had a negative impact on nematode numbers. Due to the intensity of nematode grazing on *Suillus granulatus*, the authors found that this nematode could prevent the development of mycorrhizal symbiosis with *Pinus resinosa* when present in a tripartite association in culture. It is suggested, however, that the grazing pressure of nematodes is unlikely to be intense enough to reduce the structure or function of established mycorrhizal associations in natural ecosystems. Ruess and Dighton (1996) investigated the fungal food preferences of the nematode *Aphelenchoides saprophilus* by comparing saprotrophic and ectomycorrhizal fungi. They concluded that nematode populations from a natural mixed soil community performed best and with the highest proportion of *A. saprophilus* in the community when the nematodes fed on the ectomycorrhizal fungi *Lactarius rufus* and *Laccaria laccata*. In contrast, a sustainable community could not be maintained on a diet consisting solely of *Paxillus involutus* (Table 4.7). In a more comprehensive study of the food value of mycorrhizal fungi, Ruess and Dighton (1996) offered seven ectomycorrhizal and one ericoid fungal species to pure cultures of *A. saprophilus*. Significant differences in final nematode populations were found for the different mycorrhizal fungi, and the proportion of females within these populations also varied. Nematodes feeding on *Laccaria laccata*

TABLE 4.7 Numbers of Mixed Species Populations of Nematodes in Petri Plates Supporting the Growth of a Range of Saprotrophic and Ectomycorrhizal Fungal Species

Functional group	Fungal species	Number of nematodes	(%) *A. saprophilus*
Mycorrhizal	*Lactarius rufus*	25890	99
	Laccaria laccata	2633	100
	Paxillus involutus	6	50
Saprotroph	*Agrocybe gibberosa*	349	95
	Chaetomium globosum	1427	99
	Mucor heimalis	24	13

Note: The proportion of the nematode *Aphelenchoides saprophilus* in the population is given.
Source: Data from Ruess and Dighton (1996).

TABLE 4.8 Influence of Fungal Food Species (Mycorrhizal Fungi) on the Population of the Nematode *Aphelenchoides saprophilus* and Percentage of Females in the Population (Index of Population Fecundity)

Fungal food	Population after 4 weeks ($\times 10^5$)	Mature females as percentage of population
Laccaria laccata	2.4	11.4
Cenococcum geophilum	1.5	7.3
Lactarius rufus	1.4	7.8
Hebeloma sacchariolens	0.8	2.8
Paxillus involutus	0.8	5.8
Amanita muscaria	0.7	2.0
Amanita rubescens	0.6	1.3
Hymenoscyphus ericae	2.0	6.8

Source: Data from Ruess and Dighton (1996).

produced the highest proportion of females in the population as well as the largest population (Table 4.8), suggesting that this fungus was superior to the others for both the population growth and potential fecundity of the population. In a subsequent study, Ruess et al. (2000) showed that the diet of *Aphelenchoides* sp. was not only mixed, consisting of both ectomycorrhizal and saprotrophic fungi of various higher taxa, but that the selection of the most favored fungus changed over time. It was suggested that this shift in food preference might protect the nematode from an accumulation of toxic compounds accumulated from the different fungal species.

Not only do fungi provide food for invertebrates, but invertebrate activity can change the physico-chemical properties of resources in the decomposer system to improve their exploitation by fungi. We can see in the decomposition of plant remains that there are close interactions between soil fauna and fungi, which change as the process of decomposition progresses. In his microscopic study of pine leaf litter decomposition, Ponge (1990; 1991) showed changes in fungal species invading pine needles in concert with faunal invasions. This may have been a result of animals carrying specific fungal propagules with them, but it is more likely that the physical actions of the fauna in the comminution of the litter altered its physicochemical properties, thereby altering the competitive abilities among the fungi for access to those resources. Indeed, Anderson and Ineson (1984) showed that the decomposition of leaf litter was enhanced in the presence of isopods, which by comminution of the leaf litter, increased fungal and bacterial biomass on the litter. Selective grazing on specific, preferred fungi by soil invertebrates results in changes in the competitive strengths of fungi, thus faunal grazing can alter the relative abundance of fungal species in the environment.

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A particularly good example of altered fungal competition mediated by soil arthropods is given by Newell (1984a,b). She found that of two saprotrophic basidiomycete fungi, *Onichiurus latus* preferred to feed on *Marasmius androsaceous* rather than on *Mycena galopus*. At high collembolan densities, the intensity of feeding was enough to significantly reduce the growth of *Marasimus* to such an extent that *Mycena* dominated in the leaf litter. In an optimal, ungrazed system, however, *Marasmius* had a preferred habitat of leaf litter, while *Mycena* preferred a soil habitat. The effect of collembolan grazing was therefore to shift the mycelial biomass of each fungus to suboptimal niches. As we have seen, not all fungal species are equal in their physiological attributes, and a change in species composition can have an effect on fungal-mediated processes in the ecosystem. These can be seen from examples of grazing on saprotrophic, mycorrhizal, and pathogenic fungal functional groups, although the functional effects of these interactions have only been explored to a limited degree.

The interaction between invertebrates and fungi can also be much more complex that a direct trophic interaction. In addition to the maintenance of a fungiverous invertebrate population, the fungus may reap benefits from the interaction. Over time, these close associations may evolve into near mutualisms. An example of this close association is that described by Bultman et al. (2000). In this association, the activities of the larvae of the yucca moth (*Botanophila* files) act as "pollinating" parasites of the ascomycete fungus *Epichloë elymi*. Flies transfer fungal spermatia (gametes) among fungi as they visit their hosts for egg laying, and the developing fly larvae consume ascospores. The authors measured the reproductive output of fungi, the amount of feeding by fly larvae on fungal reproductive tissues, and the mortality of fly eggs and larvae. Contrary to the expected, the reproductive output of fungi did not decrease with increasing egg load, but tended to increase as more eggs were laid (Table 4.9). Larval feeding

TABLE 4.9 Relationship Between the Number of Yucca Moth Eggs Laid on the Stroma of *Epichloë* and the Number of Perithecia Produced by the Fungus

Number of eggs per stroma	Number of *Epichloë* perithecia
0	10
1	35
2	57
3	75
>3	70

Source: Data from Bultman et al. (2000).

was only weakly associated with the number of eggs on the fungi. The mean surface area of fungal stromata decreased as egg abundance increased, but the overall effect of the flies on *Epichloe* reproduction was positive, as the number of preithecia increased with an increase in egg number. The fungus therefore appears not to be vulnerable to overconsumption by the fly larvae, suggesting that this could be an example of a balanced antagonism. Similar in associations can be seen in bark beetle–fungal interactions (Norton et al., 2000; Lombardero et al., 2000) and will be discussed later in this chapter.

4.2 EFFECTS OF GRAZING ON FUNGI AND FUNGAL-MEDIATED PROCESSES: NEGATIVE AND POSITIVE FEEDBACKS

4.2.1 Influence of Faunal Grazing on Decomposition

During decomposition, the competition for resources between microbes can be influenced by the selective grazing of fungi by soil fauna. Decomposition rates are reduced as the number of fungal species is increased, due to the fact that metabolic activity of competing fungi is greater than the activity of an equivalent biomass of a single fungal species (Wicklow and Yocum, 1982; Robinson et al., 1993). Because of the selective grazing of fungi by soil microarthropods, the diversity of fungal species effecting decomposition is often reduced (Lussenhop and Wicklow, 1985).

In agricultural systems with low densities of soil fauna the effect of faunal reduction was to reduce decomposition (suggesting a synergistic interaction). Indirect effects of faunal grazing on the decomposition of resources in soil by faunal grazing of fungi have been shown by Lussenhop and Wicklow (1985). Measuring the effect of increasing complexity of the saprotrophic fungal community on rabbit dung, they showed that as species complexity increased there was less decomposition and lower production of spores. This is similar to the findings of Robinson et al. (1993), who showed that a significantly higher level of respiration occurred when fungal species competed for a resource than could be predicted from the combination of respiration of each fungus. When Lussenhop and Wicklow (1985) introduced the mycophagous fly larvae of *Lycoriella mali*, however, there was a 10% increase in the rate of decomposition of rabbit feces at high fungal species diversity and a 1500% increase in spore production. They suggest three possible hypotheses for this effect. First they suggest that the larvae could directly compete with fungi for water-soluble compounds and that this competition becomes stronger as the complexity of fungal interactions increases. Second, larval grazing on mycelia could slow hyphal growth and thus reduce the chance of competitive interactions to such an extent that the fungi can invest more resources to decomposition. Third, the larvae

could concentrate enzymes as the number of fungal species increases. The exact effect of this interaction is unclear, however. In a microcosm experiment, Nieminen and Setälä (2001) showed that the presence of fungal-feeding nematodes and bacteria increased the fungal activity in soil. Each factor, nematodes or bacteria, had similar effects, but the two acting together were not additive. Nieminen and Setälä suggest that nutrient limitation and the dependence on fungi in this particular food web configuration contradicted previous studies that show food chain length is positively correlated with rates of nutrient-cycling processes.

Changes in the decomposition of plant litter in the absence of soil arthropods have been documented. For example, Beare et al. (1992) showed that the removal of soil arthropods reduced leaf litter decomposition by 5% in both conventional till and no-till treatments of an agricultural experiment. The increase in fungal biomass resulting from the alleviation of grazing pressure was correlated to an increase in nitrogen retention (25% higher than plots with faunal populations intact). It is suggested that this increase in nitrogen content is related to N immobilization in fungal tissue. Indeed, 85% of the net immobilized nitrogen was associated with the saprotrophic fungal community. The activities of soil fauna thus not only moderate fungal growth, but allow greater rates of nutrient mineralization than when animals are removed, leading to greater soil fertility.

Lussenhop (1992) reviewed the effects of faunal grazing on fungi on the rates of plant litter decomposition. Chen and Ferris (1999) showed that the decomposition of alfalfa residues and cellulose was increased by the presence of fungal-feeding nematodes. Where the residues were colonized by the favored fungal food (*Rhizoctonia solani*) for nematodes, both nematode populations and nitrogen mineralization was significantly higher than when the less favored fungal food (*Trichoderma* sp.) was available. This suggests that nematode feeding increased either the biomass or at least the activity of the preferred fungal food and that this increase in fungal activity was manifested in the increase in an ecosystem function. In a contrasting forest ecosystem, however, Coleman et al. (1990) showed that reduction in microbial predators in ecosystems with high densities of forest soil fauna led to increased decomposition of litter by relief of grazing pressure.

The differential grazing pressure on different fungal species by soil invertebrates can have a profound effect on the distribution of fungal mycelia, and probably on their function as well. It has often been viewed that grazing of fruiting structures by insects is inconsequential to the survival of the fungal species. Considering the mass of fungi in relation to the biomass of insects feeding upon them it was thought unlikely that the dissemination of spores, the primary purpose of a mushroom, would be impaired, regardless of the intensity of invertebrate grazing pressure (Hanski, 1989; Courtney et al., 1990). Studies of

the effect of grazing of fruit bodies of the wood-decomposing fungus *Coriolus versicolor* (Guevara et al., 2000), however, showed that the ciid beetles, *Octotemnus glabriculus* and *Cis boleti* significantly reduced the fecundity of the fungus by reducing reproductive potential by 58% and 30%, respectively. The authors suggest that this reduction in the fitness of the fungus may be significant in the environment in terms of reduction in colonization potential of this fungus.

Faunal grazing can have an effect on the nature of the growth pattern of the fungus. For example, Dowson et al. (1988) showed that arthropod grazing on the cord-forming fungus *Steccherium fimbriatum* induced the development of a fast-growing diffuse mycelium from a slow, dense growth form. Hedlund et al. (1991) also showed that the collembolan *Onychiurus armatus* caused *Mortierella isabelina* to shift from appressed hyphae to aerial hyphal growth. These changes in the growth form of the fungus can significantly alter the rate at which resources are colonized and utilized. The indirect effect of grazing may thus be to alter the rate of the processes that are carried out by the fungi concerned.

In a study of collembolan grazing in Sitka spruce plantation forests in England, Newell (1984a,b) found that of two saprotrophic basidiomycete fungi, *Onichiurus latus* preferred to feed upon *Marasmius androsaceous* rather than on *Mycena galopus*. At high collembolan densities, the intensity of feeding was enough to significantly reduce the growth of *Marasmius*, to such an extent that *Mycena* dominated in the leaf litter. It appeared that the two fungi had optimal habitats based on a vertical separation of resources, however, *Marasmius* was found to grow nearer the soil surface than *Mycena*, but by relieving the grazing pressure of the collembolan, *Marasmius* was found to grow readily at greater depth and *Mycena* into the less decomposed leaf litter at the soil surface. It was therefore suggested that the vertical distribution of these two fungal species was constrained by the effects of collembolan grazing pressure. If this is indeed true, it would suggest that the fungi are growing in suboptimal habitats and are probably functioning less efficiently than they would given ideal growth conditions. The extent to which fauna limit the effectiveness of fungal activity is not known, however.

The number of fungivorous nematodes in a community can be influenced by predation on the nematode community (Laakso and Setälä, 1999). In the study by Laakso and Setälä (1999) the presence of a specialist nematode-feeding mite (*Parazercon radiatus*) reduced the population of both bacterial and fungal-feeding nematodes by half. The omnivorous mite (*Lysigamasus lapponicus*), however, increased the density of fungal-feeding nematodes over the bacterial feeders. As a result, the specialist predator reduced nitrogen availability in soil, whereas the generalist predator caused an increase by stimulating the microbial community as a whole. The authors thus conclude that these "top-down" regulation processes are important in driving the ecosystem-level function of

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the community. Much more work is required, however, if we are to fully understand the complexities of these trophic interactions and their impact on function.

Earthworms are also selective in their feeding preferences for different fungal species. Brown (1995) cites the work of Cooke (1983) showing selection of certain fungal species and rejection of others. This selective grazing may alter the species composition on a decomposing resource by changing the diversity of fungal species and altering the physiological attributes of that community. Indeed, Tiwari and Mishra (1993) found greater numbers and diversity of fungi in earthworm casts than surrounding soil. The changes in species composition of fungal communities can thus be altered to change the rates of decomposition of resources. The activity of earthworms often results in a greater comminution of leaf litter, thus increasing the surface area for attack by saprotrophic fungi. This activity will enhance decomposition processes. Salmon and Ponge (2001) have shown that earthworm feces attract entomobryid collembola, which feed on the mucus/urine mixture contained in the feces. In addition, because of their elevated nutrient loading, these sites are foci for the development of bacterial and fungal communities. These conditions lead to the establishment of soil microbial communities that are beneficial in forming and maintaining soil aggregates that are useful for restoring degraded soils (Scullion and Malik, 2000; Görres et al., 2001).

In plant canopies herbivorous invertebrates can significantly alter the physicochemical properties of plant parts by their grazing and production of exuviae and feces. In particular, aphids produce honeydew (a pure sugar excreta produced by virtue of the fact that they need to process so much phloem sap to obtain nitrogen for growth and reproduction that most of the sugar is in excess of their energy needs) (Dixon, 1973). This sugar is a resource for fungi and bacteria in the phylloplane, in which all micro-organisms are suspected to be energy-limited (Stadler and Müller, 1996; 2000). These authors report densities of bacteria and filamentous fungi of two to three orders of magnitude higher in honeydew-contaminated leaves than in control leaves. The influence of honeydew and other resources, such as pollen, on leaf surfaces may have dramatic effects on fungal biomass and alter leaf surface fungal communities. As we have seen, the effects of fungal and bacterial communities on leaf surfaces can directly influence the success of fungal pathogen invasion of the leaf. In addition, the increased fungal biomass on leaf surfaces can alter the dynamics of nutrient absorption from throughfall precipitation. Stadler et al. (1998) and Stadler and Michalzik (1999) showed that the elevation of microbial biomass on leaf surfaces of Norway spruce trees increased the absorption of nitrogen in the tree canopy by microbial immobilization. This has a direct affect on the nutrient loading of soil under the canopy, and consequently on the growth of trees.

As we discussed earlier, edaphic abiotic factors strongly influence the nature of the fungal communities, effecting decomposition and nutrient uptake by

plants. Because of the unique properties of fungi, we showed that they were capable of tolerating low moisture levels, particularly in the form of lichens, and were able to more readily respond to rapid and short-term pulses of moisture than bacteria. As such, arid and semiarid regions tend to be fungal-dominated ecosystems (Zak, 1993), and as a result, the soil faunal community is dominated by fungivores (Whitford, 1989). In these dry ecosystems, Whitford (1989) suggests that there is indirect evidence that some fungiverous mites can remain inactive in a state of cryptobiosis. It is well known that a number of nematode species can exist in a state of anhydrobiosis (Demeure and Freckman, 1981), which affords them protection during times of desiccation and is a state in which they can be dispersed by wind (Carroll and Viglierchio, 1981).

Coûteaux and Bolger, (2000) have reviewed the current information on the effects of climate change, principally elevated CO_2, on soil fauna. They come to the conclusion that there is not enough information to suggest any significant response patterns in the populations of community structure, but also that because of the complexity of interactions in soil there may be multiple consequences of changes in soil faunal activity, including changes in food resources for soil fauna, consumption of low-quality litter by macrofauna, changes in lifespan due to elevation of temperature, enhancement of earthworm burrowing activity, and changes in the species composition of the community due to differential effects of adverse conditions on different groups of animals. As fungi form a major food source in soil and there is significant selection of fungal species by soil animals, either from the saprotrophic or mycorrhizal community, it can be assumed that because of disturbance, significant changes in either abundance or species composition of the fungal community will have a major impact on fungal grazing and the populations and communities of soil fauna. The interactive effects of climate change, fungal and fungivore community response to that change, and the subsequent effects on ecosystem process is an area that warrants further investigation.

4.2.2 Influence of Faunal Grazing on Mycorrhizal Function

Grazing of extraradical arbuscular mycorrhizal hyphae by the collembolan *Folsomia candida* was shown to decrease the effectiveness of the mycorrhizal colonization of leek roots (Warnock et al., 1982). The severing of mycelial connections between the host plant root and soil reduced the effectiveness of the mycorrhiza to increase phosphate inflow over and above that of nonmycorrhizal plants. The addition of moderate densities of the collembolan *Folsomia candida* and *Tullbergia granulata* to field-grown soybean, however, resulted in an increase of arbuscular mycorrhizal colonization of roots by 40% and in leaf nitrogen by 5% (Lussenhop, 1996). There were no effects on phosphorus content

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of the plants or on the root nodule number, however. The effect of collembola on the increase in mycorrhizal colonization of roots is contrary to the findings of McGonnigle and Fitter (1987) and Finlay (1985), who showed significant declines in mycorrhizal colonization of roots. Lussenhop suggests that the density of animals in his study (6.8×10^3 animals m^2) was considerably lower than in other studies (17×10^3 animals m^2) and that high phosphate availability may have made the response of this crop different from the other studies. He suggests that the relationship between collembolan grazing and mycorrhizal colonization is curvilinear rather than linear, and that the intermediate densities of collembola used in his study could induce compensatory growth of fungal hyphae (Bengtsson et al., 1993) and thus cause an increase in mycorrhizae. In another study of the effects of collembolan grazing on arbuscular mycorrhizae and consequences for plant growth, Harris and Boerner (1990) found that the growth of *Geranium robertianum* was maximal at low collembolan densities, as compared to either high densities or the absence of collembola. They noted that the intensity of mycorrhizal colonization of roots was inversely related to collembolan density, but that there was no relationship between the intensity of root colonization and phosphorus inflow into plants, although plants with higher root colonization had the best growth. The authors suggest that the benefit of mycorrhizal association may have been through nutrients other than phosphorus (plant tissue concentrations of other nutrients were not measured) and that at high collembolan densities collembola diversified their feeding to nonfungal resources. In addition, although they report that the mycorrhizal colonization of roots was reduced at all collembolan densities, they did not suggest that compensatory growth of extraradical hyphae may have occurred at low animal density, which may have greater benefit for plant growth than the appearance of fungal structures within the root tissue. Hiol Hiol et al. (1994) performed choice chamber experiments with the collembolan *Proisotoma minuta* and ectomycorrhizal fungi. They showed that the collembola significantly slowed the growth rate of *Suillus luteus*, *Pisolithus tinctorius*, *Thelephora terrestris*, and *Laccaria laccata* cultures and the development of mycorrhizae of these species on roots of loblolly pine seedlings. It appears that there are optimal densities of collembola to stimulate root colonization and possibly plant growth. Bakonyi et al. (2002) increased the density of the collembolan *Sinella* sp. in microcosms in which maize or red fescue were grown in the presence of spores of arbuscular mycorrhizae. Significant reductions in mycorrhizal colonization were found where the collembolan density exceeded 0.2 individuals per g of soil, but there was a significant increase in root colonization by these fungi as collembolan density increased from zero to 0.2 animals per g (Fig. 4.2).

Although soil animals have been implicated in the reduction of the mycorrhizal effect of increasing plant growth and nutrient content by their feeding on extraradical hyphae, Klironomos et al. (1999) suggest that it is highly probable

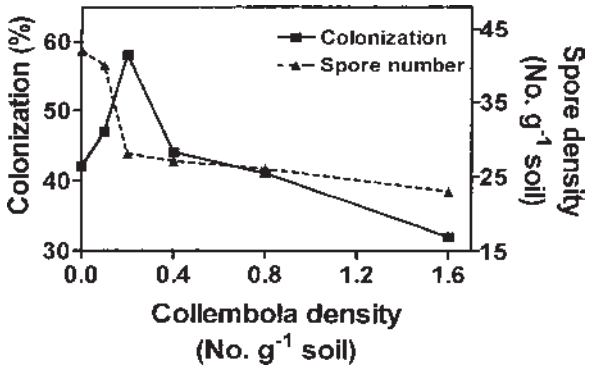

FIGURE 4.2 The effect of collembolan density on arbuscular mycorrhizal spore density and colonization of maize roots by mycorrhizae. *Source*: Data from Bakonyi et al. (2002).

that arbuscular mycorrhizal fungi are rarely grazed upon in natural ecosystems. By providing the collembolan *Folsomia candida* with a choice of saprotrophic and arbuscular mycorrhizal fungi, they concluded that the saprotroph *Alternaria alternata* was not only the preferred fungal food but that a diet of exclusively arbuscular mycorrhizal fungi reduced fecundity to the point at which no eggs could be produced by the second generation of animals (Fig. 4.3). The assumption from

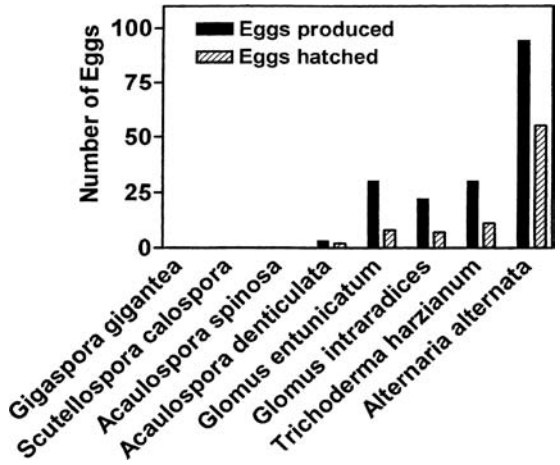

FIGURE 4.3 Numbers of eggs produced and hatched from first generation collembola (*Folsomia candida*) when fed upon a variety of arbuscular mycorrhizal fungi. *Source*: Data from Klironomos et al. (1999).

their study was that there is probably little or no effect of collembolan grazing on mycorrhizal benefit to host plants, as this functional group of fungi is avoided in favor of more nutritious saprotrophic species. This finding is in contrast to an earlier study by Klironomos and Ursic (1998), in which they suggested that despite alternate food items in the form of saprotrophic conidial fungi, collembola significantly reduced arbuscular mycorrhizal connections between the root and soil, thus reducing the beneficial effects of the mycorrhizae on plant growth. The degree of damage to mycorrhizal hyphae was shown to be a density-dependent function. These results were obtained in culture conditions, however, and it remains to be shown if indeed these animals can have a significant effect on mycorrhizal function in natural systems.

As we have seen, mycorrhizae are capable of altering the chemistry of their host plants, particularly in terms of their nutrient content. The selection of plant parts as food for invertebrates is often dependent upon the chemistry of the plant; it is possible that there could be an influence of the mycorrhizal colonization of plant roots and the palatability of above-ground plant parts to grazing herbivores. Goverde et al. (2000) attempted to test this idea using larvae of the common blue butterfly, *Polyommatus icarus*, that were fed with sprigs of *Lotus corniculatus* (Fabaceae) plants that had been inoculated with one of two different arbuscular mycorrhizal species, with a mixture of these mycorrhizae, or with uninoculated plants. Survival of third instar larvae fed with plants colonized by both mycorrhizae was 3.8 times higher than with a single mycorrhizal species and 1.6 times greater than that of larvae fed with nonmycorrhizal plants. Larvae fed with mycorrhizal plants had double the weight of those feeding on nonmycorrhizal plants after 11 days (Table 4.10). These differences are attributable to the improved chemistry of mycorrhizal plants that had three times higher leaf P concentration and a higher C/N ratio than the nonmycorrhizal plants.

TABLE 4.10 The Influence of Mycorrhizal Association of *Lotus corniculatus* on Plant Chemistry and the Performance of the Herbiverous Lepidopteran Larva *Polyommatus icarus*

Mycorrhizal treatment	Larval mortality (%)	Leaf chemistry ($mg\,g^{-1}$)			Larval fresh weight at 11 days (mg)
		P	N	C	
Nonmycorrhizal	23	3.9	5.8	40.5	13
Species 1	6	11.9	5.4	43.2	23
Species 2	6	11.6	5.2	43.4	24
Mixture	14	10.7	5.1	43.6	27

Source: Data from Goverde et al. (2000).

Furthermore, larval consumption, larval food use, and adult lipid concentrations of the butterfly differed between plants inoculated with different mycorrhizal species, suggesting that herbivore performance is mycorrhizal species-specific. On the basis that our understanding of the role of mycorrhizae in natural systems is limited and that evidence indicates that there is much less effect of mycorrhizae on plant growth in natural systems than could be predicted from laboratory and greenhouse studies (Rangeley et al., 1982; Fitter, 1985; Sanders and Fitter, 1992a,b), evidence suggesting an effect of mycorrhizae on herbivores could be a reason for the maintenance of the arbuscular mycorrhizal condition in natural herbaceous ecosystems. We thus have another example of the indirect effects of fungi on animal populations (secondary production) by the enhancement of plant food resource quality by fungal intervention.

It has been noted that the effect of root colonization by a range of ectomycorrhizal fungal species can alter the species composition of protozoa in the mycorrhizasphere (Ingham and Massicotte, 1994). Ingham and Massicotte (1994) showed that different bacterial communities were isolated from roots colonized by a variety of *Rhizopogon* species, *Thelephora terrestris*, and *Mycelium radicis atrovirens*, and that the communities were different on different tree hosts (Fig. 4.4). It is suggested that the different mycorrhizae may

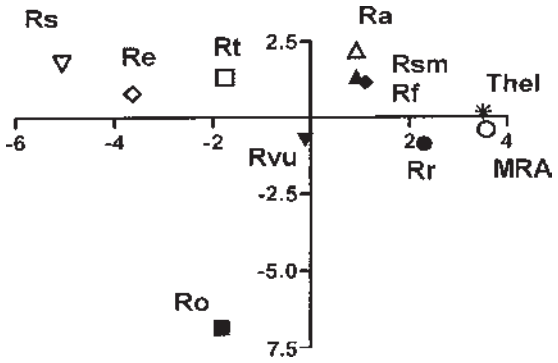

FIGURE 4.4 Principle coordinate analysis of ectomycorrhizae in protozoan species space, showing the difference in protozoan community structure of different ectomycorrhizal fungal species on roots of ponderosa pine. Four groupings appear from this analysis with similar protozoan communities on group 1 [*Rhizopogon subcaerulenscens* (Rs), *R. ellenae* (Re), and *R. truncates* (Rt)] from group 2 [*R. arctostaphylii* (Ra), *R. smithii* (Rsm), and *R. flavofibrillosus* (Rf)], from group 3 [*R. vulgaris* (Rvu), *R. rubescens* (Rr), *Thelephora terrestris* (Thel), and *Mycelium radicis atrovirens* (MRA)] from the outlier *R. occidentalis* (Ro). *Source*: The data have been reworked from Ingham and Massicotte (1994), and the first two axes account for 23% and 18.2% of the variation, respectively.

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encourage the growth of different bacterial flora, which in turn promote a different protozoan community. The authors do not, however, present any data to support the hypothesis of mycorrhizae-inducing bacterial communities that are unique to the mycorrhizal fungal species.

As it is believed that mycorrhizal plants direct much more of their photosynthates into the soil than nonmycorrhizal plants, it is anticipated that where the growth of organisms that are energy-limited, the detrital food web would benefit from the flow of C through mycorrhizal plants into the below-ground ecosystem. Setälä (2000) investigated the potential benefit of the presence of ectomycorrhizal fungi on the roots of Scots pine (*Pinus sylvestris*) on fungiverous and micobiverous representatives of soil mesofauna. Soil was defaunated and then reinoculated with 10 species of soil bacteria, 11 species of saprotrophic soil fungi, and pine seedlings, either infected or notinfected with four ectomycorrhizal fungi. Soil fauna were added with increasing levels of community complexity, including the omnivorous enchytraeid species *Cognettia sphagnetorum*, a Collembola (*Hypogastrura assimilis*), and four species of oribatid mites. After 60 weeks, pine biomass production was significantly greater in the mycorrhizal systems, the total biomass being 1.43 times higher in the presence than absence of ectomycorrhizal fungi. Similarly, almost 10 times more fungal biomass was detected on pine roots growing in the mycorrhizal than in the nonmycorrhizal systems. Despite the larger biomass of both the pines and their associated fungal community, however, neither the numbers nor biomasses of the mesofauna differed significantly between the mycorrhizal and nonmycorrhizal systems (Table 4.11). The presence of Collembola and *C. sphagnetorum* had a positive influence on pine growth,

TABLE 4.11 The Effect of the Presence or Absence of Ectomycorrhizal Associations of Scots Pine Seedlings on the Number of Soil Fauna Supported by Experimental Systems When the Fauna Are Present as Single Species or as a Mixed Community of All Species

		Faunal density (number per experimental system)	
	Faunal group	No mycorrhiza	With mycorrhiza
Faunal groups alone	Enchytraeid	83	98
	Collembola	62	18
	Mite	630	1372
Faunal groups in combination	Enchytraeid	339	44
	Collembola	14	20
	Mite	90	1235

Note: There are no statistically significant differences among the number of animals between mycorrhizal treatments because of the high variance around the mean values.
Source: Data from Setälä (2000).

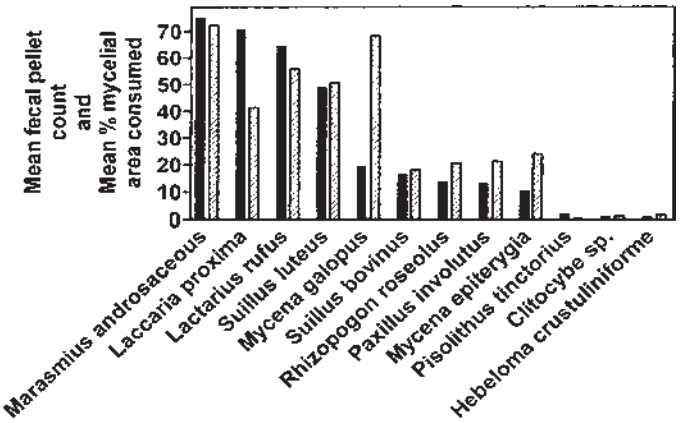

FIGURE 4.5 Hierachical feeding preference of the collembola, *Folsomia candida* on fungi as determined by mean fecal number produced by collembola and percentage consumption of the mycelial colony provided as a food source. *Source*: Data from Shaw (1988).

particularly in the absence of mycorrhizal fungi, whereas oribatid mites had no effects on pine growth. There was therefore, no simple and direct relationship between the complexity of the soil faunal community and pine biomass production. For example, the complex systems with each faunal group present did not produce more pine biomass than the simple systems in which *C. sphagnetorum* existed alone. The results of this experiment suggest that the short-term role of ectomycorrhizal fungi in sustaining the detrital food web is less significant than is generally considered to be the case. Schultz (1991) showed that there was selective grazing between different species of ectomycorrhizal fungi in pure culture by the collembolan *Folsomia candida* in the same way as Shaw (1985; 1988) (Fig. 4.5). The choice of fungal species is not taxonomically determined, as variation in palatability is seen among members of the same fungal taxon. In addition, Schultz's study also showed that the selection of fungi altered with time when fungi were combined into simple communities and direct selection between pairs of groups was allowed (Fig. 4.6). The input of plant-derived below-ground energy fuels detrital food webs. Wardle et al. (1998) suggest that negative effects on these webs could ensue from global climate change if the nature of the resources entering the system is altered as a result of increased net primary production and reduced resource quality of the litter. They suggest that this detrimental change in energy flow could be mediated through fungal–faunal interactions (Wall and Moore, 1999).

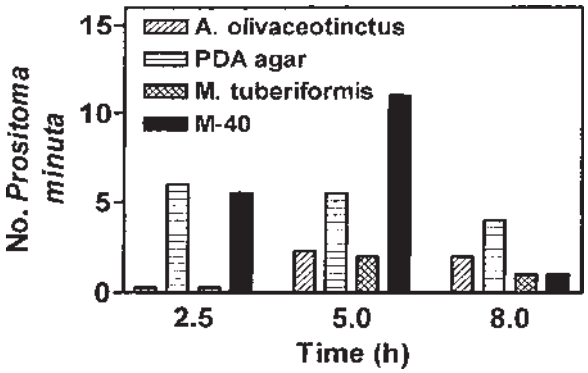

FIGURE 4.6 Changes in feeding behavior of the collembola *Proistoma minuta* over time when offered a choice of food items of the ectomycorrhizal fungi *Alpova olicaeotinctus*, *Melanogaster tuberiformis*, an unknown isolate M-40, or PDA agar in pairwise combinations. *Source*: Data from Schultz (1991).

Indirect effects of herbivory can influence fungal communities and biomass. In a study of the effects of damage to the photosynthetic apparatus of pinyon pine forest trees by the larvae of the moth *Dioryctria albovitella*, Gehring and Whitham (1991; 1994) found that there were trees that were both susceptible and resistant to moth attack. Reduction in photosynthate supply to roots of susceptible trees by moth larval grazing significantly reduced the number of ectomycorrhizal root tips formed on the trees compared to the herbivore-resistant trees. When herbivore grazing pressure was artificially removed, the mycorrhizal status of susceptible trees returned to that of resistant trees (Fig. 4.7). The effect of herbivory on mycorrhizal colonization of pine roots and growth of the host plant was greater in the stressed environment of an oligotrophic cinder soil than in a more nutrient rich, neighboring, sandy loam soil (Gehring and Whitham, 1994).

4.2.3 Influence of Invertebrate Grazing on Fungal Dispersal

McGonnigle (1997) and Dighton et al. (1997) reviewed the literature on the interactions among different soil faunal groups and fungi. Dighton et al. (1997) viewed the data with respect to faunal feeding and the ability of the animals to act as vectors of fungi, actinomycetes, and bacteria in the context of understanding the potential role of these organisms in the dispersal of genetically modified micro-organisms. The paper by Dighton et al. (1997) suggests that the most effective distribution of microbial propagules would be by larger soil organisms, which are capable of long-distance transport. Of all soil fauna the major

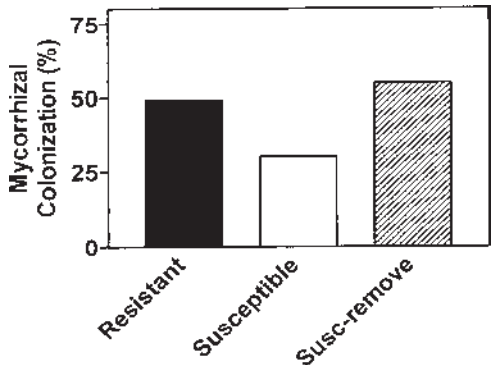

FIGURE 4.7 Degree of ectomycorrhizal colonization of roots of herbivore-resistant and susceptible strains of pinyon pine (*Pinus edulis)* under leaf-inhabiting moth herbivore (*Dioryctria albovitella*) attack and of susceptible strains of trees when herbivore pressure has been artificially alleviated by moth larva removal. *Source*: Data from Gehring and Whitham (1991) reprinted with permission from *Nature* (1991) 353:556–557. Macmillan Publishers, Ltd.

ecosystem engineers (Lawton and Jones, 1995; Lavelle, 1997) are considered to be the earthworms. As endogeic species, they are able to create burrows, which facilitate both biotic and abiotic migration of propagules from the surface soil layers to deeper soil horizons. As epigeic species, they are capable of horizontal transport of propagules for long distances. Brown (1995) reviewed the effect of earthworm activity on soil microbial and faunal community diversity. In this review he suggests the different effects of the varied ecological strategies of earthworms, depending on the size of the worm, its location in or on the soil surface, and the degree to which the worm is capable of altering the environmental conditions. Direct effects on fungi are through ingestion. These effects may alter the biomass of fungi by direct and indirect grazing, altering spore viability during passage through the gut of the worm, altering the environmental conditions by both physical and chemical means to improve or degrade the quality of microsties for fungal growth, and altering the dispersal patterns of fungal propagules. Dispersal can be enhanced by transport on or in the worm or may be reduced as leaf litter is buried and the sporulating fungi have less ability to disperse from depth in the soil. The role of earthworms in the dispersal of arbuscular mycorrhizal spores (Reddell and Spain, 1991; Gange, 1993) may be of importance in enhancing colonization of roots of newly emerging plants in the community, however. This process is of particular importance during secondary succession, during which spores from surviving vegetation can be more readily moved into areas being recolonized by plants than could be achieved via physical

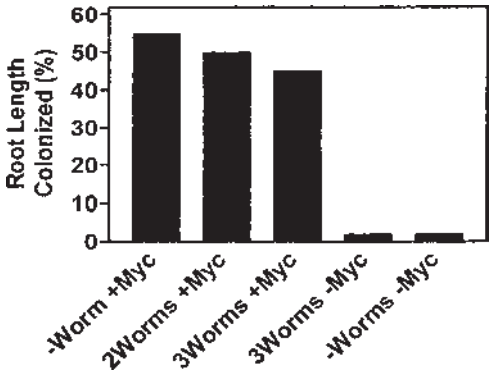

FIGURE 4.8 Colonization of roots of subterranean clover plants planted at 3-cm spacing by arbuscular mycorrhizae. The mycorrhizal inoculum and earthworms were introduced at one end of the chamber. *Source*: Data from Pattinson et al. (1997).

dispersal alone. In more recent studies, however, Pattinson et al. (1997) demonstrated that in experiments with clover plants, the presence of the earthworm *Aporrectodea trapezoids* reduced rather than increased arbuscular mycorrhizal infection of the host plant because of lateral transport of the inoculum (Fig. 4.8). They suggest that the activity of the worms disrupted the extraradical hyphal network of the arbuscular mycorrhizal fungi, preventing interplant infection by mycelial growth.

Earthworms can transport propagules of saprotrophic, mycorrhizal, and pathogenic fungi. Moody et al. (1995) showed that earthworms feed preferentially on leaf material that has been previously colonized by fungi and that they are selective with respect to the fungal species colonizing the leaf material. They used straw colonized by each of six saprotrophic fungal species, each of which had different enzymatic capabilities. They showed that there were broadly similar feeding preferences among three species of earthworms (Table 4.12). Moody et al. (1996) also showed that there was differential survival of the fungal spores on passage through the earthworm gut and that the effect was different between the earthworm species *Lumbricus terrestris* and *Aporrectodea longa*. *Fusarium* and *Agrocybe* failed to survive passage through the gut of *Lumbricus*, and both *Fusarium* and *Mucor* failed to germinate after passage through the gut of *Aporrectodea*, although the germination of spores of *Chaetomium globosum* was enhanced after passing through this worm species (Table 4.13). In a detailed study on the spores of *Mucor heimalis* Moody et al. (1996) showed that the decline in spore germination on passage through an earthworm was caused by the action of intestinal fluid, not the abrasive action of soil particles as they moved through

TABLE 4.12 Mean Number of Straw Baits Inoculated with Different Saprotrophic Fungal Species Taken by Three Earthworm Species

	Number of straw baits taken		
Fungal species	*Lumbricus terrestris*	*Aporecttodea longa*	*Allolobophora chlorotica*
Fusarium lateritium	12.8	7.9	7.4
Mucor heimalis	11.8	6.4	4.5
Trichoderma sp.	10.9	7.0	5.2
Chaetomium globosum	9.2	4.4	0.6
Agrocybe gibberosa	5.8	22	3.3
Sphaerobolus stellatus	3.6	3.0	4.8

Source: Data from Moody et al. (1995).

the gut. Indeed, they established that abrasion by soil particles stimulated spore germination.

Earthworm casts are localized sites for elevated numbers of arbuscular mycorrhizal spores and soil nutrients. In an alley-cropping agroecosystem in the tropics, Brussard et al. (1993) showed that earthworm casts had significantly higher contents of major plant nutrients derived from the interplanted tree species than from soil of the inter-row between the crops or from a monocrop (Table 4.14). This shows that the interaction between diverse resources and soil arthropods can stimuate leaf litter decomposition by fungi and bacteria to improve soil fertility.

TABLE 4.13 Viability of Fungal Spores After Passage Through the Gut of Two Earthworm Species

		Mean number of viable spores	
Worm species	Fungal species	Fed to worms	In hind gut
Lumbricus terrestris	*Fusarium lateritium*	900	0
	Agrocybe temulenta	34	0
	Trichoderma sp.	665	8
	Mucor heimalis	4060	400
	Chaetomium globosum	41	33
Aporrectodea longa	*Fusarium lateritium*	237	0
	Mucor heimalis	710	260
	Chaetomium globosum	49	76

Source: Data from Moody et al. (1996).

TABLE 4.14 Nutrient Content ($\mu g\, g^{-1}$) of Earthworm Casts in Maize—*Leucaena* Alley Cropping Tropical Agricultural Ecosystems

Position	N	P	K	Ca	Mg
Under *Leucaena*	401	8	42	191	23
Interrow	72	1.4	7.5	27	3
Monocrop	46	2	5.4	19	3

Note: The combined influence of tree derived leaf litter, consumption by earthworms, and enhancement of decomposition by fungi and bacteria significantly improve soil fertility.
Source: Data from Brussard et al. (1993).

Gange (1993) showed that earthworm feeding activity is concentrated on dead and dying root material, and as a result the worms ingest large amounts of arbuscular mycorrhizal spores. By depositing spores that are still viable in their casts, earthworms provide local sources of inoculum for establishing plant species. The number of spores per cast increases as vegetation succession proceeds (Fig. 4.9). The effect of this process is to enhance the colonization of recruits into the plant community as succession proceeds by providing available spores in patches of enriched nutrient status (worm casts), in which the opportunities for seedling establishment are increased. Doube et al. (1994a,b; 1995) have shown that earthworms of the genus *Aporrectodea* are important in assisting plant roots to be colonized by bacteria (especially species of *Pseudomonas*) that are antagonistic to root pathogenic fungi. They have shown that earthworms can be effective vectors for these biocontrol bacteria against the take-all fungus, *Gaumannomyces graminis* (Fig. 4.10).

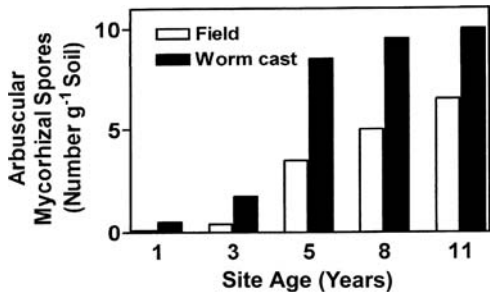

FIGURE 4.9 Mean number of arbuscular mycorrhizal spores per unit soil weight occurring in field soil and in earthworm casts at different ages of succession of a natural plant community. *Source*: Data from Gange (1993).

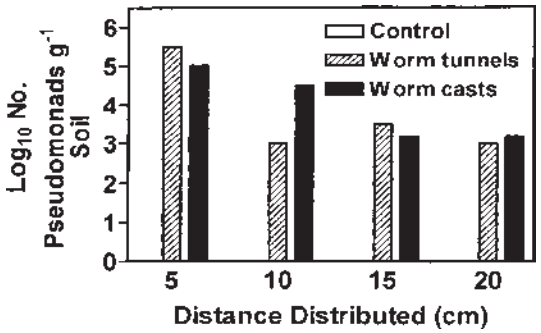

FIGURE 4.10 The effect of the earthworm *Aporrectodea trapezoids* on the distribution of the take-all biocontrol bacterium *Pseudomonas corrugata* in soil placed in a tube with earthworms and inoculum placed at one end. *Source*: Data from Doube et al. (1994b).

Dighton et al. (1997), however, point out that a number of smaller soil fauna have the capacity to transport fungal spores on their body surface and both spores and hyphal fragments in their gut. It is well known that mites are great pets of living fungal cultures, causing contamination among Petri plates. Fungal hyphae and spores are common in the gut of many mite species, particularly the Cryptosigmata (Mitchell and Parkinson, 1976; Price, 1976; Ponge, 1991). Collembola are also major fungal transporters in soil. Dispersal can be effected through carriage on the integument or by passage through the gut of spores and hyphal fragments (Visser, 1985). Visser et al. (1987) isolated over 100 fungal species from collembola in an aspen woodland ecosystem. These included saprotrophic fungi as well as plant and insect pathogens. As Lussenhop (1992) suggests, however, spores of arbuscular mycorrhizal fungi generally too large to be dispersed by microarthropods. In contrast to this suggestion, Klironomos and Moutoglis (1999) showed that the collebolan *Folsomia candida* could effect colonization of nonmycorrhizal plants from adjacent arbuscular mycorrhizal plants. They showed, however, that the effect of collembola differed among fungal species. Spores of *Acaulospora denticulata* increased their dispersal distance by 10 cm in the presence of the collembola, but the dispersal of spores of *Scutellospora calospora* was reduced when collembola were present, possibly because of spore consumption (Table 4.15). Arbuscular mycorrhizal spores may be transported by ants (Friese and Allen, 1993), which may play an important part in the colonizing of bare ground by primary plant colonizers (Allen et al., 1984). Movement of mycorrhizal spores may be greater by ants than it is by earthworms in some ecosystems (McIlveen and Cole, 1976). Apart from earthworms, the role of other soil organisms in the dispersal of fungi is little known (Dighton et al., 1997).

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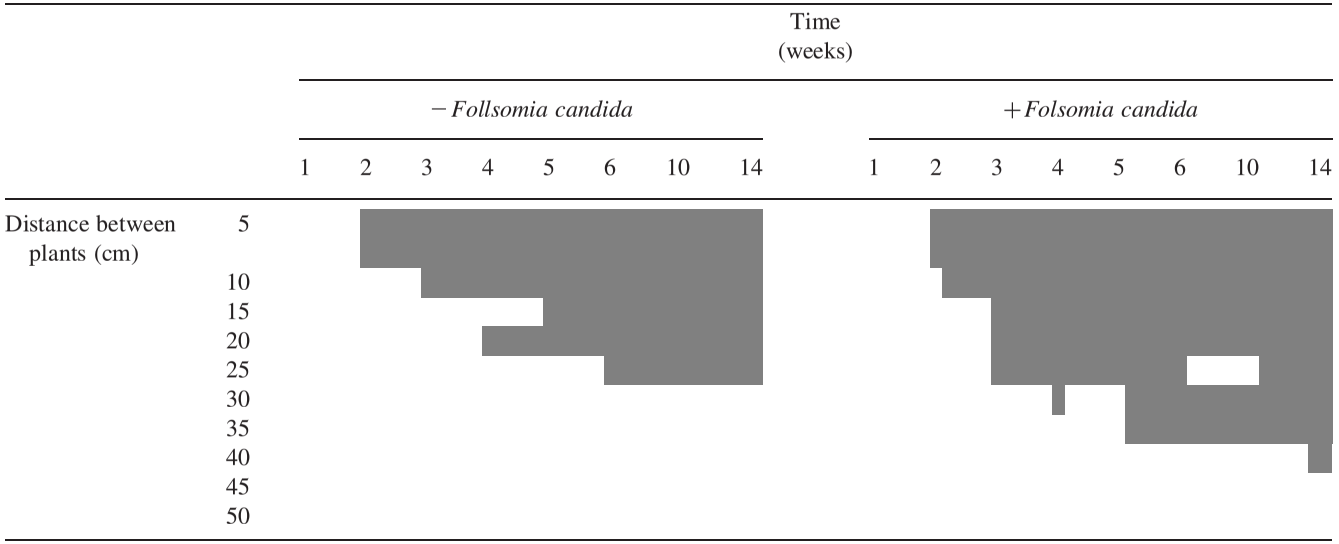
TABLE 4.15 Colonization of Nonmycorrhizal Plants by Arbuscular Mycorrhizae When Placed Adjacent to Mycorrhizal Plants and in the Presence or Absence of the Collembolan *Folsomia candida*



Note: Shaded areas indicate neighboring plants that have become colonized as a function of time (X axis) and distance (Y axis).
Source: Data from Klironomos and Moutoglis (1999).

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TABLE 4.16 The Effect of Inoculation of Seedlings of Ponderosa Pine with Feces of Tassel-Eared Squirrels and Fruit Bodies of Hypogeous Fungi

Treatment	Mycorrhizal number	(%) Seedling infection
Feces	5	33.3
Fruit body	3	20
Control	0	—

Source: Data from Kotter and Farentinos (1984).

Dromph (2001) has shown that collembola of the genera *Folsomia*, *Hypogastura* and *Proisotoma* are able to carry spores of the entomopathogenic fungi *Bauveria* and *Metathizium* on their cuticles and in their gut. Between 8%–78% of the spores carried on the cuticle and between 53–100% of the spores in feces gave rise to cultures of all three fungal species, suggesting that this type of transport of entomopathogenic fungi could be important. This work only showed the ability of these fungi to form colonies on agar, however, not in terms of infecting insect hosts. Similarly, Price (1976) and Shew and Beute (1979) showed that astigmatid mites had the ability to spread the root pathogenic fungi *Verticillium* and *Pythium myriotylum* by conidia and microsclerotia carried in the gut.

Spore dispersal of ectomycorrhizal fungi has been observed with vertebrate vectors. Trappe and Maser (1976) showed that spores of the arbuscular mycorrhizal fungus *Glomus macrocarpus* and of the hypogeous ectomycorrhizal fungus *Hymenogaster* were dispersed by small mammals (the Oregon vole, *Microtus oregoni*, and chickaree, *Tamiasciurus douglasi*). A proportion of the spores survived passage through the gut of the animals and germinated in the feces. The ability of these animals to effect spore dispersal assists in the colonization of bare ground by primary colonizing plant species during the initial phases of plant succession (Trappe, 1988). Similarly, Kotter and Farentinos (1984a,b) showed that spores of a variety (unspecified) of ectomycorrhizal fungi were viable and could develop associations with ponderosa pine after passage through the gut of the tassel-eared squirrel (*Scurius aberti*) (Table 4.16). Cázares and Trappe (1994) provide evidence to suggest that mycophagy of both hypogeous and epigeous mycorrhizal fungi results in the deposition of viable spores in feces. They show the appearance of spores of a variety of fungal genera in the feces of pika, voles, chipmunks, marmots, mountain goat, and mule deer on the forefront of Lyman Glacier, which strongly suggests that the deposition of these spores forms an inoculum source allowing colonization of the newly developing soils by early successional and slow-growing tree species (*Abies lasiocarpa*, *Larix lyalii*, *Tsuga mertensiana*, and *Salix* spp). Similar results were

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TABLE 4.17 Number of Arbuscular Mycorrhizal Spores Found in the Feces of Spiny Rats in Neotropical Forests of Central America

AM spore morphospecies	Mean number of spores in 0.05 g fecal material	SE
Glomus A	193.6	50.8
Glomus B	373.3	63.3
Glomus C	795.5	119.6
Glomus D	610.1	99.6
Sclerocystis coremioides	34.1	2.5

Source: Data from Mangan and Adler (2002).

reported by Cork and Kenagy (1989b), who demonstrated that spores of the truffle *Elaphomyces granulatus* could pass through the gut of ground squirrels and deer mouse. These spores retain viability in the feces and are thus able to colonize new seedling plants in a nutritionally favorable environment. Consumption and dispersal of arbuscular mycorrhizal spores by the Central American spiny rat (*Proechimys semispinosus*) in neotropical forests was shown by Mangan and Adler (2002) to be maximal during the fall and winter (October to December). This dispersal was positively correlated to soil moisture (good growth and germination conditions for the host tress), but unrelated to fruit availability (other food sources for the rats). These authors also showed that there was either selection of mycorrhizal spore species or differential survival through the gut, as the numbers of spores appearing in the feces differed among fungal species (Table 4.17).

4.2.4 Influence of Invertebrate Grazing on Fungal Pathogens

As worms often have higher rates of feeding at or adjacent to roots, it is not surprising that they can be involved in the activities of root pathogenic fungi. These interactions are not as simple as would be predicted by logic, however, Clapperton et al. (2001) showed that the presence of earthworms reduced the severity of symptoms of the take-all disease (*Gaeumannomyces gramminis*) on wheat. This was not due to a reduction in the abundance of fungi, but to an increase in fungi in the earthworm-colonized system. As well as increasing fungal biomass, earthworms also stimulate an increase in bacterial populations. It is suggested that the effect of earthworms on this pathogen is indirect and mediated through changes in the microbial community by as yet unknown mechanisms. It could be hypothesized, however, that an increased diversity in

the microbial community would increase the abundance of bacteria that are pathogenic to fungi and increase fungal–fungal competitive interactions.

In an indirect way, soil fauna may influence the severity of a plant fungal disease by using invertebrates as vectors of biocontrol agents. Doube et al. (1994a,b; 1995) showed that the earthworms *Aporrectodea* spp. could be used to transport *Pseudomonas* bacteria to root surfaces to protect against the take-all fungus (*Gaumannomyces graminis*).

In addition to the interactions among fungi and insect pathogens, soil fauna may also modify the efficacy of plant fungal pathogens. Recently, Sabatini and Innocenti (2000) studied the feeding preference of collembola on soil-borne plant pathogenic fungi. They determined that all of the tested species of collembola (*Onychiurus amatus, O. tuberculatus*, and *Folsomia candida*) preferred *Fusarium culmorum* mycelia, although mycelia of both *Gaeumannomyces graminis* and *Rhizoctonia cerealis* in the mixed culture continued to be grazed at a lower intensity and were capable of sustaining collembolan growth on their own. They showed that the fungus *Bipolaris sorokinaianum* was lethal to all collembolan species, however.

It can thus be seen that the dispersal of mycorrhizal spores by animal vectors can be an important component in the provision of fungal inoculum potential to sites in which vegetation regeneration is occurring. Use of this information could be made in restoration sites, in which the development of microhabitats suitable for small mammal refuges could enhance propagule dispersal and thus increase the rate of primary succession. In general, however, we do not know enough about the dynamics of fungal spore dispersal by invertebrates or the significance of faunal grazing on fungi below ground. From the few studies that have shown the propensity of soil animals to carry fungal spores or hyphal fragment, there appears to be the possibility of these animals carrying beneficial organisms to improve plant production by supplying inocula of mycorrhizal fungi or to deliver mycoparasitic fungi and bacteria to plant roots to reduce fungal pathogens (Doube et al., 1994a,b; 1995). These interactions among fungi, bacterial, and soil animals therefore requires further investigation.

4.3 SPECIFIC FUNGAL–FAUNAL INTERACTIONS

4.3.1 Ant and Termite Fungus Gardens

Soil fauna cause significant physical disturbance of soil as well as changes in the soil chemistry by the introduction of feces, leaf litter, and so on. Due to the aggregated distribution of most soil fauna, these activities increase the heterogenetity of the soil ecosystem. An example of such activity and its influence on fungi can be seen from the study of western harvester ants

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TABLE 4.18 The Effect of the Harvester Ant (*Pogonomyrmex occidentalis*) Activity on Root Length and Arbuscular Mycorrhizal Colonization of Roots of Sagebrush Community Plants

	Total root length (cm)		(%) Root colonized (cm)	
Site	Mound	Off mound	Mound	Off mound
1	49	52	34	25
2	23	118	20	11
3	127	160	27	18
4	150	180	16	12
5	255	355	21	15

Source: Data from Snyder and Friese (2001).

(*Pogonomyrmex occidentalis*) in arid and semiarid ecosystems in North America. Snyder and Friese (2001) show that the activities of these ants create nests at densities up to 30 ha^{-1}, where each nest represents an area of soil disturbance and enrichment. They found that the density of sagebrush (*Artemesia tridentata*) roots was similar in and off nest mounds, and that the root length colonized by arbuscular mycorrhizaa was similar. The intensity of root colonization was higher within the nest (Table 4.18), however. Given that nests are typically enriched in nutrients (MacMahon et al., 2000) it is surprising that there is not a greater difference in mycorrhizal colonization of roots or root length in response to this enrichment (Pregitzer et al., 1993; van Vuuren et al., 1996; Tibbett, 2000).

Of all the close associations among fungi and animals, the interaction between leaf-cutting ants and termites and their fungus gardens is an important illustration of the role of fungi in the maintenance of an insect population. This association is so close that many regard it as a true symbiosis, as the ants and termites selectively allow certain fungi to colonize and grow on the leaf pieces to provide food for their colony. Indeed, the dominant mycelium in termite nests appears to be *Termitomyces* sp., which is maintained in abundance by the constant care of the termites in the face of a greater competitor, *Aspergillus*. This balance is probably actively maintained by these animals because *Aspergillus* is less palatable or has lesser food value than *Termitomyces* (Cherrett et al., 1989; Wood and Thomas, 1989).

Bass and Cherrett (1996) found that there is a close relationship between the activities of the small worker ants of the colony "minima" workers and the production of food rewards (staphylae) produced by the fungus. The abundance of these staphylae appears to increase in smaller passages in the colony, where only

the minima workers can gain access. Indeed, activity of ants can alter the local fungal flora. Ba et al. (2000) showed that the fire ant imported into the United States from South America develops a unique yeast flora in its brood chambers. The close association between Macrotermitinae and the fungus *Termitomyces* was reviewed by Wood and Thomas (1989), and they showed that the digestive processes of termites is almost entirely dependent upon the symbiotic association with the fungus, without which wood could not be converted into a form that could be assimilated by the termite. Similarly, Cherrett et al. (1989) described the mutulaistic association in leaf-cutting ants. The fungus *Attamyces bromatificus* has never been found outside the nests of leaf-cutting ants. The ants carry a fungal inoculm to new nests in an infrabuccal pocket, a small cavity at the esophageal opening to ensure colonization of new food reserves in the new colony. Korb and Linsenmair (2001) showed that the availability of food is a limiting resource for large colonies of the fungus-cultivating termite *Macrotermes bellicosus* in two habitats in the Comoé National Park (Ivory coast). The aggregation of smaller colonies in the savannah region was probably associated with the availability of trees to provide leaves for the cultivation of fungi. This patchy distribution is also related to the availability of appropriate microclimatic conditions for fungal production, which seems to be more important for young colonies. The lower density of larger colonies in the high forest suggests a more stable environment and stable humidity for the cultivation of fungi compared to the savannah ecosystem, in which smaller colonies are more widely dispersed.

4.3.2 Bark Beetle–Fungal Interactions

The close association between wood-decomposing fungi and bark and ambrosia beetles, the evolution of the symbiotic relationship, and the physiology and behavior of the organisms involved has been reviewed by Beaver (1989). The bark beetles mainly feed on phloem which is of relatively high food value, whereas the ambrosia beetles feed on xylem, which requires a greater dependence on the fungal symbiont to improve the resource quality of the wood by partial decomposition and incorporation of nitrogen. Beaver (1989) discusses the importance of the mycangium, a specialized appendage on the insect's leg for the transport of the fungal partner, as the adult beetles have relatively little fungal material in their gut when they hatch and disperse from the tree in which they develop. In some instances there may be a tripartite interaction among plants, animals, and fungi. One of these interactions that has recently come to light and has ecosystemwide influence is the link among (1) mites, (2) specialized invaginations or tufts of hair on leaf surfaces providing refugia for mites (acarodomatia), and (3) plant pathogenic fungi. By manipulating access to diomatia by tydeid mites (*Orthotydea lambi*), Norton et al. (2000) observed the density of domatia per

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leaf and the incidence of grape mildew caused by *Uncinula necator*. They showed that the activity of mite mycophagy at high domatia densities significantly reduced the incidence of mildew on the plants.

Another complex interaction among fungi, arthropods, and plants can be seen in the blue stain fungus *Ophiostoma minus*, the mycangial fungi *Ceratocystiopsis ranaculosus* and *Entomocorticium* sp., southern pine beetles (*Dendroctonus frontalis*) a phoretic mite (*Tarsonemus* spp.,) and pine trees (Lombardero et al., 2000). *Ceratocystiopsis ranaculosus* is carried in specialized structures (mycangia) of the female bark beetle, and the fungus is necessary for the developing beetle larvae. Ayres et al. (2000) showed that the action of the fungus, when decomposing live phloem, doubles the nitrogen content of the wood/fungal matrix (from 0.4–0.86% N) (Fig. 4.11). This provides the developing beetle larvae with a nutrient-enhanced food supply, allowing for faster growth rates and more rapid maturation. The beetle also inadvertently carries the fungus *O. minus*, however, but on its body surface, not in the mycangia. Similarly, the *Tarsonemus* mite is inadvertently transported between tress by the bark beetle and has its highest population growth when feeding on *O. minus* or *C. ranaculosus*, but not on the other mycangial fungus, *Entomocorticium* sp. *Ophiostoma minus* is antagonistic to the growth of the bark beetle, so development of the two mycangial fungi into wood provides food for developing beetle larvae, but also provides fungal competition against *O. minus*. The high growth rate of the mite when feeding on *Ceratocystiopsis* reduce the growth of this fungus, allowing greater wood colonization by *O. minus*, and hence greater antagonism with the developing beetle population. There thus exists an indirect negative effect of

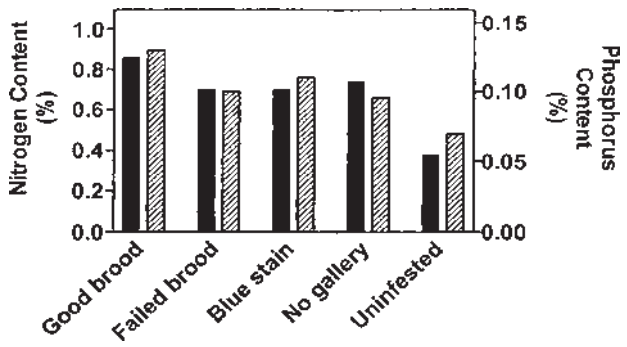

FIGURE 4.11 Concentrations of nitrogen (solid bars) and phosphorus (hatched bars) in phloem of *Pinus taeda* trees with or without infestation of *Dendroctonius frontalis* and its associated mycangial fungi. Blue stain is where the bark is also infected with the blue stain fungus *Ophiostoma minus*, which inhibits the growth of the mycangial fungi. *Source*: Data from Ayres et al. (2000).

a phoretic mite on the population of a bark beetle that appears to be regulated by induced changes in competitive abilities between fungi.

Similarly, other bark beetles and wood wasps are vectors of other fungal pathogens of trees. Redfern (1989) discussed the role of the bark beetle *Ips cembrae* in transmitting the fungal disease *Ceratocystis lariciola* and the wasp *Urocerus gigas* in transmitting *Amylostereum chailletii*, both of which cause dieback and death of larches. The degree of damage to the tree by fungal pathogens introduced by both the bark beetle and the wood wasp appears to be density-dependent. Where the population of the insects is high and causes severe attack of the tree, tree death is a likely outcome. Where insect density is low, the effect of the fungus is relatively minor (Fig. 4.12).

4.4 FUNGI AS ANIMAL PATHOGENS: NEGATIVE IMPACTS ON FAUNAL PRODUCTIVITY

In addition to the positive effects of fungi on vertebrates in terms of providing a consistent or intermittent food source, fungi can have detrimental effects on animal populations. There are many fungal diseases of humans and other vertebrates that are particularly critical when they infect individuals with compromised immune systems. Details of some of the important human fungal pathogens can be seen in texts such as those by Bulmer (1989); Evans and Richardson (1989). A discussion of these pathogens is outside the scope of this book, however. Many of these disease are not fatal on their own, but can exert enough influence on the health of their host to reduce growth and fecundity, which has consequential effects on the population of the animal.

Such pathogenic fungi can have negative effects on insect populations. In her presidential address to the Mycological Society of America, Blackwell (1994) discussed the evolution and life histories of some of these strange members of the Laboulbenales that are carried by and negatively affect many arthropods. Although these fungi are small and often obscure, they may have important effects of insect populations and are being investigated as possible biocontrol agents (Charnley, 1997; Leite et al., 2000; Freimoser et al., 2000). Charnley (1997) discussed the effect of these fungal pathogens, which are able to breach the insect defenses of an exoskelton and a variety of immune responses. Charnley (1997) lists some 20 commercial products, containing the five most commonly used insect pathogenic fungi (*Verticillium lecanii*, *Metarhizium anisopliae*, *Bauveria basiana*, *B. brongniartii*, and *Paecilomyces fumosoroseus*) for use against a variety of plant insect groups. Johnson and Goettel (1993) report that the application of spores of *Beauvaria bassiana* in fallow fields reduced the population of grasshoppers by 60% and 33% within 9 and 15 days, respectively, after application. The incidence of fungal disease in the insects declined from

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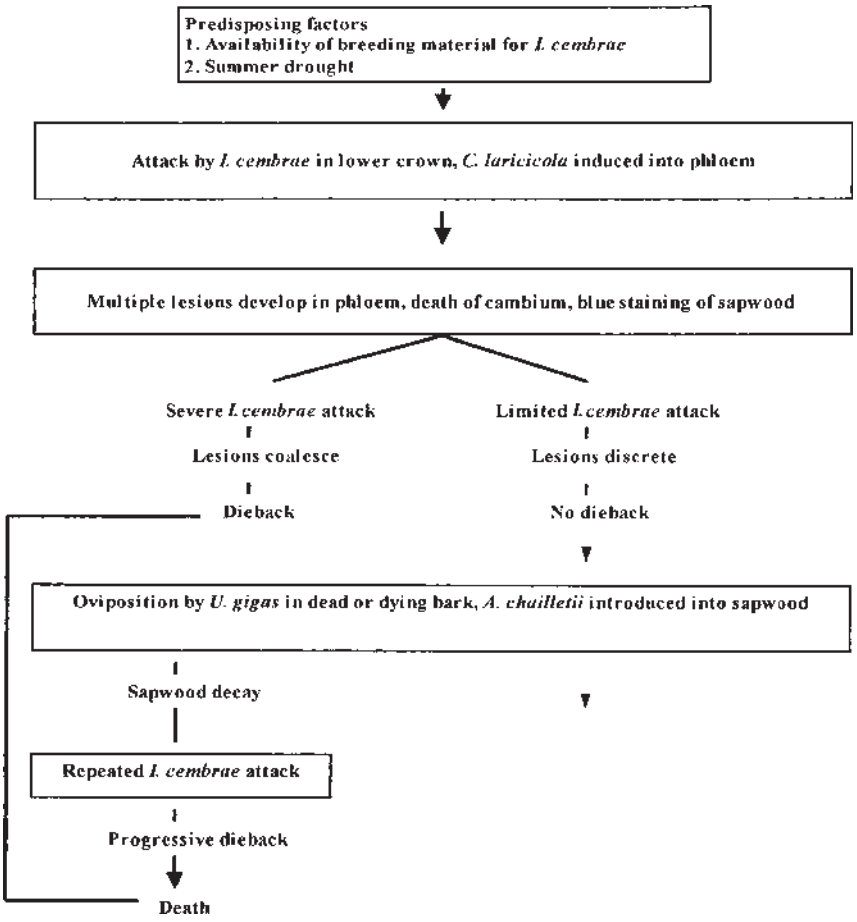

FIGURE 4.12 Interactions among the bark beetle, *Ips cembrae*, the wood wasp, *Urocerus gigas*, and the two larch fungal pathogenic fungi, *Ceratocystis lariciola* and *Amylostereum chailletti*, showing how the severity of the diseases depends on interactions between the two insects. *Source*: From Redfern (1989).

70% 2 days after spore application to 41% by 13 days, and subsequently to 5% after 19 days. Pickford and Riegert (1964) showed that the fungus *Entomophthora grylli* caused an almost complete eradication of the grasshopper *Cammula pellucida* in Saskatchewan in 1963. The high incidence of this fungus was correlated to unusually high precipitation and high humidity in June and July of that year, compared to the long-term average and previous 2 years, which favored fungal growth and reproduction.

In natural ecosystems, entomopathogenic fungi may be important density-dependent population regulators (Kamata, 2000). Hajek and Leger (1994) reviewed the literature on the biology and ecology of entomopathogenic fungi. Blakwell (1994) has specifically reviewed the literature on the Laboulbenales. Kamata (2000) considered the effect of the pathogenic fungus *Cordyceps militaris* in conjunction with avian predators, parasitoids, and abiotic factors on the population of the beech caterpillar *Syntypistis punctatella*. He concluded that the periodic population fluctuations of these larvae were caused by delayed density-dependent regulators. The fungus was the prime suspect. This causal agent was suspected as the disease started to induce population decline before it reached outbreak densities, but the delayed induced defensive response of the trees was not as closely related to the changes in the insect population (Fig. 4.13). *Cordyceps* is also reported as frequently occurring on insects in tropical forest

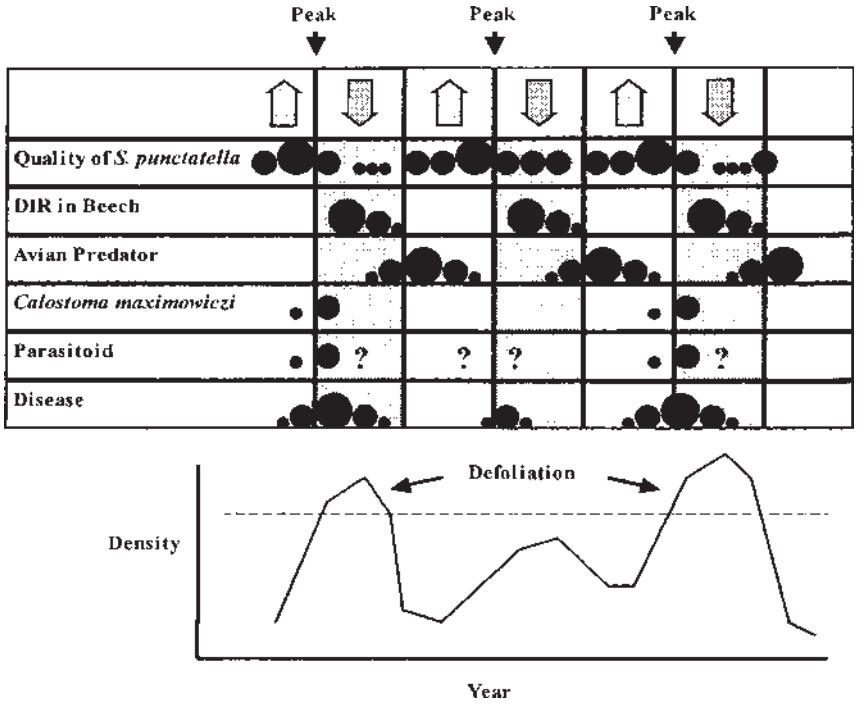

FIGURE 4.13 Model of the regulation of the population dynamics of the beech caterpillar *Syntypistis punctatella* by the delayed induced defensive response (DIR) of the beech trees and other density-dependent factors. The main correlation between caterpillar density and a regulator appears to be with insect diseases, which are mainly fungal. *Source*: Data from Kamata (2000).

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ecosystems (Evans, 1982). Evans (1982), however, stated that pathogenicity of this fungus was not tested. There was circumstantial evidence, however, that suggests that *Cordyceps* is one of the most common pathogens of arthropods. The sudden decline in the population of gypsy moth *Lymantria dispar* in Appalachian forests in 1996 was reported to be due to the high abundance of the fungus *Entomophaga maimaiga* (Butler and Strazanac, 2000), again showing how this fungus could be important in regulating insect populations. The incidence of fungal disease may be related to environmental conditions, however. Hicks et al. (2001) showed that there was a significant increase in entomopathogenic fungi in warm, wet conditions. During these weather events the populations of pine beauty moth in Scottish lodgepole pine forests were reduced mainly by fungal pathogens, whereas at other times predators were the main regulators of moth populations.

The isolation and culture of insect and other arthropod pathogenic fungi (Leite et al., 2000; Freimoser et al., 2000) may ultimately be useful in the discovery and use for the biocontrol of human pests. Onofre et al. (2001) have tested two isolates each of two species of entompathogenic fungi against the bovine tick *Boophilus microplus*. The fungus *Metarhizium flavoviride* proved to be more effective against adult ticks, reducing both larval emergence from eggs, and reproductive efficiency, than *M. anisopilae* (Table 4.19).

Mankau (1981) mentions nematode-trapping fungi that occur in the rhizosphere of plants such as *Arthrobotrys dactyloides*, *Dactylaria brochopaga*,

TABLE 4.19 Mean Lethal Dose (LD_{50}) and Conidial Density of the Entomopathogenic Fungi, *Metarhizium flavoviridae* and *M. anisopliae*, Required for Control of the Engorged Tick *Boophilus microplus*

	Mean percentage control (C%)			
	M. flavoviride		*M. anisopliae*	
Conidia ml^{-1}	CG-291	MF-3	CG-30	CG-46
0	0	0	0	0
10^4	10.7	23.7	3.1	10.3
10^5	54.6	50.9	5.1	32.4
10^6	57.3	45.7	19.5	31.9
10^7	77.9	63.2	51.6	54.8
10^8	75.9	66.8	57.2	60.0
	LD_{50}			
Conidia ml^{-1}	3.4×10^5	4.2×10^5	2.3×10^7	1.4×10^7

Source: Data from Onofre et al. (2001).

Monacrosporium ellipsosporum, and *M. gehyropagum*. These fungi, he suggests, are in the prime position to predate plant parasitic nematodes. Although research has suggested the potential of these fungi as biocontrol agents for plant pathogenic nematodes, there has been limited success in their use. Nematode egg parasitic fungi, such as *Rhopalomyces elegans*, and cyst pathogenic fungi, *Verticillium* and *Cylindrosporium* species, may also be important in regulating nematode densities. Studies suggest that 14–50% of cysts and 70–90% of eggs of nematodes may be infected with pathogenic fungi. There appears to be little information regarding the effects of these fungal pathogens on nematode population regulation, however.

Fungal diseases have been reported as important regulators of anuran populations (Kaiser, 1998; Morell, 1999; Lips, 1999; Reed et al., 2000; Warkentin et al., 2001; Fellers et al., 2001). Widespread records of frog population decline in Panama have been reported by a number of authors. Lips (1999) showed data reporting an increase in the number of dead frogs found in her surveys over recent years. Necropsies of all dead frogs showed skin abnormalities, especially around the mouth, consistent with fungal pathogens. Previously, Kaiser (1998) had reported an increase in the incidence of a chytrid fungal disease of frogs in Panama. Also, a chytrid, *Batrachochytridium dendrobatidis*, has been found in Australia, where it has been reported to be the major mortality factor in motorbike frogs (Morell, 1999). It is believed that climate changes are one of the reasons for the increase in the incidence of skin infections caused by this fungus, which can be considered to be an "emerging infectious disease" (Reed et al., 2000). These chytrids have caused oral deformities of up to 41% of larval mountain yellow-legged frogs (*Rana mucosa*) in the Sierra Nevada of California (Fellers et al., 2001). Reed et al. (2000) reported the occurrence of a variety of Chlamydia species that causes respiratory disease of up to 90% of African clawed frogs (*Xenopus tropicalis*) imported into the United States. One breeding colony lost 90% of its individuals within 4 months because of this fungal infection. The fungal infection is not confined to adult and larval frogs. Warkentin et al. (2001) showed that a filamentous ascomycete fungus was found on 7% of the egg clutches of the Panamanian red-eyed tree frog (*Agalychnis callidryas*) and accounted for 40% of egg deaths (Fig. 4.14).

Similarly, aquatic fungi, particularly members of the Phycomycetes, are important pathogens of freshwater fish. Ogbonna and Alabi (1991) isolated some 24 fungal species from fish in a Nigerian freshwater pond. With an increasing development in fish farming in this country, the authors discuss the greater need for evaluating the species of fungi responsible for infecting fish, their relative pathogenicity, the need to find either chemical or biological methods of control, as this developing economy could be of importance to the country as a whole.

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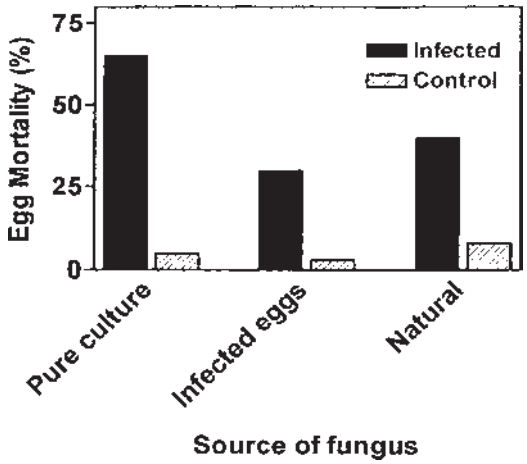

FIGURE 4.14 Percentage of red-eyed treefrog egg mortality in laboratory-cultured egg masses when infected by a pure culture of an ascomyete fungus inoculm introduced by contaminated eggs, and from a natural population. *Source*: Data from Warkentin et al. (2001).

4.5 FUNGAL–FAUNAL INTERACTIONS IN AQUATIC AND MARINE ECOSYSTEMS

The role of fungi in aquatic ecosystems has been reviewed by Wong et al. (1998). They suggest that some 600 fungal species are associated with aquatic ecosystems and that their function ranges from saprotrophs to pathogens of both plants and animals. In aquatic ecosystems interactions among fungi and leaf-shredding fauna (Amphipoda, Isopoda, Diptera, Plecoptera, and Trichoptera) have been studied (Suberkropp, 1992). It has been suggested that fungal degradation of the leaf litter "conditions" the leaf material to make it more palatable for faunal grazing. These fungi alter the palatability of the litter resource, alter its chemical composition, and appear to increase its food value. Indeed, Bärlocher and Kendrick (1975) regard aquatic hyphomycetes as intermediaries in the energy flow in stream ecosystems. They showed that the amphipod *Gammarus* increased in weight faster in relation to the amount of food ingested when provided by the fungi *Humicola*, *Anguillospora*, *Clavariopsis*, *Tricladium*, or *Fusarium*, compared to a diet of elm or maple leaves.

The selection of leaves varies among animal species, the animals are selective in the choice of fungal colonizers of the leaf material. Although the larvae of *Tipula* spp. do not select leaves that have been colonized by fungi, other shredder species do select colonized leaves. The amphipod (*Gammarus*

pseudolomnaeus) has been shown to be selective among fungal species colonizing leaf litter by favoring leaves colonized by some fungal species and not by others. *Gammarus pseudolimnaeus* has been shown to have greater growth on leaves colonized by four fungal species than six other fungal species. Trichopteran larvae have also been shown to have significantly improved rates of growth on leaf litter colonized by fungi than on uncolonized leaves. Contrary to the reports of Bärlocher and Kendrick (1975), however, Suberkropp (1992) suggests that it is not the fungus per se that elicits greater productivity of animals. Suberkropp (1992) cites work showing that certain animals, such as the amphipod *Gammarus* and the isopod *Asellus*, grew better on leaves colonized by fungi that when fed with the fungi alone or the leaf litter alone. There is thus the suggestion of some synergistic benefit. The mechanism for this, however, is unclear, as estimates show that fungal biomass accounts for 1–5% of the detrital biomass in aquatic ecosystems. Fungi make up 90–95% of the microbial biomass on decaying leaves, however, which suggests that bacteria are possibly less important as decomposers, at least in the initial stages of leaf decomposition. This fungal biomass has been shown to be insufficient to account for the increased rate of respiratory loss of carbon from fungal colonized leaves. The fungal contribution to respiration accounts for 1–57% of the total carbon respired. The most logical mechanism for enhanced growth of animals grazing on fungal-colonized leaf litter is that the biochemical changes in leaf chemistry caused by fungal attack improve the availability of essential nutrients (particularly nitrogen) and readily assimilable energy sources. In a study of the decomposition of alder and willow leaves in streams, Hieber and Gessner (2002) showed that the shredder community counted for 64% and 51% of the leaf litter mass loss for alder and willow, respectively. Fungi accounted for 15% and 18% mass loss, respectively, and that for bacteria was only 7% and 9%, respectively. Within this community of organisms, fungi were found to compose 95–99% of the total microbial biomass, which is in line with values reported in other studies. (See above.) Although fungi appear to dominate in these ecosystems, Wong et al. (1998) conclude that we still know relatively little about the diversity and functional role of these fungi.

In contrast to the terrestrial ecosystem, there is little evidence suggesting a faunal grazing effect on the fungal community structure or biomass. Suberkropp (1992) cites work showing that leaves incubated in fine mesh bags supported a more diverse fungal community with a lower mass-specific sporulation rate than leaves incubated in coarse mesh bags. This indicates a reduced biomass of fungi under potentially higher grazing intensity, the stimulation of sporulation under a more stressed (grazed) environment, and selective feeding by fauna or differential resistance to grazing within the fungal community, leading to a reduced fungal diversity in more heavily grazed conditions.

Fungi are important in marine and estuarine ecosystems. Although information on their diversity, biomass, and function is limited and less than

that for terrestrial and aquatic ecosystems, there is evidence to suggest that they play a role in supporting faunal populations. Fungal biomass in the decomposing material in salt marsh ecosystems is also important for the sustaining invertebrate herbivore populations. The amphipod (*Ulorchestia spartinophila*) has been shown to have complex dietary requirements and appears to grow best and produce the most offspring when fed on decaying leaves containing a high fungal biomass.

Kohlmeyer and Kohlmeyer (1979) show a table of 107 fungal species isolated from decomposing wood in marine habitats. These include 73 Ascomycotina, two Basidiomycotina, and 29 mitosporic species. As in terrestrial ecosystems, the low resource quality of wood appears to encourage tight linkages between fungi and fauna for its decomposition. Evidence suggests that wood-boring marine mollusks preferentially settle and feed on wood that has previously been colonized by fungi and partially decomposed rather than invading fresh wood. The associations have become so tight that, for example, the wood-boring crustacean the gribble (*Limnoria tripunctata*) has increased longevity when feeding on wood colonized by fungi. More important, it is incapable of reproduction on any substrate unless marine fungi are included as part of its diet. This may be due to the enhanced availability of proteins, essential amino acids, and vitamins, which are unavailable in the absence of fungi.

Fungi are major pathogens of marine animals (Hyde et al., 1998). Mitosporic fungi have been shown to cause disease of crustaceans (Smolowitz et al., 1992) and to cause damage to corals (Raghukumar and Raghukumar, 1991) and juvenile clams (Norton et al., 1994). Norton et al. (1994) isolated dematiatious fungal hyphae (*Exserohilum rostratum* and *Curvularia* spp.) from mantle and shell of juvenile *Tridacna crocea* clams where they were associated with decline in health. Many oomycetes are highly destructive pathogens in finfish, mollusks, and shellfish (Noga, 1990). Very few fungi have been reported as pathogens of marine plants, although some have been observed on leaves and roots of mangrove. Many marine algae are susceptible to fungal pathogens, however, primarily with chytrids and oomycetes. The impact of these pathogens on production and fitness of their hosts has not been adequately investigated. Certainly, Hyde et al. (1998) conclude in their review that the role of fungi in this ecosystem requires considerably more research than has hitherto been devoted to it. Although numerous fungal species have been isolated from marine habitats, their function is largely unknown. Similarly, Wong et al. (1998) state that the role of fungi as plant pathogens in aquatic ecosystems appears to be minor, but that many fungi are pathogenic to animals. Citing the work of Thomas (1996), they show that fungi are pathogens of fish, turtles, tadpoles, adult anurans, and many invertebrates. There are, suggestions that fungi may potentially be used as biocontrol agents for mosquitoes.

Like many terrestrial and aquatic arthropods, marine isopods contain fungi in their gut to assist in the breakdown of plant food. Cafaro (2000) showed that

several genera and species of Patagonian intertidal isopods contained Trichomycets of the genus *Palavascia*. A variety of gut symbionts, including the cultured fungus *Termitomyces*, are found in the gut of termites for the same reason (Wood and Thomas, 1989). In aquatic ecosystems, trichomycetes are also found as endosymbionts in black fly larval guts (Beard and Adler, 2002). These authors showed that there were significant differences in the abundance of different fungal species among seasons, within sites, and among sites, although no reason was given for the between-site differences. Beard and Adler (2002), however, demonstrated than new recruits to the black fly larval population rapidly became colonized by *Harpella melusinae*, suggesting a strong dependence on this fungus as a gut symbiont.

4.6 SUMMARY AND CONCLUSIONS

As a component in the ecosystem, fungi are a good food resource for grazing animals. Numerous vertebrate and invertebrate animals consume either the fruiting structures or mycelia of fungi as the main component of their diet, or more usually, as part of their diet. The fact that mushroom collecting and consumption is a tradition in many European countries is testament to their food, medicinal, and cultural value (Hudler, 1998). Indeed we point out in this chapter that the cultivation of mushrooms for human consumption is a multimillion dollar industry in the United States alone. It is thus not surprising that many animals use fungi as a food source.

For vertebrate animals, the consumption of fungi for food is often part of their diet. This part is especially important at times of the year when other foods are scarce. In artic regions, for example, when the ground is snow-covered there is little vascular plant food available. At this time, reindeer forage for lichens as their main food source. In the same way, other vertebrates around the world, particularly small mammals, make use of fungi at times when other food sources are depleted or fungi are abundant. Many small mammals also forage below ground for hypogeous fungi, whose spore dispersal is dependent on these creatures. The degree of dependence of many animals on fungi as a food source is still not entirely clear. What would be the impact on faunal populations and communities of the removal of fungi from ecosystems?

For invertebrates, both the fruiting body and the mycelium form a food base. The nutritional value of this food item is high, especially for certain groups, such as nematodes. We have documented above the role that fungi play in the maintenance of populations of fungivorous nematodes and that by selectively feeding on specific fungal species the proportion of females in the population, their fecundity, and hence the size of subsequent populations, can be strongly influenced (Ruess and Dighton, 1996; Ruess et al., 2000). Soil arthropods are also somewhat

dependent on fungal mycelia for their growth and development. Without fungi many collembola and mite populations would be reduced in the soil.

As animals graze on fungi, they are able to affect the rate of fungal-mediated ecosystem processes. The rate of decomposition of leaf litter is affected by the rate of colonization of the litter by fungi. The rate of colonization can be helped by the invasion of soil animals by the physical breakdown of leaf litter into smaller parts (comminution) and the active transport of fungal inocula (spores of hyphal fragments) into the leaf litter by animals (Ponge, 1990; 1991). The actual effect of grazing on fungal mycelia can significantly alter its growth. Intense grazing reduces hyphal growth, whereas moderate rates of grazing can stimulate compensatory growth and actually increase fungal growth. This latter effect can help fungi to grow and colonize new resources. As we have seen above, however, like humans, animals are selective in what they eat. Selection of preferred fungal species can benefit the animal by having a higher nutritional value than other species or by avoidance of poisonous secondary metabolites. This selection cannot be seen in the same way as fungal toxicity to humans, as many fungi that are poisonous to us are the preferred choice of many invertebrates, which will consume the fungi with no apparent harm! Selection of one fungus compared to another provides an asymmetric selection pressure on the preferred fungal species. Under intense grazing pressure, the growth of the preferred fungus will decline in relation to the less preferred fungus. Grazing selection and intensity can thus alter the outcome of competition of fungi within the community. A classic example of this is given above, where the preferred grazing of *Marasmius and rocaceous* over *Mycena galopus* by the collembolan *Onychiurus armatus* resulted in both fungal species being displaced from their optimal habitat in the forest floor of a Sitka spruce stand (Newell, 1984a,b). The impact of changes in the distribution of fungi in the decomposer community can affect the rate of decomposition of leaf litter and the rate of mineralization of nutrients. How important are fungal grazers to the decomposition process? Given observations of the feeding behavior of collembola in rhizotrons (Lussenhop, personal communication, 2002) it would appear that collembola spend a great deal of time grooming and then wandering around "nibbling" at fungal hyphae rather than consuming large quantities at once. How important is their grazing, given that once a fungal hyphum has been severed its translocatory function is inhibited?

In the same way that soil fauna selectively graze saprotrophic fungi, they also selectively consume mycorrhizal fungi. Again, given that a severed hyphum is useless for the transport of water or nutrients to a host plant, how important is the grazing of mycorrhizal mycelia to plant growth and fecundity? Much information is given above on the detrimental effect of faunal grazing on mycorrhizal fungi. Much of this information, however, has been gained from studies in the greenhouse or laboratory or in the field at unrealistic densities of

animals. How important is this grazing in natural ecosystems? Is it enough to cause significant decline in plant yield? Could this grazing be selective enough to affect one plant species to a greater extent than another, thus altering plant community structure?

It was mentioned above that animals are able to carry fungal propagules either on their bodies or in their gut. This ability to transport fungal propagules is important in spreading inocula through the ecosystem. It is so important that some fungal groups have evolved to rely on faunal dispersal of their spores. Hypogeous fungi, such as truffles, rely entirely on small mammals to consume the fruit body and disseminate spores in their feces. Other fungi, such as the members of the Phallales in the Gasteromycetes, have involved sticky, malodorous spore masses that attract flies, which then disperse the spores. The dispersal of fungal propagules can be important in providing, for example, mycorrhizal inoculum for plants invading bare ground during primary or secondary succession. This aspect is discussed in greater detail in the next chapter. Fungal spores can survive passage through the guts of earthworms and soil arthropods, thereby being spread to new resources, such as new organic sources for the saprotrophic fungal community or roots for the mycorrhizal fungal community. Indeed, we have seen that some animals, particularly earthworms, have potential as delivery systems of pathogenic fungi to sites in which other pests reside in soil, and thus help in biological control (Doube et al., 1994a,b; 1995).

During evolution, the close association between animals and fungi has occasionally grown to be so close that the two are inseparable. Some species of ants and termites rely on fungi as a food source to such an extent that they actively cultivate the preferred fungal species within their colony's nest. By selective grazing, the most nutritious fungal material is fed to the developing young. The colonies of fungi are also cleaned of any contaminating fungi that are either less palatable or that may compete against the preferred fungal species. In order to decompose high C:N ratio plant material of plant materials containing high levels of lignin, fungal-derived enzymes are often necessary. In addition to providing these enzymes, fungi are also able to translocate nutrients (particularly nitrogen) into such recalcitrant plant materials. It is for this reason that we think that bark beetles carry fungi in a specialized structure, or mycangium, on their legs. The fungi decompose the wood in the phloem of the tree, translocate into this wood nitrogen from more N-rich surrounding plant material, and make this resource more palatable and nutritious for the developing beetle larvae. As we note above, however, there may be more complex interactions with many more players in the game. How many different scenarios are there in nature that make use of multispecies interactions in the same way as that of bark beetle, phoretic mite, and two competing fungi (Lombardero et al., 2000)?

Thus far we have seen that fungi are important as food sources for the growth of faunal populations and that animals can help to alter fungal communities to either

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benefit or harm ecosystem processes. Fungi also act in a negative way on animal populations. Almost all animals are subject to attack by pathogenic fungi. In some animals the effect of a fungal pathogen is more dramatic than others. In particular, entomopathogenic fungi that attack insects can be of importance in natural ecosystems as regulators of populations. The effect of fungi appears to follow the rules of density-dependent interactions, whereby the effect of the fungus on the population is maximal when the animal population is at its peak (Kamata, 2000). When environmental conditions are favorable for fungal growth, these pathogens can cause devastating effects on a host animal. It is for this reason that many of these fungi are being investigated as biocontrol agents of pests of crop plants. We outline an interesting case in which nematode-trapping fungi can be introduced into pastures through the feces of cattle to such densities that they significantly reduce the population of juvenile forms of gut parasitic nematodes that reside in the soil. The effect of these fungi significantly reduces the incidence of gut parasitic nematodes in cattle and thus improves the yield of cattle and their products.

Fungal pathogens of frogs and fish can cause major declines in populations, and fungal diseases of economically important mollusks, particularly bivalves, can have serious economic impacts. From the perspective of conserving biodiversity in the tropics, the decline in anuran populations due to fungal pathogens is disturbing. Given the scenario of climate change producing conditions conducive for fungal growth, how much more important will fungal diseases of animal become?

From the information provided in this chapter we may conclude that Rayner's statement that fungi regulate populations of organisms is true for animals. The degree to which fungi are involved in different groups of animals is variable, and for some groups is largely unknown. Where fungi are not directly involved in regulating the population of animals, either for the benefit or detriment of the population, interactions among fungi and animals can take a multitude of forms and have significant effects on ecosystem processes. One problem that we still face is trying to interpolate to the real world from studies conducted under unrealistic conditions. The effects of interactions among fungi and fauna seen in contrived studies may not resemble those actually occurring in nature. This problem is not confined to the study of fungi, but is common in many ecological studies.

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5

Fungi and Population and Community Regulation

Population and community regulation can result from either promotion or reduction in the growth, fitness, or reproduction potential of an organism. If the fitness of one organism in the community is altered to a greater extent than another, the result is a changed dominance of the favored species in the community that occurs over successive generations.

In Chap. 3 we showed how primary production was positively influenced by mycorrhizal fungi that assisted plants in obtaining essential nutrients and water and by endophytes that reduced the effects of faunal grazing on the plant. In addition, we saw how plant pathogenic fungi could reduce plant production, as measured by biomass, and also by the fecundity of the plant, as measured by seed production and offspring survival. If the growth promotion or suppression is asymmetric among plant species in a plant community (i.e., not all species in the community respond in the same way or in the same direction to the influence of a fungus), there will be selective pressures exerted on members of the community. Those species exhibiting enhanced growth and fecundity will increase their abundance and standing in the community, whereas those species exhibiting reduced growth and fecundity will be reduced in their contribution to the community. In a similar way we may consider that fungal pathogens of animals could also influence both the population of the animal and its occurrence in the community of animals of the same trophic or functional group. Despite the extensive literature on the effects of fungal pathogens on a variety of faunal groups, however, there is little documented evidence on the effects of fungi on animal communities. Recent concerns, however, have been raised concerning the high incidence of fungal diseases of, for example, frogs, leading to a significant decline in their populations in

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the tropics. This is especially important, as tropical areas are being looked to as havens of biodiversity.

A variety of direct and indirect effects of fungi can both cause changes in populations of organisms and alter community composition. The interactions considered in this chapter are summarized in Table 5.1.

5.1 MYCORRHIZAE AND PLANT SUCCESSIONS

Pedersen and Sylvia (1996) suggest that one of the major components determining the success of early colonizing plants during plant seral succession is the availability of nutrients. In this context the ability of plants to associate with mycorrhizal fungi and enhance their ability to sequester nutrients from a limited resource is of benefit to the success of the plant species in the community. Indeed, it has been shown that the dispersal of spores of hypogeous fungi by rodents is an important determinant of mycorrhizal inoculum for plants in the early stages of succession on bare ground. The distribution of mycorrhizal fungal spores by animals is rarely random, however. Small mammals defecate in middens and are likely to deposit more spores in areas of active feeding sites than in other localities. This patchy distribution of mycorrhizal inoculum potential has an influence on the type of plant that can be successful in each microhabitat. For example, M.F. Allen (1991) suggested that the presence of mycorrhizae increased the diversity of plant species colonizing new areas. The patchy distribution of mycorrhizal spores, and hence inoculum potential, would allow the establishment of both mycorrhizal and nonmycorrhizal plant species in the community. It has been shown that during primary colonization, mycorrhizal inoculum potential can vary from none to abundant in locations only centimeters apart (Allen and MacMahon, 1985). In his book, M.F. Allen (1991) compares the importance of mycorrhizae in the re-establishment of vegetation following disturbance in a variety of ecosystems. From his own work he showed that vegetation colonizing Mount Saint Helens consisted entirely of mycorrhizal species, both arbuscular mycorrhizal and ectomycorrhizal forms. In contrast he cites the work of Schmidt and Scow and Hendrix and Smith in the Galapagos, where a mixture of arbuscular mycorrhizal and nonmycorrhizal plants established. In this case the distribution of mycorrhizal associations was related to soil nutrient content, with nonmycorrhizal plants developing in the more fertile, lowland soils and mycorrhizal plants establishing in the poorer rocky soils. From these and other studies, Allen and Allen (1990) hypothesized a number of patterns of mycorrhizal dependence in developing ecosystems in relation to nutrient and water availability. The pattern for regulating plant competition is given in Fig. 5.1. In a recent study of mycorrhizal colonization of plants in a primary succession on volcanic substrates of Mt. Koma, Japan, however, Titus and Tsuyuzaki (2002) found no effect of microsite on the arbuscular mycorrhizal colonization of

TABLE 5.1 Ecosystem Services Provided by Fungi

Ecosystem service		Fungal functional group
Soil formation	Rock dissolution	Lichens, Saprotrophs, Mycorrhizae
	Particle binding	Saprotrophs, Mycorrhizae
Soil fertility	Decomposition or organic residues	Saprotrophs (Ericoid and ectomycorrhizae)
	Nutrient mineralization	Saprotrophs (Ericoid and ectomycorrhizae)
	Soil stability (aggregates)	Saprotrophs, Arbuscular mycorrhizae
Primary production	Direct production	Lichens
	Nutrient accessibility	Mycorrhizae
	Plant yield	**Mycorrhizae, pathogens**
	Defense against pathogens	**Mycorrhizae, Endophytes, Saprotrophs**
	Defense against herbivory	Endophytes
Plant community structure	**Plant–plant interactions**	**Mycorrhizae, pathogens**
Secondary production	As a food source	Saprotrophs, mycorrhizae
	Population/biomass regulation	**Pathogens**
Modification of pollutants		Saprotrophs, mycorrhizae
Carbon sequestration and storage		Mycorrhizae (Saprotrophs)

Note: Services and fungal groups discussed in this chapter are in bold face type. Fungal groups in parentheses are regarded as of lesser importance in that function.

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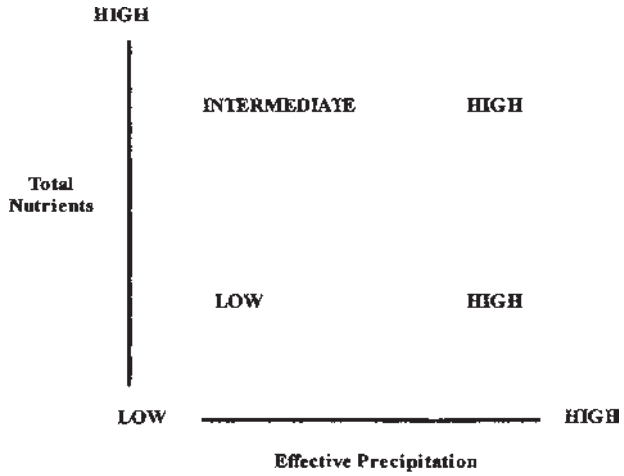

FIGURE 5.1 Hypothesized pattern of succession showing the importance of mycorrhizae in regulating plant competition during seral succession. *Source*: Data from Allen and Allen (1990).

Agrsotis scabra. *Campanula lasiocarpa*, on the other hand, showed a higher rate of root colonization by arbuscular mycorrhizae near rock than on flat sites and those occupied by *Polygonum*. In all sites, willow (*Salix reinii*) was heavily ectomycorrhizal. These data suggest that the models proposed by Allen and Allen (1990) are not only dependent on environmental factors but are also plant species-dependent.

Trappe and Maser (1976) showed that spores of the arbuscular mycorrhizal fungus *Glomus macrocarpus* and the hypogeous ectomycorrhizal fungus *Hymenogaster* were dispersed by small mammals, such as the Oregon vole, *Microtus oregoni*, and the chickaree, *Tamiasciurus douglasi*. A proportion of the spores survived passage through the gut of the animals and assisted in the colonization of bare ground by primary colonizing plant species by providing mycorrhizal inoculm (Trappe, 1988). Similarly, Kotter and Farentinos (1984a,b) showed that a variety of ectomycorrhizal fungal spores could survive passage through the gut of the tassel-eared squirrel, *Scurius aberti*, and develop mycorrhizal associations with ponderosa pine. Cazares and Trappe (1994) showed that mycophagy of both hypogeous and epigeous mycorrhizal fungi results in the deposition of viable spores in feces. In part the local deposition of feces in middens by small mammals may account for the patchy distribution of mycorrhizal spores in the environment, as seen by Allen (1991).

The appearance of spores of a variety of fungal genera in the feces of pika, voles, chipmunks, marmots, mountain goat, and mule deer on the forefront of

Lyman Glacier forms an inoculum source, allowing colonization of the newly developing soils by early successional and slow-growing tree species (*Abies lasiocarpa, Larix lyalii, Tsuga mertensiana*, and *Salix* spp). Jumpponen et al. (1999) identified "safe sites" on this glacier outwash where plant colonization was most likely. These sites consisted of concave surfaces of coarse rocky particles, which were ideal for trapping tree seeds and protecting them from desiccation. It is likely that these sites also formed foci for foraging small mammals, as they were a site of abundant food in the form of seeds. The deposition of mycorrhizal spore-laden feces in these microsites would thus further enhance the survival of germinating tree seedlings. In these harsh environmental conditions, Jumpponen et al. (1998) showed that the dark-septate mycorrhizal fungus *Phialocephalia fortinii* significantly enhanced growth of lodgepole pine (*Pinus contorta*), which is an early colonizer of the glacier forefront, but only in the presence of added nitrogen. Total plant phosphorus, however, was significantly enhanced in the presence of the mycorrhiza with no added nitrogen (Table 5.2). During the succession of plants in this recent glacial till, microbial communities change from bacterial domination to fungal-dominated communities. During this change, carbon-use efficiency changes from a high rate of carbon respiration to an accumulating phase, thus indicating that

TABLE 5.2 Effects of Mycorrhizal Colonization on the Growth and Nutrient Content of Lodgepole Pine (*Pinus contorta*) Seedlings by the Dark-Septate Fungus *Phialocephalala fortinii* in the Presence and Absence of Added Organic Matter and Nitrogen to Lyman Glacier Forefront Soil

Treatment	Plant dry weight (mg)	Total N (percentage dry wt.)	Total P (percentage dry wt.)
No N added			
No OM, No Myco	52.9	0.69	0.074
OM, No Myco	40.3	0.63	0.076
No OM, Plus Myco	48.8	0.60	0.087
OM, Plus Myco	43.1	0.62	0.100
$100\,kg\,N\,ha^{-1}$			
No OM, No Myco	81.7	1.41	0.072
OM, No Myco	104.1	1.78	0.066
No OM, Plus Myco	129.9	1.64	0.092
OM, Plus Myco	146.2	2.11	0.128

Note: Organic matter only is significant in no N added treatment for biomass, but for P content only mycorrhiza is significant. In the N added treatment, mycorrhiza is significant for biomass and P content and organic matter is significant only for N content.
Source: Data from Jumpponen et al. (1998).

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fungi are a stabilizing force in the developing ecosystem and facilitate net carbon fixation into biomass (Ohtonen et al., 1999).

The existence of successions of ectomycorrhizal species during primary succession is supported by the findings of Jumpponen et al. (1999; 2002) on the Lyman Glacier forefront. In the different plant succesional stages they identified, they found 68 ectomycorrhizal species belonging to 25 genera, with no single ectomycorrhizal species occurring on all three successional sites. The authors also found that ectomycorrhizal species diversity increased to a maximum where tree canopies started to overlap. This information corresponds to that of other studies (Dighton et al., 1986; Last et al., 1987; Visser, 1995), in which the increase in diversity of ectomycorrhizal fungi at canopy closure may be related to both the relative paucity of available nutrients (phosphorus) (Dighton and Harrison, 1990) and an increasing proportion of nutrients locked up in organic forms. It has been speculated (Dighton and Mason, 1985) that this increased diversity of mycorrhizal fungi allows the greater expression of mycorrhizal function in order to utilize the mixed available resources of inorganic and organic nutrients. Some degree of validation of this hypothesis has come from the study of Conn and Dighton (2000), in which the diversity of ectomycorrhizae growing into different tree litters reflects appropriate enzyme functions in relation to the relative availability of inorganic nutrients. Where phosphorus is immobilized during early stages of leaf litter decomposition, the ectomycorrhizal community of pine tree seedlings contained a greater proportion of acid phosphatase producing mycorrhizal types.

The succession of arbuscular mycorrhizal fungi on roots of herbaceous plant species is probably less obvious than that of ectomycorrhizal fungi. We have seen, however, that different species of arbuscular mycorrhizae may have contrasting effects on the performance of the host plant species, thus, as in the ectomycorrhizal scenario above, we may anticipate changes in the arbuscular mycorrhizal community on plants in association with changes in available resources in the environment. Indeed, Hart et al. (2001) propose two hypotheses to explain the examples of successional changes in arbuscular mycorrhizal fungal species. One of these hypotheses suggests that the mycorrhizal fungi are the driving force (drivers); the second suggests that changes in mycorrhizal species are dependent on the plant and environmental conditions and the mycorrhizae are considered "passengers" (Fig. 5.2).

The importance of maintaining a continuous mycelial mat of mycorrhizal fungi to encourage rapid development of mycorrhizal associations during colonization has been demonstrated. Amaranthus and Perry (1989) showed that when Douglas fir was planted into partially cleared sites in which mycorrhizal roots are maintained on the roots of the remaining trees, the survival of the newly planted trees was approximately 90%. Where trees were planted into totally cleared areas, the newly planted tree survival after 2 years was only 50%. They

FIGURE 5.2 A model proposing two alternate mechanisms for changes in community structure of arbuscular mycorrhizal (AMF) communities through time. The "passenger hypothesis" proposes that mycorrhizal communities are determined by the plant community, whereas in the "driver hypothesis" the mycorrhizae determine the plant species by interspecific differences in colonization and persistence potential of the fungi. *Source:* From Hart et al. (2001).

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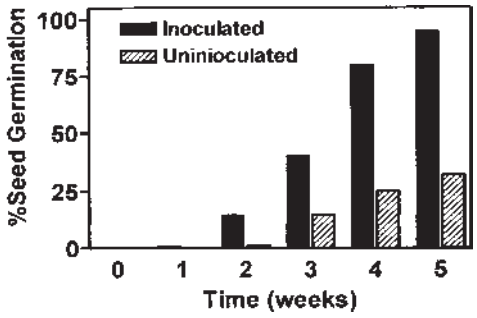

FIGURE 5.3 Effect of seed inoculation with *Chaetomium bostrychodes* on the germination of *Gmelina arborea* seeds. *Source*: Data from Osonubi et al. (1990).

attributed the reduction in survival to the lack of a viable communal ectomycorrhizal network into which the new trees could connect. It is probable that this existing mycelial network provided greater stability of the system, allowing carbon and nutrient exchange to take place between connected plants. This allows new recruits to access a larger pool of nutrients and carbon than they would be able to on their own. This synergistic activity between surviving mature plants and recruits into the ecosystem allows greater ecosystem stability and survival of the same plant species composition of the ecosystem following disturbance.

Even saprotrophic fungi can influence plant establishment. Inoculation of the seed of the pulp wood tree *Gmelina arborea* with the fungus *Chaetomium bostrychodes* has been shown to improve seed germination (Osonubi et al., 1990) (Fig. 5.3). It is probable that enzyme production by the fungal hyphae assist in seed stratification or replacement of the scarification process.

5.2 MYCORRHIZAE AND PLANT FITNESS

In addition to improving plant growth, the effect of mycorrhizal associations can lead to improvements in overall plant fitness. This improved fitness, if asymmetric, can be a method of providing competitive advantage to those plant species or individuals that respond the most to the effects of mycorrhizal colonization. These highly responsive plants will therefore become more dominant in the community. Examples of improved fitness are scattered in the literature. For example, Sanders et al. (1995) showed that plants with arbuscular mycorrhizae had improved phosphate nutrition. In addition to the enhancement of vegetative growth, which was supported by greater nutrient acquisition, there was a significant increase in flower bud and seed production in mycorrhizal

plants. These increases are related to overall plant growth and lead to greater performance of the plant as a whole rather that just becoming a larger plant. The effects of mycorrhizae on the increase in reproductive potential of plants has been noted by Koide et al. (1988), Stanley et al. (1993), Lewis and Koide (1990), Bryla and Koide (1990), and Koide and Lu (1992), the increased reproductive potential leading to improvement in offspring vigor by increased seedling germination, leaf area, root:shoot ratio, and root enzyme production. Heppell et al. (1998) showed that offspring of arbuscular mycorrhizal-infected *Abutilon theophrasti* were significantly larger than offspring of nonmycorrhizal parents, and under high-density conditions, improved even more because of the effects of early self-thinning in the mycorrhizal condition. This advantage was also transferred to the next generation in terms of total seed production (Table 5.3). The influence of mycorrhizae can, however, differ significantly among plant species, and according to Janos (1980) can be a significant factor in determining plant species composition in the tropics.

The effect of mycorrhizae on the composition of the plant community they colonize was reviewed by Francis and Read (1994). Many of the examples they cited were of two species interactions. They came to the conclusion that the effect of arbuscular mycorrhizae is most beneficial to K-selected plant species and has an adverse effect on ruderals. Francis and Read (1995) thus proposed a continuum of responses from mutualism, with positive mycorrhizal effects to antagonistic, negative effects of mycorrhizae, depending on the host plant species (Table 5.4).

Benefits of mycorrhizal colonization of the bluebell (*Hyacinthoides non-scripta*) in natural ecosystems have been shown to enhance phosphorous nutrition of the host plant at specific times of the year. Greatest phosphate uptake

TABLE 5.3 Plant Fitness Parameters of *Abutilon theophrasti* Offspring of Mycorrhizal or Nonmycorrhizal Parents

Offspring age (days)	Fitness parameter	Mycorrhizal parent	Nonmycorhizal parent
20	Shoot height (cm)	12.5	9.4
	Shoot dry mass (g)	61.2	30.9
	Leaf number	3.6	3.0
47	Shoot height (cm)	30.6	19.8
	Shoot dry mass (g)	521	154
	Leaf number	4.4	3.4
94	Survivors per box	59.1	26.6
	Seeds per survivor	17.9	10.6

Source: Data from Heppell et al. (1998).

TABLE 5.4 Responses of Different Plant Families to Arbuscular Mycorrhizal Infection Showing a Continuum of Responses from Positive at One End to Negative at the Other

+ ve				− ve
Mutualism	Commensalism	Neutralism	Antagonism	
Asteraceae	Burmanniaceae	Gramineae	Boraginaceae	Brassicaceae
Ericaceae	Gentinaceae		Caryophyllaceae	Chenopodiaceae
Fabaceae	Monotroaceae		Resedaceae	Polygonaceae
Liliaceae	Orchidaceae		Scrophulariaceae	
Pinaceae	Triuridaceae			
Plantaginaceae				
Ranunculaceae				

Note: This variation in plant response is thought to invoke differences in competitive fitness of plant groups and thus determining plant community structure in any given set of environmental conditions.
Source: Data from Francis and Read (1995).

occurred when there was reallocation of nutrients from the resting bulb to rapidly growing above-ground plant parts (Merryweather and Fitter, 1995a). The degree of dependency of bluebell plants on their mycorrhizae appears to increase through age. Young bulbs are phosphate rich and inhabit upper soil layers; however, because of their susceptibility to frost, summer desiccation, and herbivory, the bulbs at greater depth have higher rates of survival. The trade-off for this enhanced survival at depth is a reduction in the availability of soil phosphate at deeper depths; thus the plants supported by deeper bulbs become more dependent upon their mycorrhizal fungi (Merryweather and Fitter, 1995b). In contrast, Sanders and Fitter (1992a) found that the level of arbuscular mycorrhizal colonization of roots of mixed plant assemblages in a natural grassland varied among plant species but not significantly within species over time. They could thus not come to any conclusion about the benefits of mycorrhizal associations. Sanders and Fitter (1992b) also could not correlate plant phosphorus, heavy metal content, and biomass to the degree of root colonization by mycorrhizal structures. They thus suggest that the influence of mycorrhizae in altering plant fitness may be nonnutritional, but as yet is unspecified.

The distribution of fungal species in a mixed community of arbuscular mycorrhizal plant species is not homogenous. Johnson et al. (1992) showed that the arbuscular mycorrhizal community differed among five plant species of a grassland community. In the same way, Eom et al. (2000) showed that the different species of plants in a tallgrass community have differing arbuscular mycorrhizal fungal associates (Fig. 5.4). This information lends credence to the idea that there are feedbacks between the mycorrhizal fungal associate and

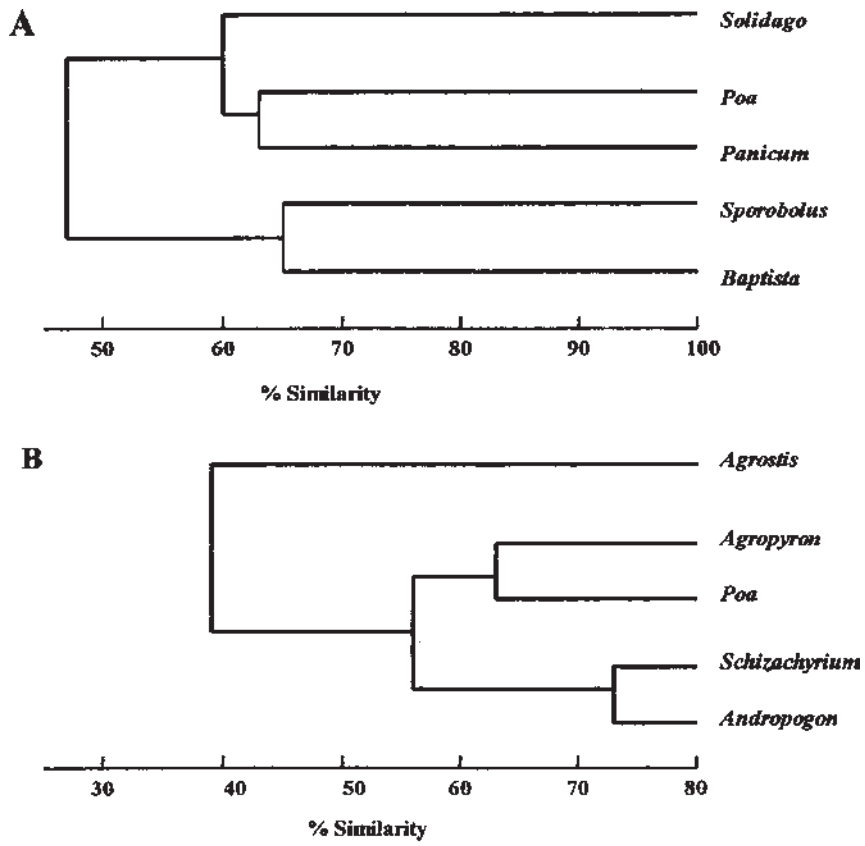

FIGURE 5.4 Cluster analysis of the similarity of arbuscular mycorrhizal fungal species associated with five host plants from: A, a mixed species tallgrass prairie ecosystem (data from Eom et al., 2000); and B, garden plots in a native grassland (data from Johnson et al., 1992).

the plant that enable the plant species to dictate the fungal species assemblage and vice versa. In a similar way, van der Heijden et al. (1998) showed that the arbuscular mycorrhizal fungal community strongly influenced the plant species composition of members of a European calcareous grassland ecosystem that was constructed in mesocosms. At low mycorrhizal species diversity the plant species diversity varied widely as the arbuscular mycorrhizal species in the community we are altered. Altering the species composition of the mycorrhizal fungi did not cause such large changes in the plant species composition at high mycorrhizal species diversity. At these high mycorrhizal diversities, nutrient acquisition by

the host plant community increased, leading to greater biomass accumulation. This information shows that the variability in function (nutrient acquisition) between a low diversity of mycorrhizal fungal species results in greater asymmetric beneficial effects for plant growth. The resultant patchy effect on growth among plant species would have considerable effects on the structure of the plant community if the growth of some species is enhanced more than others. At high mycorrhizal diversity, however, each plant and each plant species has a greater chance of associating with an efficient mycorrhizal species. In this case, the asymmetry in benefit is lost, a more even beneficial effect of the mycorrhizae is seen throughout the plant community, and a shift in plant species community structure is unlikely.

In a study of the effects of different arbuscular mycorrhizal fungi on the growth of the clonal plant *Prunella vulgaris*, Streitwolf-Engel et al. (2001) showed that the number of ramets produced by the plant was significantly related to the mycorrhizal species (Fig. 5.5). They also showed, however, that stolon length and spacing between daughter plantlets was determined by host genotype, not directly under the influence of the mycorrhizal partner. As was the case in the study of McHugh (unpublished) on *Spartina* spp., we can see that both the presence of arbuscular mycorrhizal fungi and the species composition of the mycorrhizal community influence the ability of clonal plants to colonize new areas by the production of stolons. This attribute provides the plant with greater competitive abilities, which could be used to enhance site restoration.

The differential influence of different mycorrhizal species in the community may in part explain the effects of fungicide on plant species

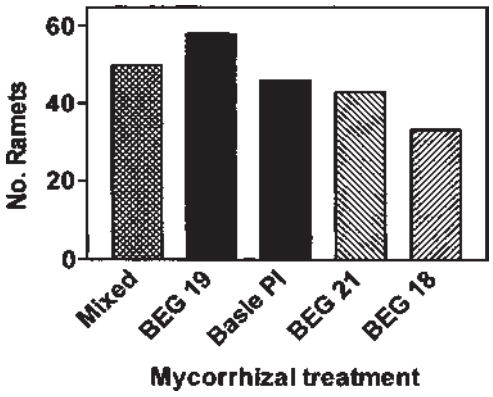

FIGURE 5.5 Mean number of ramets produced by the clonal plant *Prunella vulgaris* when roots are colonized by a mixed community or specific strains of arbuscular mycorrhizae. *Source*: Data from Streitwolf-Engel et al. (2001).

diversity shown by Gange et al. (1993). Here, the addition of fungicide reduced the total root colonization of the plant community by arbuscular mycorrhizae, which in turn reduced plant species diversity. It is possible that the fungicide had differential effects on different species of mycorrhizal fungi, thus reducing mycorrhizal diversity. It must be remembered however, that soil factors may also confound these interactions (Johnson et al., 1992).

The effect of the degree of mycorrhizal infection on the outcome of two competing plant species should explain the results shown above. Watkinson and Freckleton (1997), however, modeled the interactions between the grasses *Holcus lanatus* and *Dactylis glomerata* in the presence and absence of mycorrhizal infection. Although the effect of mycorrhizal colonization of roots altered the competition/plant density response surface slightly, *Holcus* always dominated over *Dactylis*, suggesting that the increase in plant performance conferred on the plant by the mycorrhizal association was compensated for by changes in the intra- and interspecific competition strengths.

The competition among plants for nutrients is often given as a reason for the evolution of specific plant assemblages, by which some plant species are more able to access limiting nutrients than others. This is one of the prime reasons why plant succession occurs. The role of different mycorrhizal associates in the process of competition among plants for available soil phosphorus was investigated by Pedersen et al. (1999). They grew slash pine (*Pinus elliottii*) intentionally inoculated with the ectomycorrhizal fungus *Pisolithus arhizus* or fortuitously colonized by *Thelephora terrestris* and a native grass (*Panicum chamaelonche*), which associates with arbuscular mycorrhizae. Pine inoculated with *P. arhizus* took up more P when competing with the nonmycorrhizal grass than when competing with another pine, irrespective of the mycorrhizal status of the competing pine seedling. From an analysis of the phosphate uptake kinetics, it was found that pine is more competitive at higher nutrient concentrations, while the grass is more competitive at lower nutrient concentrations, suggesting a separation in niche between the two plants.

The degree of response to mycorrhizal infection by each of the component plants in a community may or may not be similar. Taking Simpson's paradox as the basic model, by which the response of the whole may not be based on the response of the individual parts, Allison and Goldberg (2002) explored the responses of individual plant species in communities to both arbuscular mycorrhizal association and the availability of phosphorus in soil. Their data set was derived from the published literature. Their conclusion was that they could not predict an overall community response that was the sum of consistent trends in response of the component plant species. They were therefore forced to reject the first hypothesis that the degree of dependence of all plant species increased as available phosphate levels declined, based on the fact that all individual plant species had consistent response trends in the same direction (Fig. 5.6a). Their

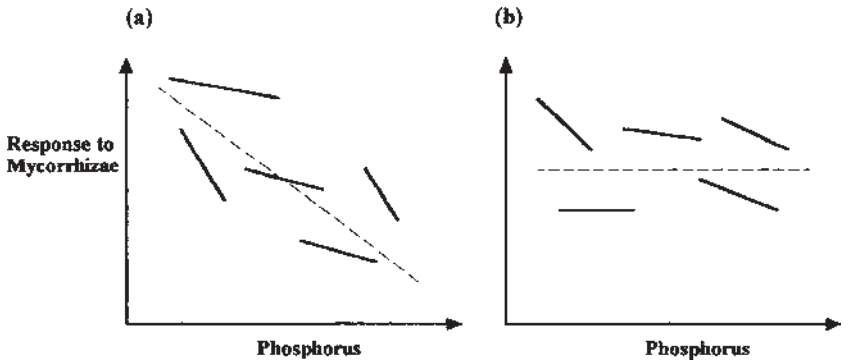

FIGURE 5.6 Models of the response between arbuscular mycorrhizal plants to mycorrhizal infection and soil phosphorus availability. Graph a depicts each plant species in the community responding in the same way, with a reduction of mycorrhizal colonization of roots with increasing P supply. In this situation, the net ecosystem effect is for a general reduction in mycorrhizal associations. Graph b depicts a variable response of each plant species in the community, resulting in a net lack of mycorrhizal response throughout the ecosystem. *Source*: From Allison and Goldberg (2002).

second hypothesis stated that the direction of response of each individual plant species to degree of mycorrhizal infection in relation to P supply was different. As a consequence, there was no net community response (Fig. 5.6b). If this second hypothesis is really what happens in plant communities, it is easy to see how the varied responses of the individual plant species to both mycorrhizal colonization and environmental variables would lead to changes in community structure as conditions changed. The magnitude of the effect of mycorrhizal fungi to influence this change would be proportional to the relative effect of plant fitness enhancement provided by the mycorrhizal fungi to each individual plant species.

The influence of mycorrhizae on plant performance is influenced by edaphic controls exerted by changes in soil chemistry. Bever et al. (1997) developed a model to explain the importance of feedback mechanisms between the soil community and plant population dynamics. Using mixtures of four plant species, they demonstrated that growth could be enhanced or inhibited by soils in which the same or different plant species had been previously grown (Fig. 5.7). They suggest that changes in the soil organisms and nutrients or plant-antagonistic chemicals can act in either a positive or negative feedback mechanism to affect growth of subsequently planted species. Similar changes in plant fitness can be related to small-scale in soil nutrient availability heterogeneity. Farley and Fitter (1999) showed that root proliferation of seven

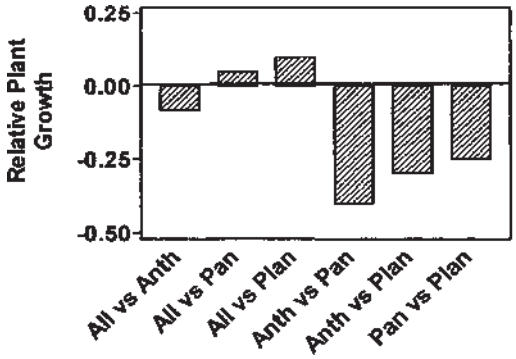

FIGURE 5.7 Test of feedback of soil communities and plant growth for the species *Allium* (All), *Anthoxanthum* (Anth), *Panicum* (Pan), and *Plantago* (Plan). The Y axis is the growth of plants in their own soil relative to that in each other's soil. *Source*: Data from Bever et al. (1997).

co-occurring woodland plant species responded differently to localized nutrient-rich patches in soil. This difference in response was not affected by mycorrhizal status, but the differential growth response led to an improved level of competition by the plant species that responded by producing more root biomass.

The effect of leaf litter chemistry on the growth of roots and ectomycorrhizal community structure has been shown many times (Baar and de Vries, 1995; Baar et al., 1994; Walker et al., 1999; Conn and Dighton, 2000; Dighton et al., 2000). The effect of weed species leaf litter on the growth and mycorrhizal development of a native tree species was shown by Walker et al. (1999). They showed that leaf litter of *Rhododendron maximum*, an invasive weed of southern Appalachian forests, affected the growth of native hemlock (*Tsuga canadensis*). Hemlock tree seedlings planted under hemlock litter had three times the intensity of ectomycorrhizal colonization of their root system, four times the root ramification (branching), and twice the biomass of trees planted into leaf litter form rhododendron thickets (Fig. 5.8). In addition, trees in rhododendron litter had a significantly higher proportion of *Cenococcum geophilum* mycorrhizae than trees outside rhododendron litter. It is suggested that these changes are important in driving the trajectory of vegetation community development in regenerating forests in this ecosystem. This gives us a hint of the effects of leaf litter leachates or root exudates from one plant that affects a second plant. This activity is often referred to as allelopathy and will be discussed further later in this chapter.

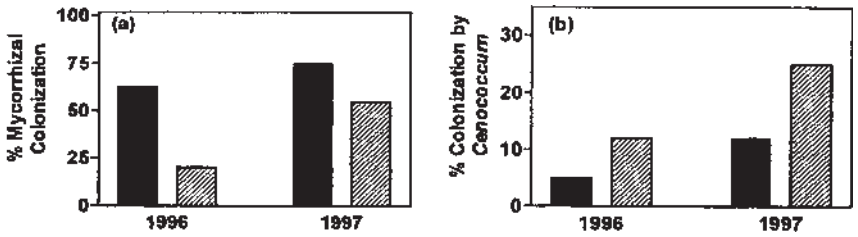

FIGURE 5.8 Total mycorrhizal colonization (a) and proportion of *Cenococcum geophilum* mycorrhizae (b) on hemlock trees in the presence (solid bars) and absence (hatched bars) of *Rhododendron maximum* leaf litter. *Source*: Data from Walker et al. (1999).

Recently direct net transfer of carbon or nutrients between plants in the community has been shown to occur in natural ecosystems. Formerly this ability of interplant linkage through mycorrhizal bridges has only been demonstrated in controlled conditions. Simard et al. (1997a,b,c) showed transfer of carbon from paper birch (*Betula papyrifera*) to Douglas fir (*Pseudotsuga menziesii*) in both partial and deep shade. They showed that the amount of carbon transferred between plants represented 13–45% of the carbon contained in shoots for *P. menziesii* and 45% for *B. papyrifera*, respectively. This represents a considerable supplement of photosythetically derived carbon to the recipient plant. Wu et al. (2002) also showed that 24% of ^{14}C label occurring in the underground parts of pine seedlings was allocated to the extraradical hyphal component of their ectomycorrhizal association. They concluded that much of this carbon would be available to other plants that could share the same mycorrhizal symbiont. This sharing of resources between different plant species within the community thus alters our concept of the stability of plant assemblages being based on competition among plants for available resources (nutrients, water, and light). The new paradigm should incorporate both competition and synergism between plants within a community. We do not know the extent of this sharing of resources between plants via mycorrhizal connections, however. The examples shown here represent conditions in which one plant is at a disadvantage by being in the shade. If source-sink relations do not differ between connected plants, does the linkage become redundant? One could also envisage that these connections could be used for parasitism of one plant upon the other. Examples exist in the natural ecosystem in which this occurs, such as the achlorophyllous plant *Monotropa*, which shares mycorrhizal associations with the roots of trees (Smith and Read, 1997). This association was used as one of the first demonstrations of carbon transfer between plants, assumed to be via the mycorrhizal connection

(Björkman, 1960) and considered by Björkman to be an example of epiparasitism.

These interplant connections may be important in determining the coexistence of arbuscular mycorrhizal plant communities. Walter et al. (1996) demonstrated the existence of interplant transfer of phosphorus in tallgrass prairie communities. The amount of phosphorus transferred from donor to recipient plant was species-dependent and decreased with increasing distance between neighboring plants. The transfer between plants was greater within forbs and cool season C_3 grasses than in C_4 grasses, indicating selectivity in the interplant transfer. This difference may alter the competitive abilities of the plant. The effect of benomyl as a fungicide to reduce mycorrhizal infection did not alter rates of transfer of phosphorus, probably as mycorrhizae were still present in the benomyl-treated plants. In an experiment to demonstrate the effects of arbuscular mycorrhizal association on intraspecific interactions, Ronsheim and Anderson (2001) surrounded a target *Allium vineale* plant with genetically identical neighbors, neighbors from the same population, or neighbors from a different population. The presence of mycorrhizal fungi was beneficial for plant growth, especially if the neighbors were genetically identical or from the same population as the target plant. There is thus specificity in the interaction between *A. vineale* plants and the soil fungal community at the population level that specifically favors intraspecific interactions among plants from the same population. This finding suggests that plants from the same population are able to share a more efficient hyphal network than if individual plants were spatially separated.

5.3 PLANT PATHOGENS AND PLANT FITNESS

Harper (1990) casts some doubt on the role of pathogens in altering populations and communities of their hosts. He cites examples of dramatic negative effects of fungal pathogens on introduced or alien plants or on native plants by alien fungal pathogens. He suggests, however, that such dramatic effects of pathogens are rarely seen where there has been evolution of communities of organisms in their natural environment. Is it possible that the extreme interactions have already been played out earlier in the development of the plant communities, and that the current interactive responses of alien and native species of plants or fungi only represent what has happened in the past?

Much of the effect of plant pathogens on plant populations or plant production has been recorded from exotic pathogenic fungal species or the effect of resident pathogens on exotic plant species. Indeed, the problems associated with the global movement of invasive plants and fungi are attracting increasing interest from researchers, farmers, and economists (Rossman, 2001). In particular, the rapid evolution of introduced plant pathogens by genetic change, induced by their new environmental conditions, is of great concern in terms of

devising potential control methods (Brasier, 2001). The survival of economically important exotic crops continues to be challenged by the emergence of local diseases that adapt to new host plants. Wingfield et al. (2001) discuss the impact of exotic fungi on exotic plantation forest trees in the tropics that can induce severe loss of forest trees with disastrous economic consequences. Brasier (1990) reviews the devastating effects of the chestnut blight fungus *Cryphonectria parasitica*, which was probably imported from China, on chestnuts in North America. The rapid spread of this disease, at about 37 km per year, and significant reduction in fitness of the host tree, which now exists as an understory shrub species rather than a dominant canopy tree, is witness to the effect of an introduced pathogen. In a similar way, the fungus *Ophistoma ulmi* caused extensive decline in the elm populations of Europe and North America. Resistance of the trees was seen to occur, however. Some of this apparent resistance is because of the genetic variation in host plants producing actual resistance (Burdon et al., 1990; Crute, 1990), but some was due to the presence of fungal pathogenic mycoviruses (Brasier, 1990) that reduced the effectiveness of the fungal pathogen.

In a similar way, the decline in oaks in southern Europe due to the destructive effects of the oomycete pathogen *Phytophthora cinnamomi* has been reviewed by Brasier (1996). In the Mediteranean regions, this fungus has been responsible for significant decline in the evergreen oaks *Quercus suber* and *Q. ilex*, thus significantly altering the community structure of the oak forest ecosystems of this region in Spain, Portugal, Tunisia, and Morocco. The spread of this fungus through soil is by virtue of motile oospores that require wet or waterlogged soil for optimum dispersal. Climate change models of this area predict increasing rainfall in these regions, which would result in a potential increase in the rate of spread of the disease. Brasier (1996), however, suggests that the severity of cold winters in central and northern Europe would limit the northward spread of *Phytopthora*

Alexander (1990) chronicles the effect of a fungal pathogen (*Ustilago violacea*) on the alien plant species (*Silene alba*) in the eastern United States. This anthersmut fungus invades the stamens and replaces them with fungal structures. In female flowers, the fungus causes abortion of the ovary. Even if the fungus systematically infects the plant, there appears to be little effect on the survival of the plant other than a loss of its reproductive potential. Some plants within the community develop resistance to the pathogen, so the ready dispersal of fungal spores and the patchy occurrence of resistant plants results in a fragmented community of plants with varying degrees of fungal infection within them. It is therefore likely that this heterogeneity maintains some equilibrium between the abundance of host plants and the pathogenic fungus. This may be what occurs during the evolution of plant communities, exploring why there is no evident effect of fungal diseases on natural plant communities.

Paul (1990) suggests that the interactions among the host plant, pathogenic fungus, and environment can significantly vary the outcome of the severity of the pathogenic symptoms. For example, he suggests that the degree of loss of photosynthetic capacity of a plant due to fungal invasion will be greater in a plant growing in the shade than one growing in full light. Similarly, he cites work to support the fact that fungal pathogen effects are greater in nutrient-poor or droughty conditions, in which the fungus competes with the host plant for limited resources. The level of the impact of a pathogen thus may be greater on plants growing in marginal habitats than those in optimal habitats. This would certainly alter the competitive abilities of plants growing in marginal conditions. This reduction in fitness of a pathogen-infected plant is significant when the host plant is grown in a mixture with a nonhost plant. The reduced performance of *Senecio vulgaris* in the presence of the fungal pathogen *Puccinia lagenophorae* was shown to improve the competitive abilities of *Lactuca salvia* (Paul and Ayres, 1987), *Euphorbia peplus* (Paul, 1989), and *Capsella bursa-pastoris* with which they were grown.

Hansen and Goheen (2000) reviewed the effects of the root rot fungus *Phellinus weirii* in coniferous forests western North America: which are, largely composed of hemlock and Douglas fir. The fungal pathogen slowly kills trees and the infection spreads from a central infected tree to neighbors in such a way that on death, gaps are created in the forest, allowing invasion by other plant species. Within these gaps the diversity of vegetation during successional colonization increases in both species richness and evenness, compared to the original species composition. Changes in the resistance of trees to the pathogen appear to be due to the nutrition of the host tree. As the infection front advances, dead trees contribute to the nutrient pool in the soil, and the elevated level of nitrogen available to the succeeding generation of trees confers a greater resistance to the pathogen. Indeed, Zhang and Zak (1998) showed that the changes in bacterial and fungal activity in gap soils was significantly different from that under closed canopy forest in subtropical forest ecosystems. This change in metabolic activity increased plant litter decomposition in gaps, creating greater mineralization of nutrients.

Alexander and Mihail (2000) determined if the effect of seed and seedling mortality due to a fungal pathogen on plant population dynamics depended on the degree to which growth and reproduction of surviving individuals compensate for deaths. Using the annual plant *Kummerowia stipulacea* at three planting densities and the root fungal pathogen *Pythium* species, they found that high sowing density reduced seedling establishment and size. In the presence of the pathogen, seed and seedling survival was low and plants were initially smaller, but at maturity, the average surviving pathogen-infested plants were larger than in the other treatments. This suggests that the effect of the pathogen allows the surviving plants to be released from intraspecific competition. There thus may be a role for

fungal pathogens in determining interplant spacing to minimize competition and increase fitness. Interactions between shade and available water levels in the competition between oak and woody shrub species in savanna ecosystems suggests that the intervention of oak wilt fungi can cause a difference between competition between oaks and woody shrubs and facilitation of shrub layer communities (Anderson et al., 2001). Water tables around healthy mature oaks were lowered, thus reducing shrub layer community development, but shrub layer communities were able to establish where oak wilt reduced the growth of oak trees.

The effect of reduction of plant fitness during the process of primary or secondary succession can alter the trajectory of the assembly of plant species in the community. Holah et al. (1997) showed that the effect of the root-rotting fungus *Phellinus weirii* reduced the development of Douglas fir (*Pseudotsuga menziesii*) in areas of pathogen abundance (infection centers). These areas were colonized more successfully by shrubby growth of western hemlock (*Tsuga heterophylla*), thus changing both the species composition and the canopy architecture of the forest (Fig. 5.9). In contrast, the effect of introduced anthracnose of dogwood caused by *Discula destructans* has caused a change in the plant community structure of forest ecosystems of the Cumberland Plateau in Tennessee. By selectively reducing the population of dogwood trees, the vegetation has become dominated by two bird-dispersed tree species, blackgum and spicebush. In addition to the change in the forest community, loss of the dogwood trees has reduced the cycling of calcium in the ecosystem, with the consequential effects of the reduced availability of calcium to birds through their insect food, resulting in poor egg survival (Hiers and Evans, 1997).

A rather more remote interaction between plant pathogens and plant performance is discussed by Whitham and Schweitzer (2002). The ecosystem-level effects are brought about by changes in leaf litter chemistry as a result of leaf-inhabiting fungal pathogens. Pathogens induce the development of higher levels of plant-defense chemicals (polyphenols), especially tannins. The higher content of these chemicals reduces the palatability of dead leaves to soil fauna, and by increasing the C:N ratio of leaf material, reduces the ability of saprotrophic and mycorrhizal fungi to decompose the leaf litter and obtain nutrients from within (Hättenschwiler and Vitousek, 2000). Hättenschwiler and Vitousek conclude that with repeated or sustained high pathogen levels in plants, this positive feedback mechanism could reduce soil fertility at a local and possibly regional level.

Interest has also arisen in the potential role of fungal pathogens as biocontrol agents for commercially important and exotic plant species. For example, Pieckenstain et al. (2001) showed that the fungus *Epicoccum purpuascens* produces antifungal compounds to inhibit *Sclerotinia* head rot in sunflowers. In agriculture, Tsahouridou and Thanassoulopoulos (2002) have

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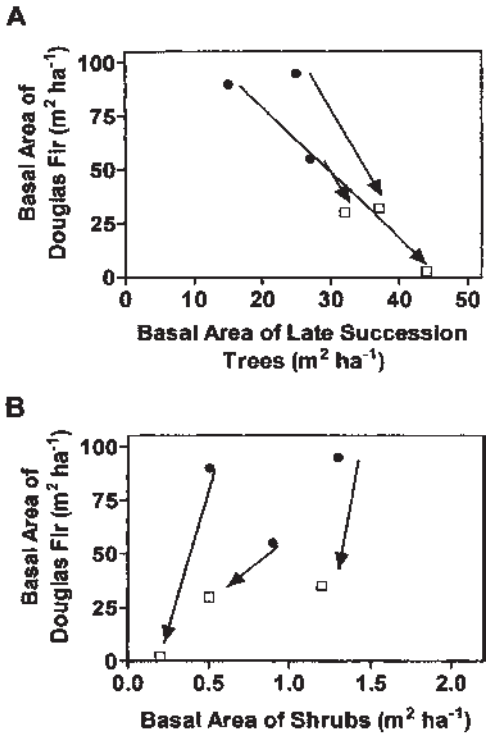

FIGURE 5.9 Changes in the relative basal area of Douglas fir trees in relation to late successional trees (A) or shrubs (B) in the H. J. Andrews forest as a result of the root-rotting fungal pathogen *Phelliunus weirii*. Changes are indicated by arrows showing trends in response from plants outside infection centers (solid symbols) to areas within infection centers (open symbols). *Source*: Data modified from Holah et al. (1997).

shown that *Trichoderma koningii* is a good biological control agent for damping off of tomato by *Sclerotium rolfsii*. In the tropics, Evans (1995) suggests that it is impractical and undesirable to use herbicides in more fragile agroecosystems and natural areas because of the unknown secondary effects of these chemicals. In contrast, biocontrol agents, such as pathogenic fungi, may be more desirable for use in reducing the abundance of exotic plant species. Although the science of fungal biocontrol of weeds has not been perfected in these ecosystems, there are indications that the fungal pathogen flora of plants changes significantly from its native range to that its exotic range (Table 5.5). The fact that there is minimal overlap of fungal pathogen species in both the native and exotic ranges suggests

TABLE 5.5 Tropical Weed Plant Species and the Number of Pathogenic Fungi Associated with Them in Their Native Range and in the Range in Which They Are Common Exotics

Plant species	Native range	Number of fungal species	Exotic range	Number of fungal species	Number of fungal species in common
Chromolaena odorata	Neotropics	17	Paleotropics	21	4
Mikania micrantha	Neotropics	29	South-east Asia	14	6
Lantana acmara	Neotropics	28	Paleotropics	26	6
Cyperus rotundud	Sudan, Pakistan, India	19	Neaotropics, Southeast Asia, Oceania, Australia	32	6
Euphorbia heterophylla	Neotropics	21	Paleotropics	33	7
Euphorbia hirta	Neotropics	15	Paleotropics	19	4

Source: Data from Evans (1995).

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that there is scope for the selection of effective pathogen species in the plant's exotic range to effectively reduce its fitness.

Interestingly, it is not only the plant whose fitness may be affected by a pathogenic fungus. The interactions between pathogens on a plant may affect the fitness of the pathogenic fungi themselves. In a study of rust fungi on wheat leaves, Newton et al. (1997) showed that the relative fitness of a number of strains of the rust *Puccinia graminis* was controlled by density-dependent relationships. For example, relative fitness of the fungal strain SR22 was much greater at low spore densities on the leaf than at high density. At these low densities, which were well below the carrying capacity, the high infection efficiency of SR22 gave it a competitive edge. As spore density of a mixed spore inoculum on the leaf increased, however, the strong competitive abilities of strain SR41 allowed it to dominate in the community. In the natural ecosystem, the effect of fungal pathogens on individual plants thus may depend upon the outcome of competition of the fungal pathogens within their own community as much as the competition between saprotrophic fungi and pathogens.

5.4 SAPROTROPH–PATHOGEN INTERACTIONS: BIOCONTROL

The presence of saprotrophic fungi on plant surfaces is a long accepted fact (Last and Deighton, 1965). Leaves of terrestrial plants support extensive and diverse communities of both pathogenic and nonpathogenic fungi (Dickinson and Preece, 1976; Preece and Dickinson, 1971; Farr et al., 1989; Kenerley and Andrews, 1990; Blakeman, 1992; Donegan et al., 1996). Many saprotrophic members of the phylloplane have been shown to be antagonistic toward plant pathogens. For example, Omar and Heather (1979) showed that *Alternaria* and *Cladosporium* species were more effective inhibitors of *Melampsora larici-populina* on poplar leaves than *Penicillium* (Fig. 5.10). Sharma et al. (1988) and Singh and Khara (1984) examined changes in radial growth of mycelial inoculum discs in interactions of one saprotroph antagonist and a single pathogen (*Alternaria solani*). In a study conducted by Blakeman and Brodie (1977) competition for nutrients among the epiphytic members of the phyllosphere of beetroot leaves was shown to negatively affect the germination of spores of plant pathogens. Upadhyaya and Arora (1980) evaluated the effect of fungal growth-staling products on phylloplane fungi. In a study of the development of the fungal pathogen *Pestalotiopsis funereal* on *Eucalyptus globules*, they found that leaf discs treated with the growth-staling products isolated from the leaf-inhabiting microfungi of *E. globulus* resulted in a significant decrease in the number of fungal pathogens.

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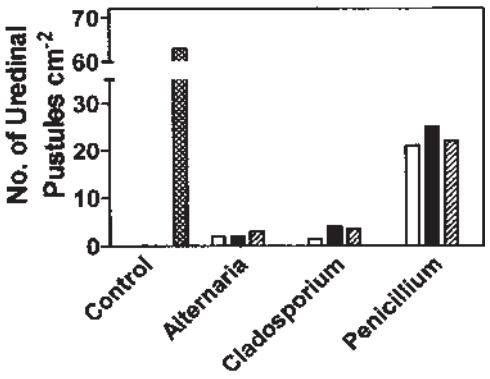

FIGURE 5.10 Effect of saprotrophic leaf surface fungi on the development of uredinal pustules of *Melampsora larici-populina*. Saprotroph conidia incubated before uredinospores added (open bar), conidia, and uredospores as a mixed inoculum (solid bar) and uredinospores added before conidia (hatched bar) compared to infection without saprotroph (control). *Source*: Data from Omar and Heather (1979).

Most studies of this type have observed interactions between a single saprotroph and a single plant pathogen; very few have looked at two or more saprotrophs in combination as antagonists. Members of the phyllosphere fungal community have been shown to coexist, however, but the functional role of the organisms as a community rather than as isolated individuals has not been adequately investigated (Fokkema, 1991; Bills, 1995).

The inhibitory attributes of phylloplane fungi have been used to develop fungal pathogen biocontrol agents. In a review of the interactions between phylloplane microorganisms and mycoherbicide efficacy, Schisler (1997) discusses only single species interactions or the effects of microbial metabolites without discussing the individual organisms or communities of organisms that might produce these metabolites. Janisiewicz (1996), however, evaluated the effects of multispecies combinations of yeasts and bacteria for their abilities to control blue mold (*Penicilium expansum*) on harvested apples. He suggested that the optimal species mix occurred when there was minimal niche overlap among the species. The resultant minimal competition among antagonist microbial species allowed maximal competitive interaction between the antagonist and the pathogen.

Because of the documented inhibitory effect of leaf saprotrophs against foliar pathogens, other work has evaluated the effects that current management practices of fungicide application has on the phylloplane community and how it might increase the pathogen's ability to initiate disease where the saprotrophic members of the phylloplane community have been eliminated or reduced by

the fungicide. Fokkema and de Nooij (1981)found that some fungicides reduced the ambient mycoflora while others had no effect. Thomas and Shattock (1986) also tested this idea by applying three different fungicides (benomyl, triadimefon, and chlorothalonil) to *Lolium perenne* that had the pathogens *Drechslera siccans* and *D. dictyoides* in addition to other saprotrophic filamentous fungi. They found that the three fungicides altered the incidence of the phylloplane mycoflora in very different ways. Benomyl reduced most saprotrophs but allowed the levels of *D. siccans* and *D. dictyoides* to increase over control levels by 37% and 90%, respectively. This showed that in the absence of saprotrophs to antagonize them, the pathogens were able to flourish beyond the established controls. Triadimefon reduced the level of pathogenic species and increased the abundance of most other common saprotrophs. Chlorothalonil removed virtually all fungi from the surface of the leaves. For agricultural purposes, there thus needs to be a balance between encouraging natural competitors against plant pathogens and the use of traditional fungicide treatments. The importance of a protective saprotrophic fungal community on leaf surfaces, however, may only play an important part in reducing pathogenic fungal invasion during the short time the host plant is susceptible and when the spores of the pathogenic fungus are abundant for leaf inoculation.

The community interactions in the phylloplane and their ecological significance have been explored in the review by Bélanger and Avis (2002). They suggest that the diversity of fungal inhabitants on a leaf surface occur as a result of niche separation based on the temporal and spatial diversity of resources. Moy et al. (2000), however, showed that the fungal endophyte *Neotyphodium typhinum* formed epiphyllous networks of hyphae on the leaf surface of a number of grass species, particularly *Bromus setifolius* and *Poa ampla.* They suggest that these epiphyllous fungal networks could possible act antagonistically toward fungal pathogens. The mechanism of this protection may be by direct fungal–fungal interactions or by virtue of prior space occupancy; thus, they contest, many of the fungi may not be in competition with each other, but are utilizing unique resources. They argue further that if this niche separation is true then evidence in the literature would not support the hypothesis of a saprotrophic fungal community affording protection to plant pathogens. Citing the experiments of Rishbeth (1963) on competition between *Peniophora giganta* and the pathogen *Fomes annosus*, they argue that the defense is merely a delay in allowing access of the pathogen to its optimal resources. Whether this is defense or inadvertent competition is somewhat semantic, as the result is a delay in the colonization of plant tissue by a pathogen. Similarly, Bélanger and Avis (2002) suggest that the hyperparasitism shown by *Trichoderma* spp. is probably the main mode of action of members of this genus. They reason, however, that this parasitism of other fungi that occur in nature have rarely been shown to be an effective means of biocontrol when the density of *Trichoderma* has been

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artificially increased. Jeffries (1997) reviewed the subject of mycoparasitism and came to the conclusion that this modus operandi is difficult to quantify in regard to its effect on populations of either fungal species. Evidence is cited in his review of positive correlations between host fungal hyphal density and that of the parasitic fungus, suggesting a direct trophic effect. He does, however, suggest that this aspect of fungal ecology could have great importance in reducing plant pathogenic fungi, although much of this information originates from the study of agricultural crops rather than the natural plant communities. Marois and Coleman (1995) also suggest that understanding the ecology of successions of phylloplane fungi could point to the appropriate species to combat pathogenic fungi. They suggest that the succession of fungi colonizing developing leaves is analogous to the colonization of freshly fallen dead leaves in the decomposer community. Their hypothesis is that an r-selected plant pathogenic fungus would best be controlled through competition, whereas a K-selected pathogen would be effectively combated by a mycoparasite.

The competitive interactions between saprotrophic and pathogenic fungi also occur in the rhizosphere. Whipps (1997) reviewed some of these fungal–fungal interactions, showing that the types of interactions could be classified as "direct antagonism" by mycoparsitism, antibiosis, or direct competition, or through "indirect interactions" by the fungal induction of resistance and by plant growth promotion. An example of sustained mycoparasitism in the rhizosphere is that of the control of *Rhizoctonia* by *Verticillium biguttatum* (Van den Boogert and Velvis, 1992; Van den Boogert and Deacon, 1994). The production of antibiotics by fungi in the rhizosphere has been reviewed by Lynch (1990). The introduction of nonvirulent forms of pathogenic fungal species has been shown to induce disease resistance to plants (Mandeel and Baker, 1991; Martyn et al., 1991). Most of these studies, however, have been conducted in agricultural settings or in artificial conditions; the importance of these interactions in natural ecosystems and their influence on plant fitness is largely unknown.

5.5 MYCORRHIZAL–PATHOGEN INTERACTIONS

Mycorrhizal fungi have been known to be effective in the prevention of root pathogen fungal attack on the host plant (Garbaye, 1991). As Smith and Read (1997) suggest in their review of the effects of ectomycorrhizae in pathogen resistance, however, much of the work has been conducted in unrealistic nursery conditions. The actual role of these mycorrhizae as antagonists to plant pathogens in nature are largely unknown. Indeed, even recent work of Branzanti et al. (1999) that demonstrated the significant effect of inoculation of chestnut trees with the ectomycorrhizal fungi *Laccaria laccata, Hebeloma crustuliniforme, H. sinapizans*, and P*axillus involutus* on preventing chestnut ink disease caused by *Phytophthora cambivora* and *P. cinnamomi* was conducted on seedling trees

(Table 5.6). Suppression of root rot, caused by *Cylindrocarpon destructans* by arbuscular mycorrhizal inoculation of peach trees by *Glomus aggeragatum*, was similarly demonstrated in an experimental system with tree seedlings (Traquair, 1995) (Fig. 5.11).

In contrast, the effect of arbuscular mycorrhizae and defense against plant pathogenic fungi has been studied to a greater extent, especially in annual plants. Much of this work has concentrated on agricultural crops, however, and therefore may be equated to the artificial conditions identified for research on ectomycorrhizal fungi. An example of this kind of work is that of Lui (1995) on cotton. Here the effect of inoculation with the arbuscular mycorrhizae *Glomus hoi, G. mosseae*, and *G. versiforme* significantly improved growth and established a significant defense against the wilt fungi *Verticillium dahliae* (Table 5.7). Similarly, Abdalla and Abdel-Fattah (2000) showed that peanut plants had a reduced incidence of root fungal pathogens when inoculated with the arbuscular mycorrhizal fungus *Glomus mosseae* than they did in the absence of mycorrhizae. The benefit of mycorrhizal colonization of roots was both an antagonism against the two fungal pathogens, *Fusarium solani* and *Rhizoctonia solani*, and a growth enhancement of the host plant, leading to greater fitness expressed in terms of seed production (Table 5.8).

From the data derived from mixed-species grassland, Sanders and Fitter (1992a,b) suggest that the role of arbuscular mycorrhizal colonization of plant roots may be nonnutritional. In a study of the annual winter grass *Vulpia ciliata* in a natural plant community, Newsham et al. (1994) used two fungicides, benomyl and prochloraz, to selectively reduce infection by arbuscular mycorrhizae and pathogenic fungi, respectively. Their determination of plant performance suggested that there was direct interference between the mycorrhizal and pathogenic fungi, and although the plants did not show pathological symptoms,

TABLE 5.6 Effect of Inoculation of Chestnut Seedlings (*Castanea sativa*) with Ectomycorrhiza Against the Effects of the Chestnut Ink Stain Fungal Pathogen *Phytopthora cambivora*

Fungal treatment	Leaf area (cm^2)	Plant weight (g)
Control	21.3	9.3
Phytopthora alone	15.6	5.2
Phytopthora + *Laccaria laccata*	28.1	9.4
Phytopthora + *Paxillus involutus*	19.5	6.1
Phytopthora + *Hebeloma crustuliniforme*	22.0	5.9
Phytopthora + *H. sinapizans*	28.1	10.2

Source: Data from Branzanti et al. (1999).

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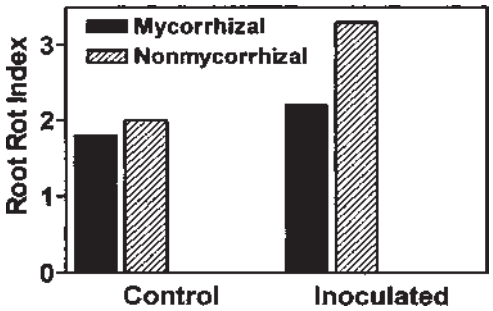

FIGURE 5.11 Degree of cylindorcarpon root rot in peach tree seedlings inoculated with the mycorrhizal fungus *Glomus aggregatum*. Inoculated trees received a conidial suspension of *Cylindrocarpon destructans*. *Source*: Data from Traquair (1995).

the mycorrhizal fungi induced greater fitness in the plants as a result of competition with the pathogen. It was also inferred from the data that this was the prime function of the mycorrhizal association, rather than improving phosphorus uptake by the host plant. This type of study on natural plant communities is altering the

TABLE 5.7 Growth and Disease Status of Cotton Plants Grown in Association with the Wilt Pathogen *Verticillium dahliae*, Arbuscular Mycorrhizae, and Combinations of the Two

Treatment	Plant height (cm)	Disease incidence (%)
C	10.5	0
Vd_1	9.7	43.3
Vd_2	8.3	35.5
Gh	12.8	0
Gm	13.1	0
Gv	13.1	0
Gh + Vd_1	11.1	23.3
Gm + Vd_1	11.7	23.3
Gv + Vd_1	12.3	20.0
Gh + Vd_2	8.9	23.3
Gm + Vd_2	9.9	23.3
Gv + Vd_2	12.5	16.7

Note: C = control of no fungal additions, Vd_1 and Vd_2 are two strains of *Verticillium dahliae*, Gh, Gm, and Gv are the mycorrhizae *Glomus hoi, G. mosseae*, and *G. versiforme*, respectively.
Source: Data from Lui (1995).

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TABLE 5.8 Effect of the Arbuscular Mycorrhizal Fungus *Glomus mosseae* on Growth and Fecundity of Peanut Plants at Maturity Infected with the Root Pathogenic Fungi *Fusarium solani* and *Rhizoctonia solani*

	Growth parameters		Yield biomass	
Treatment	Shoot weight (g)	Number of branches	Pods per plant	100 seed weight (g)
Control	9.3	6.3	9.7	64.5
Mycorrhizal	13.0	8.3	12.3	72.5
Fusarium	6.7	5.0	8.0	45.9
Myco + *Fusarium*	7.8	6.5	10.6	65.9
Rhizoctonia	6.9	5.0	7.0	39.8
Myco + *Rhizoctonia*	9.1	6.7	8.7	60.5
Fusarium + *Rhizoctonia*	5.8	5.0	5.3	38.4

Source: Data from Abdalla and Abdel-Fattah (2000).

dogma of the function of mycorrhizae as being enhancement of host plant nutrition alone. Much more research needs to be done, however, to show the relative importance of mycorrhizae in nutrient uptake and plant defense. A discussion of the arbuscular mycorrhizal benefits afforded to host plants in terms of nutrient acquisition and growth enhancement on the one hand and the protection of the host plant against fungal root pathogens on the other led Newsham et al. (1995) to conclude that the benefits were related to the root architecture of the host plant. In their model (Fig. 5.12), Newsham et al. (1995) suggest that the derived benefit of a mycorrhizal association is predominantly nutrient acquisition if the host plant root system is poorly branched. In contrast, the benefit shifts toward pathogen prevention where the host root system is highly branched.

The distribution of root pathogens in soil and their ability to infect host plants may be an importance determinant in the germination and survival of certain plant species. Augspurger (1990) shows how the effect of damping off fungi (*Phytophothora, Rhizoctonia, Pythium*, and *Fusarium*) influences the development of tropical forest tree species that develop in forest gaps. In many of these tropical tree species, seed dispersal is limited to within 100 m of the parent tree. Augspurger's research suggested that seedlings that germinated close to the parent tree had a higher percentage of loss due to damping off than seedlings developing further from the parent tree. These findings substantiate the hypothesis proposed by Janzen (1970) and Connell (1971) referred to as the Janzen–Connell hypothesis. The essence of this hypothesis is outlined by Clark and Clark (1984), in which both the effects of root pathogens and the higher

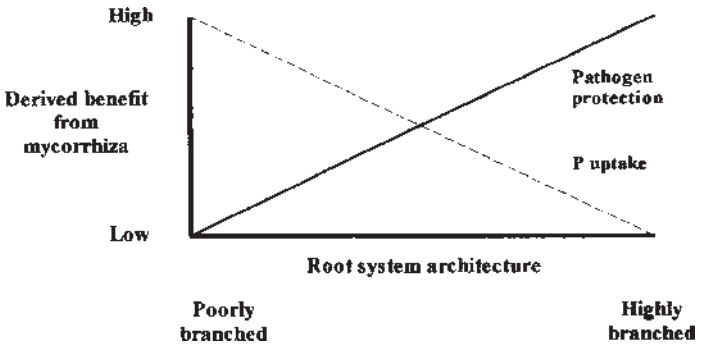

FIGURE 5.12 Nature and magnitude of the benefit derived from plant associations with arbuscular mycorrhizae, depending on the branching pattern of the host plant root system. *Source*: Redrawn from Newsham et al. (1995).

incidence of herbivore grazing on seedling plants restricts the development of conspecific species under the canopy of mature tropical trees (Fig. 5.13). The hypothesis suggests that this is a mechanism favoring dispersal of seeds away from parent trees and stimulates colonization of forest gaps. Recent evidence from controlled experiments supports this hypothesis (Packer and Clay, 2000; van der Putten, 2000). In their studies, the alleviation of the pathogenic effect of soils under a parent tree was achieved by soil sterilization. This sterilization process reduced the incidence of *Pythium* damping off of black cherry tree seedlings (Fig. 5.14). It is difficult to argue, however, if the pathogen alone is influencing the spatial pattern of successful seedlings. Seedlings growing in the shade of a parent tree probably exhibit signs of stress because they are growing at suboptimal light levels. This may make them more vulnerable to root pathogens than those seedlings growing in optimal light conditions toward the centers of the gaps. A similar mechanism has been shown to affect recruitment of *Ocotea whitei* seedling trees under canopies of adults of the same tree species on Barro Colorado Island, Panama, because of the presence of a fungal tree canker. Seedling survival is significantly higher under the canopy of a nonsusceptible tree, *Beilschmiedia pendula* (Gilbert et al., 1994).

In contrast to this hypothesis, the links among conspecific plants by mycorrhizal bridges has been shown to confer advantages to the seedlings because of interplant transfers of carbon and nutrients (Amaranthus and Perry, 1994; Read, 1998; Rayner, 1998). Amaranthus and Perry (1989) showed that when Douglas fir seedlings were planted into forest gaps close to adult trees, survival approached 90%. Where seedlings were planted at great distances from parent trees, survival after 2 years was only 50%. Amaranthus and Perry attributed the reduction in survival to the lack of a viable, communal ectomycorrhizal network into which

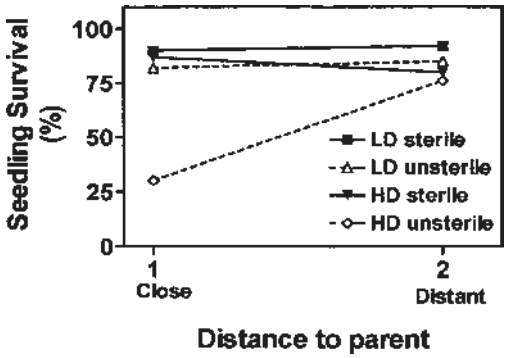

FIGURE 5.13 Effect of distance from parent tree and soil sterilization on the survival of black cherry seedlings. The regression model included density, density × distance, density × sterilization, and distance × density × sterilization. Removal of any variable significantly reduced the model fit. *Source*: Data from Packer and Clay (2000) reprinted by permission from Nature (2000) 404:278–281 Macmillan Publisher Ltd.

the new trees could connect to allow new recruits to be able to access a larger pool of nutrients and carbon than they would be able to on their own. Demonstration of direct net transfer of carbon or nutrients between trees in the field shows that there is benefit to seedlings of the same and different parental tree species. Simard et al. (1997a,b,c) demonstrated transfer of carbon from paper birch (*Betula papyrifera*) and Douglas fir (*Pseudotsuga menziesii*) in both partial and deep shade, which

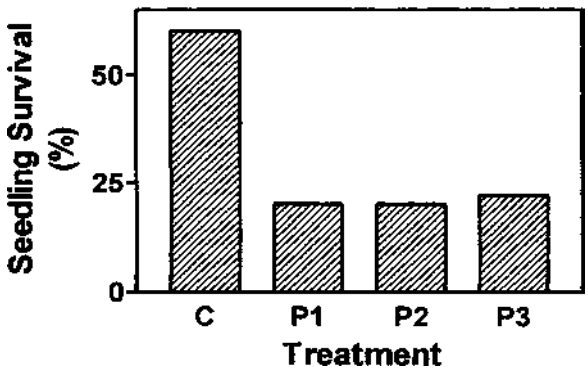

FIGURE 5.14 Black cherry seedling survival in control soil (C) of potting mix and sterilized fungal growth medium and fungal pathogen-inoculated soils (P1–P3) containing 5 ml of inoculum of *Pythium* spp. *Source*: Data from Packer and Clay (2000) reprinted by permission from Nature (2000) 404:278–281 Macmillan Publisher Ltd.

considerably supplemented photosythetically derived carbon in the seedling, recipient plant. This mechanism has been shown to enhance the survival of tropical, ectomycorrhizal tree seedlings under the canopy of parent trees in the Cameroon (Onguene and Kuyper, 2002) (Table 5.9). Newbery et al. (2000) however, did not find such conclusive proof of the beneficial effects of ectomycorrhizae in the enhancement of tropical legume seedlings under conspecific adult trees. In the case of *Tetraberlinia bifoliata*, enhancement of seedling growth was only significant at high densities of adult trees (Table 5.10). Their data suggested that a beneficial effect could be found in some cases in which seedling growth was enhanced, but that in other tree species, this benefit was not evident. The interaction between root pathogens and mycorrhizae in the establishment of conspecific trees seedlings under the canopy of parent trees is thus not simple. There are probably many interactions among the mycorrhizal and pathogenic fungi that result in an advantage of one or the other, depending on local environmental conditions (Connell et al., 1984).

5.6 ENDOPHYTES AND ANTIHERBIVORE ACTION

The interactions among plants and their bacterial and fungal endophytes have recently been reviewed by Bacon and White (2000). Clay (1990) defines endophytic fungi as those that grow within a plant for a period and then egress to sporulate. In general, these fungi cause no apparent damage to their host plant. Indeed, Clay (1997) states that fungal endophytes are a model system showing how fungi can have important effects upward through the whole community by virtue of their interactions with grazing animals. Of particular interest are the interactions among members of the Clavicepitales and grasses. The presence of these fungi in the leaves of grasses reduces the incidence of insect herbivory (Table 5.11), grazing by ungulates, and oviposition on the plant by insects.

TABLE 5.9 Seedling Shoot Biomass of *Paraberlinia bifoliolata* When in Contact with or Isolated from the Root and Mycorrhizal System of Different Tropical Tree Species After 8 months

Adult tree species	Seedling shoot biomass in contact with adult tree (g)	Isolated seedling shoot biomass (g)
Afzelia	1.59	1.16
Brachystegia	1.48	1.24
Paraberlinia	2.43	1.52
Tetraberlinia	2.19	1.78

Source: Data from Onguene and Kuyper (2002).

TABLE 5.10 Survival of Seedling Tropical Ectomycorrhizal Trees After 16 Months of Growth Under the Canopy of Conspecific Adults at Low and High Stem Density

	Percentage seedling survival	
Tree species	Low adult stem density	High adult stem density
Microberlinia bisulcata	25	33
Tetraberlinia bifoliata	33	65
Tetraberlinia moreliana	70	76

Source: Data from Newbery et al. (2000).

The effect of the fungi is to both alter the nutrient content of the host plant and the production of secondary metabolites that act as deterrents to the animals. For example, species of the genus *Baccharis* have been shown to produce high concentrations of macrocyclic tricothecenes that are toxic to cattle (Jarvis et al., 1987). Indeed, Clay (1990) suggests that there are complex interactions among endophytes and host plants that vary along a continuum between herbivory defense and pathogenicity, which strongly influences the fitness of the host plant (Table 5.12). The close association between plant and endophyte has been shown to have evolved to a great extent in grasses, in which the two partners are inseparable. Examples of this are the fungi *Acremonium lolii* and *A. coenophialum*, associated with ryegrass and tall fescue, respectively. Wilson (1993) suggests that the improved fitness of alkaloid production by the endophyte has led to vertical transmission of the endophyte from plant to plant via the seed. In this way, all new plants can start life with the endophyte and the advantages the fungus confers. In contrast, Wilson suggests that the endophytes of many other plants, such as the fungus *Discula quercina* of oak, are transmitted horizontally via rain splash from tree to tree. The chances of a plant becoming colonized by the appropriate fungus is therefore, dependent upon environmental conditions. This will result in a mosaic of both colonized and uncolonized plants, in such a way that the resulting community will be dependent upon the competitive and fitness advantages conferred on the plant by the endophytic fungi. Additionally, these fungi infect seeds where the pericarp is missing or damaged, in such a way that the fungus acts as an antagonist against pathogenic fungi. Fitness of the host plant is also enhanced by the presence of endophytes in its seeds. Clay (1990) cites a number of examples in which grass seeds were rendered ineffective in germination due to insect damage in the absence of endophytic fungi in the seed. Where the endophyte was present, the level of seed germination was normal. The degree of endophyte development within the host plant and proportion of seeds infected thus can be an important aspect of actual

TABLE 5.11 The Influence of Fungal Endophytes of Grasses in Reducing Damage by Animals

Insect herbivore	Host plant genus	Effects of endophyte
Rhopalosiphum padi	*Festuca*	Avoidance
Spodoptera frugiperda	*Cenchrus*	Avoidance, reduced survival and development rate
S. eridania	*Cyperus* *Danthonia* *Festuca* *Glyceria* *Lolium* *Panicum* *Paspalum* *Stipa* *Tridens*	
Sphenophorus parvulus	*Lolium*	Reduced feeding, oviposition
Blissus leucopterus	*Festuca*	Reduced feeding, oviposition
Acheta domesticus	*Lolium*	Reduced survival
Agrotis segetum	*Dactylus*	Reduced survival, growth
Tribolium castaneum	*Festuca* *Lolium*	Reduced survival, population growth
Crambus spp.	*Lolium*	Reduced feeding, oviposition
Listronotus bonariensis	*Lolium*	Reduced feeding, oviposition

Source: Data from Clay (1990). with permission from the Annual Reviews of Ecology & Systematics Vol 21 © 1999 by Annual Reviews: www.annualreviews.org.

TABLE 5.12 Relation Between Host Plant Fitness and Types of Fungal Mutualism

Fitness relationship	Type of ecological association
$A > B > C$	Pathogenic—endophyte provides no defense against herbivory
$A > C > B$	Conditionally mutualistic—endophyte gives some defense against herbivory
$B > A > C$	Unconditionally mutualistic—herbivore is detrimental
$B > C > A$	Unconditionally mutualistic—herbivore has beneficial effect
$C > A > B$	Conditionally mutualistic—endophyte is pathogenic in absence of herbivory
$C > B > A$	Unconditionally mutualistic—mutualism is strongest when herbivory is present

Note: A = uninfected plant with no herbivory, B = endophyte infection with no herbivory, and C = endophyte infection with herbivory.
Source: Data from Clay (1990).

fecundity and competitive ability, which may be overlooked if the measure of plant success is only made in terms of seed production and not seed germination potential.

Richardson (2000) briefly catalogs the history of endophyte research in grasses, showing that the effect of infected plants on grazing animals has been noted since the early 1980s. He continues to discuss the importance of the production of alkaloids by these endophytic fungi as being the causal agent of herbivore avoidance. These alkaloids are secondary metabolites of the fungi and are considered to have evolved as an adaptation to confer competitive advantage to the endophyteinfected host plant. Indeed, Lane et al. (2000) show that the infection of grasses with asexual *Neotyphodium* endophyte exerts a natural selection in favor of the host plant, increasing its fitness in competition with other plant species due to antiherbivore and plant-growth-promoting factors. It would appear that the degree of protection afforded to a host plant by an endophyte does not change under changing environmental conditions. In a study of the influence of elevated carbon dioxide on the rate of grazing of grasses by the fall armyworm *Spodoptera frugiperda*, Marks and Lincoln (1996) saw an increase in grazing intensity with elevated CO_2, but the proportion of plant consumed by the insects was similar to that of plants grown in ambient conditions (Fig. 5.15). Indeed, Clay (1997) showed that endophyte-infected plants outperformed uninfected plants in the presence of herbivory and suggested that the evolutionary trajectory of increasing endophyte infection of plants will be associated with the level of herbivory (Fig. 5.16). Use of fungal endophytes for pest management is appearing as a new science. Prestidge and Ball (1997) cite evidence of the adverse effects of *Acremonium*-infected tall fescue on 12 species of beetle, two species of flies, 16 species of Hemiptera and Homoptera, and eight species of lepidopteran larvae, thus suggesting that endophytes could be important biological control agents of agricultural pests.

In addition to reducing the potential impact of herbivore grazing on plants, fungal endophytes in the Clavicepitales have also been shown to alter the vegetative growth and reproduction of the host plant (Table 5.13) (Clay, 1990). In his review, Richardson (2000) goes on to postulate that the evolution of alkaloid production may have additional properties that influence plant fitness. He suggests that in other fungal–plant interactions secondary metabolites can influence host plant physiology. He cites the example of the fungal pathogen *Cercospora*, which produces cercosporin, which kills the host plant cells to make more nutrients available to the fungus. Indeed, he shows that the presence of endophytic fungi in host plants increases the concentration of apoplastic carbohydrates in leaves, allowing a greater supply of energy to be made available to the fungus (Table 5.14). He also suggests that the production of alkaloids is nitrogen-demanding and cites evidence to show that these fungi are capable of altering the nitrogen balance within the host plant in favor of making more

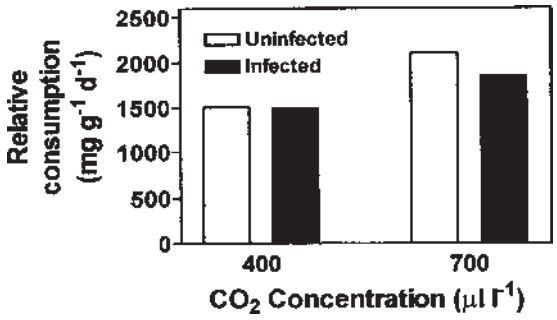

FIGURE 5.15 Relative consumption rates of tall fescue plants by the fall armyworm *Spodoptera frugiperda* when the plants are infected with the fungal endophyte *Acremonium coenophialum* or not. *Source*: Data from Marks and Lincoln (1996).

nitrogen available to the fungus. This evidence supports the idea that mutualistic associations (mycorrhizae and endophytes) may be in the middle of a continuum of fungal physiologies, ranging from saprotrophy at one end and pathogenicity at the other.

Kruess (2002) also showed that the plant pathogenic fungus *Phoma destructiva* acted in a similar fashion to endophytic fungi known to reduce herbivory in infected plants. Pathogen-infected plants proved to be less palatable than noninfected plants to larvae of the beetle *Cassidia rubiginosa*. Beetle development and pupal survival were also retarded on infected plants (Fig. 5.17).

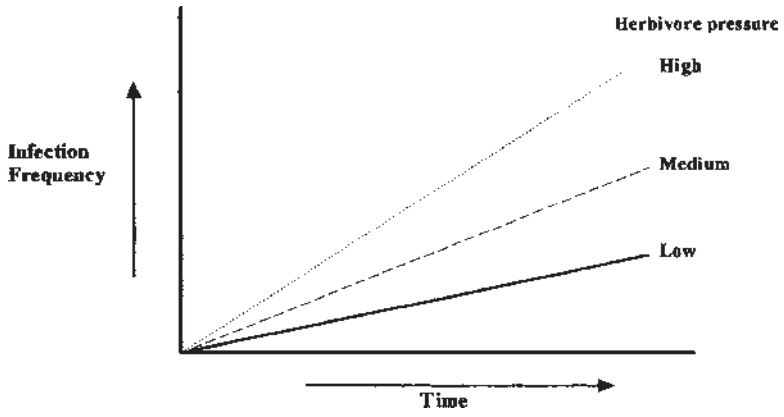

FIGURE 5.16 Hypothesized relationship between the evolution of endophytic infection of plants and the intensity of herbivory over time. *Source*: From Clay (1997).

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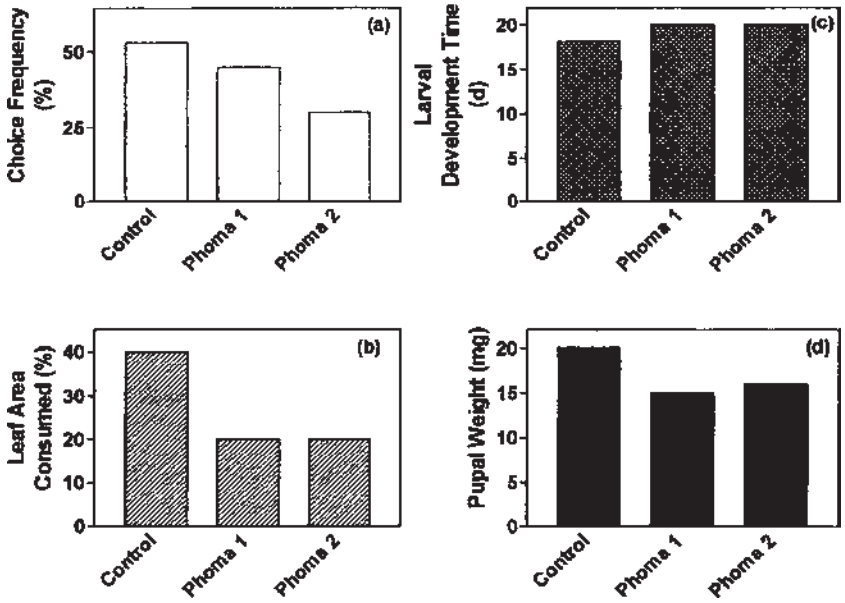

FIGURE 5.17 Influence of infection of the thistle *Cirsium arvense* with the plant pathogenic fungus *Phoma destructiva* on (a) choice of leaf for feeding, (b) leaf area consume, (c) larval development time, and (d) pupal weight of the herbiverous beetle *Cassida rubiginosa*. *Source*: Data from Kruess (2002).

It can thus be seen that known plant pathogenic fungi have a similar effect to leaf endophytes that are considered to be mutualists. This begs the question of our definitions of mutualism and parasitism, where it is likely that there is a continuum of degrees of magnitude of observed effect on the host plant.

Fungal endophytes are not restricted to grass species and agricultural crops. Wilson (2000) reviewed the endophytes of woody plants and showed similarities in the effects of these fungi on host plants to those cited above. The major grazers of woody plant leaves are insect larvae, and it has been shown that the presence of endophytes reduces grazing. This can lead to both spatial and temporal alteration of the grazing insect abundance within the canopy of the host plant. Wilson (2000) points out that much of the evidence for this is correlatory, but could have impacts on the success of the insect population with respect to predator avoidance and maturation time. In contrast to this idea of protection against herbivores, Faeth and Hammon (1997a,b) showed that there was a positive association between populations of Emory oak leaf miner, *Cameraria* spp., and infection by the endophytes *Ophiognomonia cryptica, Plectohomella*, and *Asteromella*. The incidence of endophyte infection was not affected by the population of insects,

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TABLE 5.13 Effects of Members of the Clavicepitales as Endophytes of Plants on Herbivore Resistance and Plant Growth

		Effect on host		
Endophyte genus	Number of host species	Vegetative growth	Reproduction	Herbivore resistance
Acremonium	100	Increase	No effect	Yes
Atkinsoniella	4	Increase	Suppressed	Yes
Balansia	100	Increase and decrease	Suppressed	Yes
Epichloe	100	Increase	Suppressed	Yes
Myriogenospora	20	Decrease	Suppressed	Yes

Source: From Clay (1990).

however. Faeth and Hammon (1997b) also showed that the survival and larval growth of the leaf miners was not related to the degree of infection of the leaves by the endophytes (Fig. 5.18). This evidence would indicate that the effect of the endophyte is not for plant protection, but for the later finding of Wilson and Faeth (2001) that the presence of the endophytes significantly reduces oviposition by the adult leaf miner, hence the potential detrimental effect of the endophyte is partially mitigated by the reduced colonization by the insect that acts as its vector.

Wilson (1993) and Faeth and Hammon (1997b) showed that endophyte-infected leaves of trees were more likely to abscise earlier than uninfected leaves. Little is known, however, about how this affects the rate of retranslocation of nutrients prior to leaf abscission and the consequences for this on the resource quality of this leaf litter to the decomposer community on the forest floor. If nutrient resorption is restricted in endophyte-infected leaves, a higher resource leaf litter would have considerable effects on the rates of leaf litter breakdown, nutrient mineralization, and the fertility of the soil under endophyte-infected trees. Indeed, it has been postulated that endophytes may effect leaf litter decay in the early stages of decomposition. Petrini et al. (1992), however, have shown that "typical" saprotrophic fungi in decaying leaf litter usually rapidly replace endophytes.

Certainly the body of evidence cited by Clay (1997) shows that there is strong inference from controlled greenhouse studies and a limited number of field studies that fungal endophytes can play a significant role in determining the community composition of plants by selectively altering competition and fitness of infected species. How closely the evolution of current plant assemblages is related to the coevolution of endophytic fungi, plants, and their herbivores is not known. Evidence suggests, however, that the presence of fungi within host plant

TABLE 5.14 Concentration of Apoplastic (Outside the Host Cell) Carbohydrates of Endophyte-Infected and Endophyte-Free Big Bluegrass (*Poa ampla*)

Carbohydrate	Endophyte-infected	Endophyte-free
Glucose	94.5	51.1
Fructose	205.5	132.2
Sucrose	n.d.	n.d.
Mannitol	trace	n.d.
Arabitol	n.d.	n.d.
Total	300.1	183.8

Source: Data from Richardson (2000).

tissues is an ancient association dating back to the Silurian period (Kidston and Lang, 1921; Pirozynski and Malloch, 1975).

5.7 NEMATOPHAGOUS FUNGI AND ANIMAL PATHOGENS

We saw in Chap. 4 that fungal pathogens of animals are capable of directly influencing faunal populations by causing the death of individuals or by reducing or increasing their fecundity. There are, however, more subtle interactions between fungi and animals that can affect their populations and health. One example of this interaction is the part played by nematode-trapping soil fungi and the health of ruminant animals. Nematophagous fungi have adopted a variety of ways by which they are capable of trapping free, living nematodes. This ability may be by the production of sticky secretions from the hyphae or from specialized structures derived from modified hyphae (sticky knobs of *Nematoctonus* sp.). In addition, a number of species (*Arthrobotrys* and *Dactylella*) produce constricting rings or nets of hyphae that close around nematodes by an almost instantaneous tactile-induced change in turgor pressure, with the hyphae cells creating the noose. The fungus secretes enzymes and digests the nematode, which is used as a source of nitrogen.

Many free-living nematodes in soil have a pathogenic stage as gut intestinal parasites of ruminant animals, such as *Trichostrongylus colubriformis* and other strongyles. It has been show that conidia and chlamydospores of the nematophagous fungi *Duddingtonia* and *Arthrobotrys* are capable of surviving passage through the gut of ruminants (Faedo et al., 1997). *Duddingtonia flagrans* spores consistently survived better than spores of *Arthrobotrys* spp. These spores

germinate in the dung, in which the free-living stage of the nematode develops high population densities and from which it becomes a potential source of infection for other grazing animals. The nematophagous fungi, however, offer an effective control of the population of the free, living stage of the nematode. By trapping and killing nematodes, these fungi are able to significantly reduce the infective potential of the nematode population (Faedo et al., 1997; Hay et al., 1998) (Fig. 5.19).

The potential use of nematophagous fungi as biocontrol agents for intestinal nematode parasites has been investigated (Larsen et al., 1997; Bird et al., 1998; Manueli et al., 1999). The reduced ability to recover fungi from the feces of animals in the tropics (Manueli et al., 1999), however, suggests the use of these fungi as biocontrol agents may be restricted.

Kerry and Jafee (1997) reviewed the literature on nematophagous fungi as biocontrol agents for plant pathogens. They highlight two factors that influence the success of these fungi as pathogen controls. One of these factors is the survival of conidia and trapping structures produced by these fungi. There appears to be little information on the survival of these fungi or their role as food for other soil-inhabiting fauna. This information relates to the second factor of density-dependent parasitism, where the efficiency of nematode trapping is closely correlated to the density of nematode-trapping fungal structures in soil, which is related to conidial density in soil. The ability to provide an adequate inoculum density to effect a significant nematode kill rate may be a limiting factor to the success of a specific fungal species as a biocontrol agent.

Other fungi may also be important regulators of plant parasitic nematodes. Viaene and Abawi (1998) showed that not only were nematophagous fungi of the genera *Arthrobotrys* and *Monacrosporium* important in reducing populations of juvenile nematodes of the genus *Meloidogyne*, but parasitic fungi of the genera *Fusarium, Verticillum*, and *Alternaria* were found to parasitize nematode egg masses (Table 5.15). Kerry (1988) showed that populations of the cereal cyst nematode could be controlled by the fungi *Nematophthora gynophial* and *Verticillium chlamydosporium*. These fungi parasitized female nematodes and eggs. They found approximately 150 fungal species that had these properties. It is possible that these fungi may also be important regulators of nematode populations and have the potential for use as biocontrol agents. In the presence of arbuscular mycorrhizal fungi, Elsen et al. (2001) found that the population of the plant-burrowing nematode *Radopholus similes* was significantly reduced. The major effect of the mycorrhizae was seen in the females, suggesting potential long-term population regulation by the reduction in fecundity (Fig. 5.20).

The nematicidal properties of fungi are not limited to Deuteromycetes. Barron and Thorn (1987) found that the basidiomycete fungi *Pleurotus ostreatus, P. strigosus, P. subareolatus*, and *P. cornucopiae* produced minute spathulate secretory cells that produced droplets of toxins that killed nematodes on contact

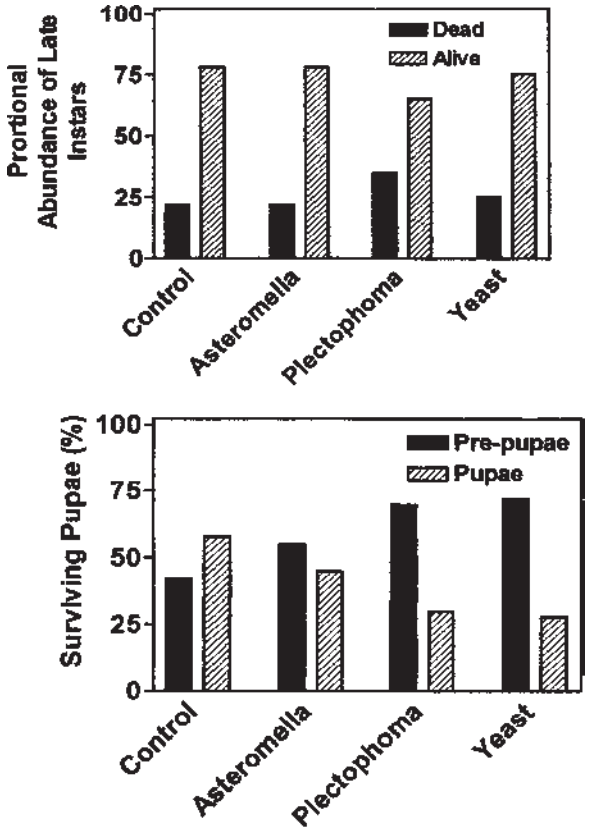

FIGURE 5.18 Proportion of dead and alive late instar larvae of the leafminer *Cameraria* subsequent to the injection of spores of phylloplane and endophytic fungi (upper graph) and pupal survival of the leafminer *Cameraria* in the presence of phylloplane and endophytic fungi (lower graph). *Source*: Data from Faeth and Hammon (1997).

within 30 s. Subsequent to the death of the nematode, fungal hyphae penetrated orifices of the nematode and destroyed it.

Fungal diseases have been reported as important regulators of a number of groups of animals. Anuran populations have recently been shown to decline as a result of the effects of fungal pathogens (Kaiser, 1998; Morell, 1999; Lips, 1999; Reed et al., 2000; Warkentin et al., 2001; Fellers et al., 2001). These reports are of concern, especially as the decline in frogs appears to be greatest in the tropical

regions (e.g., in Panama), in which efforts are underway to conserve biodiversity. Lips (1999) reported increasing numbers of dead frogs in her surveys over recent years. Frogs showed symptoms of fungal pathogens around the mouth and eyes. Previously, Kaiser (1998) and Morell (1999) reported an increase in the incidence of a chytrid fungal disease of frogs in Panama and in Australia to such an extent that Reed et al. (2000) consider this fungal group as an "emerging infectious disease." Indeed, the outbreak of a variety of Chlamydia species that cause respiratory disease of African clawed frogs (*Xenopus tropicalis*) imported into the United States was so extensive that one breeding colony lost 90% of its individuals within 4 months (Reed et al., 2000). Reports do not indicate, however, that such losses in numbers of frogs within a population affect the community structure of frogs. This information is, however, very difficult to obtain without a complete understanding of frog metapopulation dynamics and niche overlap among species.

In natural ecosystems, entomopathogenic fungi may be important density-dependent population regulators (Kamata, 2000). Kamata (2000) concluded that the periodic population fluctuations of the larvae of the beech caterpillar *Syntypistis punctatella* were caused by delayed density-dependent effects of the fungal pathogen *Cordyceps militaris*. *Cordyceps* is also reported as frequently occurring on insects in tropical forest ecosystems (Evans, 1982) and may be one of the most common pathogens of arthropods. Again, both these studies and that of Butler and Strazanac (2000)—of the dramatic effect of the fungus *Entomophaga maimaiga* on populations of the gypsy moth, *Lymantria dispar*, in Appalachian forests in 1996—show the dramatic effects of insect fungal pathogens on populations, but not on community structure.

The regulation of invertebrate populations by fungi may have effects on vegetation community structure. If the degree of faunal grazing is such that impaired plant fitness results, leading to a shift in the competitiveness of that species, then alleviation of the grazing pressure by fungal pathogens would alter the trajectory of vegetation community change. I am unaware of any studies that have demonstrated these linkages.

Indirect effects of fungi on animal populations can be seen in the effects of fungi on animal food sources. The effect of fungal pathogens on plants is to reduce photosynthesis and growth to such an extent that either vegetative or crop yield is reduced. Perhaps one of the classic stories of the effect of a plant pathogen on both populations and community structure would be that of the potato blight in Ireland in the 1800s. As reported earlier, the effect of the devastating appearance of the potato blight fungus *Phytopthora infestans* caused such a loss in yield in potatoes in sequential years that it caused famine in Ireland. Not only did the population of the Irish people decline, but since so many people emigrated to the United States, it has subsequently significantly changed the "community" composition of the American people. Although there is little

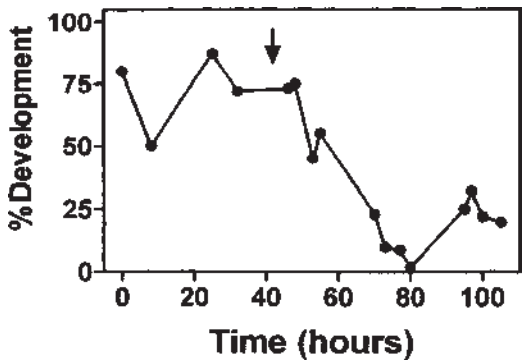

FIGURE 5.19 Mean percentage development of eggs of the intestinal parasitic nematode *Trichostrongylus colubriformis* into infective larvae in sheep feces before and after oral administration of a spore inoculum of the nematophagous fungus *Duddingtonia flagrans*. *Source*: Data from Faedo et al. (1997).

documentation that fungal pathogens can influence the population or community structure of other organisms, one can see that the catastrophic effects of chestnut blight and *Phytophthora*-induced decline of oaks in Europe and Eucalyptus in Australia not only have an effect on the plant communities in these areas but will also have an effect on the grazing fauna specific to those tree species. The potential use of nematode-trapping fungi and fungi that parasitize plant-pathogenic nematode eggs (Mankau, 1981) may reduce the incidence or severity of plant yield decrease caused by plant-infecting nematodes. The knock-on effects to other fauna grazing on other parts of the plant would also be expected to be affected.

5.8 ALLELOPATHY

Allelopathy is usually regarded as the interactive effect of one plant species upon another by the excretion of toxic metabolites. If we take a rather broader view of this competitive interaction, however, we can invoke the effect of one plant on the soil microbial community, both fungi and bacteria, that may have subsequent effects on the establishment, growth, and survival of another plant species.

Lichens are particularly well known for containing plant-inhibitory substances. Brown and Mikola (1974) found that the foliose lichen *Cladonia cristatella* significantly inhibited the germination of seeds of a number of plant species. A number of *Cladonia* species were shown to reduce the growth of a number of both saprotrophic and ectomycorrhizal fungi, thus potentially reducing

TABLE 5.15 Percentage of Plant Parasitic Nematode (*Meloidogyne hapla*) Egg Masses Infected with Parasitic Fungi and Juveniles Attacked by Nematophagous Fungi from organic Soils in New York

	Egg masses and J2 stage nematodes with fungi (%)	
Soil sample	Eggs	J2 juveniles
A	21	5
B	15	9
C	13	15
D	30	24
E	29	11

Source: Data from Viaene and Abawi (1998).

the efficacy of the mycorrhizal association, although the effect of this reduction in mycorrhizal function was not correlated to a reduction of phosphorus uptake by the plants (Brown and Mikola, 1974).

The addition of *Cladonia alpestris* lichen to the soil surface significantly reduced the growth and survival of pine and spruce seedlings in a tree nursery, but had little effect on birch growth or survival (Table 5.16) (Brown and Mikola, 1974), and a ground cover of greater than 10% of *Cladonia alpestris* in natural ecosystems was shown to reduce Scots pine seedling growth in comparison with

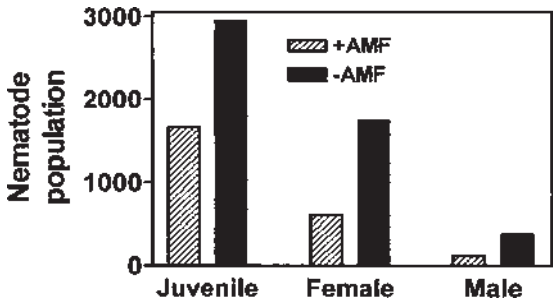

FIGURE 5.20 The effect of arbuscular mycorrhizal inoculation on the population of the root burrowing nematode *Radopholus similis*. *Source*: Data from Elsen et al. (2001).

similar and higher ground cover of *C. rangiferina* or *Arctostaphylos uva-ursi*. In similar studies, Fisher (1979) grew white spruce and Jack pine seedlings in the greenhouse in acidic sandy soil with mulches of the lichens *Cladonia rangifera* or *Cladonia alpestris*. After 15 weeks of growth, the soil was spiked with radioactively labeled phosphorus (^{32}P-PO_4), and the uptake of the radiolabel measured in plants harvested at 17 weeks. The presence of lichen mulch significantly reduced tree seedling growth and phosphate uptake. Nitrogen and phosphorus plant content were reduced, but nitrogen was reduced less than phosphorus. Potassium, calcium, and magnesium plant content was not affected (Table 5.17).

Lawrey (1986; 1989) made acetone extracts from lichen species (*Aspicilia gibbosa* and *Lasallia papulosa*) that were shown to be readily eaten by the slug *Pallifera varia*, and from lichens that were avoided by the slug (*Flavoparmelia baltimorensis* and *Xanthoparmelia cumberlandia*). The extracts were added to cultures of the bacteria *Bacillus megaterium, B. subtilis, Staphylococcus aureus, Escherichia coli*, and *Pseudomonas aeruginosa*. The lichens that were avoided by the herbivore had the greatest antagonistic effects against the bacteria *Bacillus megaterium, B. subtilis*, and *Staphylococcus aureus*, whereas the growth of both *Escherichia coli* and *Pseudomonas aeruginosa* were unaffected by any lichen. Defensive chemicals produced by the two lichens avoided by the herbivore included norstictic, stictic, usnic, constictic, connorstic, gyrophoric, caperatic, and protocetaric acids. In a controlled experiment, Lawrey (1989) also showed that vulpinic, usnic, and stictic acids reduced the growth of the same susceptible bacterial species. There thus appears to be a universal defensive role of these chemicals, before against herbivory or microbial attack and as an allelopathic agent (Table 5.18).

Changes in the microfungal flora of soils as a result of continuous agricultural practices have been shown to affect the ability of that soil to support plant growth and to effectively carry out the processes of leaf litter decomposition. This has been suggested to be a form of allelopathy (Golovko, 1999). In a comparative study between virgin cereal-meadow steppes of chernozem soils in the Mikhailovsky Reserve of the Ukraine and similar land in which the vegetation was periodically or frequently cut, Golovko (1999) showed that the microfungal community increased from 14 to 24 species as disturbance increased (Table 5.19). Using cress as a bioassay plant, Golovko (1999) showed that many of the fungi associated with highly disturbed sites inhibited plant growth. Indeed, *Aspergillus fumigatus* completely inhibited cress growth. Along with changes in polyphenols in soil, he suggested that the change in the fungal and bacterial communities were causal agents of allelopathy.

Increased development of plant defense chemicals in leaves can be induced by the presence of leaf-pathogenic fungi. This increased concentration of

polyphenols causes a significant reduction in the decomposition of plant litters (Whitham and Schweitzer, 2002). The higher content of these chemicals reduces the colonization of litter by saprotrophic and mycorrhizal fungi. Koide et al. (1998a,b) demonstrated a significant reduction in the growth of ectomycorrhizal fungi as a result of the effects of high concentrations of polyphenols. This effect could be considered analogous to an allelopathic effect if the reduction in mycorrhizal colonization of a host plant led to a reduction in the host plant's fitness. Molofsky et al. (2000), however, contest that the survival and fitness of the annual plant *Cardamine pensylvanica* is related to leaf litter mass and persistence rather than litter quality. It is thus possible that the controls exerted by leaf litters are different for annual and perennial plants.

5.9 SUMMARY AND DISCUSSION

Interactions between plants and animals are discussed in Chap. 3 and 4, especially in relation to plant productivity and population regulation. In this chapter I have attempted to translate some of these interactions into the community perspective. How do the interactions between plants or between animals result in the assemblages or communities that we see in ecosystems? How much of these interactions is due to environmental effects and how much to the intervention of other organisms in the ecosystem? How important are fungi in this process?

The evolution of fungi, along with the emergence of plants onto dry land, have been very closely related (Kidston and Lang, 1921; Pirozynski and Malloch, 1975), and these close associations are still observed today in the form of mycorrhizae, endophytes, and plant pathogens. The fact that these close associations still exist suggests that there is some benefit to each of the partners. It is therefore not surprising that there is a benefit to plants to being associated with mycorrhizal fungi during the initial stages of primary succession of vegetation

TABLE 5.16 Seedling Plant Height and Survival of Three Tree Species in a Tree Nursery in Which the Soil Surface was Left Bare or Had been Covered with the Foliose Lichen *Cladonia alpestris* Collected from a Surrounding Forest

	Cladonia alpestris plots		Control plots	
Tree species	Height (cm)	Survival (%)	Height (cm)	Survival (%)
Pinus sylvestris	22.2	93	25.8	100
Picea abies	21.4	84	31.2	100
Betula verrucosa	105.0	70	108.0	67

Source: Data from Brown and Mikola (1974).

onto new land. We have seen in this chapter how the presence of mycorrhizal inocula carried into newly colonized areas benefits the plants in terms of nutrient and water acquisition. The patchy distribution of these pockets of inoculum, together with patchy distributions of suitable rooting media, lead to spatial variability in the benefits derived by the plant from mycorrhizal associations. In very resource rich areas, it would seem that nonmycorrhizal ruderals are capable of surviving. It is the combination of this heterogeneity in the environment, patchily distributed beneficial fungi, and the increased growth and fitness of individuals and individual species in this mosaic that gives rise to the plant community structure that develops.

After the initial colonization of bare ground, there is a succession of dominant plant species and functional groups as the plant community develops toward a stable climax. During this succession of plants we also see successions of fungi, both as saprotrophs and mycorrhizae (and probably pathogens). Are these successions linked or coincidental? There seems to be compelling evidence to suggest that successions of both plants and fungi are linked and the linkage is through changing environmental conditions. Most of these edaphic (soil) changes are related to the resource quality of the materials that provide the plant nutrients during decomposition. What do we know of the feedback mechanisms that elicit changes in species communities or functional groups? Conn and Dighton (2000) suggest a link among edaphic factors, the supply of nutrients, and the development of different functional groups of ectomycorrhizal fungi. Where leaf litters immobilize phosphorus in the early stages of decomposition, ectomycorrhizal fungal communities that develop on the root systems invading that litter have a higher proportion of acid phosphatase-producing types, effecting mineralization of phosphorus that is tied up in organic resources. Although they did not prove the same for nitrogen, it is likely that the feedbacks among nutrient dynamics, plant demand for nutrients, and the ability to "select" appropriate mycorrhizae maintain an optimal community of both plants and associated fungi. This model

TABLE 5.17 Allelopathic Effect of the Lichen *Cladonia* spp. on Tree Species

Tree species	Lichen species	Dry weight	^{32}P uptake	N content	P content
Jack pine	*Cladonia alpestris*	56	62	85	81
	Cladonia rangifera	60	56	83	71
White spruce	*Cladonia alpestris*	58	48	77	62
	Cladonia rangifera	64	43	79	54

Note: Values are expressed as percentage of the control trees without a lichen mulch.
Source: After Fisher (1979).

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TABLE 5.18 Reduction in Spore Germination of the Moss *Funaria hygrometrica* in the Presence of Lichen Compounds

Lichen compound	(%) Germination
Vulpinic acid	37
Usnic acid	62
Evernic acid	69
Psoromic acid	72
Lecanoric acid	94
Atranoric acid	97
Stictic acid	99
Fumarprotocetaric acid	100

Note: Germination is expressed as a percentage of control.
Source: From Lawrey (1986).

still needs to be completely evaluated. This is especially true if the benefit to the host plant is nonnutritional. Perhaps the burden on the plant to sustain a mycorrhizal habit is less than we previously thought (Fitter, 1991) (Table 5.20), and compared to the production of roots, may have multiple benefits.

Even in a patchy environment, stability can be maintained by the development of linkages between patches. In this case the abilities of fungi to bridge between resources and translocate material between patches is of great importance. We have seen in this chapter that the development of a mycelial web or network in the environment is beneficial for the establishment of new recruits into the plant community. If plants can "plug into" an existing mycorrhizal network, their chance of survival is enhanced. This is especially important during the initial stages of colonization of bare ground. The recent demonstration of interplant transfer of carbon and nutrient in the field (Simard et al., 1997b,c) is altering our view of the rule of plant community assembly. It was previously thought that communities developed as a result of competition among species. This new finding implies that synergistic activities also exist that need to be incorporated into models of plant community dynamics. How much of these interplant connections help with establishing and maintaining the stability of the ecosystem?

How much do mycorrhizae differentially affect plant performance and fitness, thus stimulating change in plant community structure by altering the dominant species? Many lines of evidence point to different fungi having different properties and efficiencies (Dighton et al., 1990), thus by chance some plants in the community get a better deal than others by associating with a "better"

TABLE 5.19 Soil Microfungal Species of the Mikhailovsky Reserve as Influenced by the Intensity of Cutting

Virgin ecosystem	Periodically cut	Frequently cut
Mortierella stylospora	*Mortierella alpina*	*Absidia corymbifera*
Alternaria alternata	*Aspergillus flavus*	*Mortierella alpina*
Aspergillus versicolor	*A. nidulans*	*Rhizopus oryzae*
Cladosporium herbarum	*Botrytis cinerea*	*Acremonium murorum*
Penicillium citrinum	*Cladosporium cladosporioides*	*Alternaria alternata*
P. duclauxii	*Fusarium solani*	*Aspergillus amstelodamia*
P. funiculosum	*Gloeosporium* sp.	*Botrytis cinereas*
P. lanosum	*Penicilium chrysogenum*	*Cladosporium cladosporioides*
P. nigricans	*P. citrinum*	*C. herbarum*
P. olsoni	*P. glauco-lanosum*	*Gliochladium roseum*
P. rubrum	*P. lanosum*	*Penicillium chrysogenum*
P. rugulosum	*Trichoderma album*	*P. decumbens*
Trichoderma viride	*T. viride*	*P. frequentans*
T. koningii	*T. koningii*	*P. implicatum*
	Mycelia sterilia	*P. lanosum*
		P. multicolor
		P. restrictum
		P. spinulosum
		P. steskii
		P. variabile
		Scopulariopsis brevicaulis
		Sporocybe byssoides
		Trichoderma koningii
		Mycelia sterilia

Source: From Golovko (1999).

mycorrhizal fungus. Is this variability smoothed out over the population and community, as suggested by Allison and Goldberg (2002), or does the asymmetry of the beneficial effect of the mycorrhizae persist? Is this asymmetric effect enough to alter the trajectory of plant community development (sequential change of dominant plant species or groups)?

TABLE 5.20 Estimated Relative Cost of Maintenance of Arbuscular Mycorrhizal Symbioses and Roots

Biomass of fungus	10% of root biomass (may be up to 20%)
Cost of growth and maintenance of fungus	1–10% of fungal biomass $d^{-1} \equiv 0.1$–1% of root biomass d^{-1}
Cost of root maintenance	1.5% of root biomass d^{-1}

Note: Thus the cost of maintenance of mycorrhizal fungus $\approx$ root maintenance cost.
Source: Data from Fitter (1991).

On the negative side of plant fitness and growth, we have seen that pathogenic fungi can have a significant effect. The most extreme examples of the effects of fungal pathogens on plants, however, is that of interactions between exotic plants and fungi or exotic fungi and plants. In these instances, it is probable that there has not been time for disease resistance to evolve in the plant species. Here we get dramatic and rapid changes in plant communities as dominant plant species are eradicated from the ecosystem (chestnut blight, oak decline, Dutch elm disease, etc.). How strong are the pathogenic effects in natural ecosystems? Evidence from the effects of less acute pathogens (Alexander, 1990; Paul, 1990; Hansen and Goheen, 2000) suggests that their action increases heterogeneity in the gene pool of the same plant species, leading to patchy dispersion of disease-susceptible and disease-resistant plants in the community. The separation of these two groups of plants is maintained by the rate of the spread of the fungal pathogen and the rate of recolonization of blighted areas by the host plant. Where patches of diseased plants are not recolonized by the same plant species, gap replacement by other species leads to an increase in biodiversity in the community. Also, if one plant is replaced by another rather than by the same species, the architecture of the community and the chemistry of the leaf community is also increased. This gives rise to an increased diversity of resources that can be used by grazing animals. Gap replacement by a nonconspecific thus not only leads to an increase in plant diversity, but also to an increase in the diversity of grazing fauna.

Fungi interact with each other in a variety of ways. In this chapter we have mentioned interactions between plant-pathogenic fungi and saprotrophs on leaf surfaces and plant-pathogenic fungi and mycorrhizae. In both cases the interference may be physical, as a result of resource competition or by the production of biocides. It is probable that a fine balance has evolved in natural ecosystems between plant pathogens and other fungal functional groups that

regulate them. In agroecosystems, however, this balance is upset by the development of monospecific crops and the effects of disturbance, fertilizers, and other chemicals. In these ecosystems a science of biocontrol is emerging, in which the benefits of saprotrophic and mycorrhizal fungi are being sought to control disease-causing fungi. This science also extends to the control of invertebrate pests of plants. Nematophagous and entomopathogenic fungi are being used to control important pests of crop plants. These fungi exist in natural ecosystems, but their effects do not seem to be seen until the population of their host invertebrate increases to high levels. It is here that the density-dependent regulation of invertebrate populations by fungal pathogens can be seen (Kerry and Jafee, 1997). Interest has recently been raised regarding the decline in tropical anuran populations by fungal pathogens. Concern is twofold. One concern is the potential loss of diversity in tropical ecosystems, which are one of the main biomes in which public opinion is high. The second concern is the effects of predicted climate change. If conditions are likely to become warmer and wetter, then conditions for the propagation of fungal pathogens are going to increase, thus exacerbating the situation. What is still unclear is how important fungi are in the regulation of other vertebrate populations. Do fungi also regulate changes in vertebrate community structure?

Two final interactions between plants and fungi affect both the plant and grazing animals. Fungal endophytes produce alkaloids that are poisonous to grazing animals. These fungi act as grazing inhibitors, and thus impart protection and greater growth and fitness to the host plant. In turn, these endophytes regulate the feeding of animals and limit their populations. Both vascular and nonvascular plants and lichens produce polyphenolic and other toxic chemicals. These chemicals, which are released into the environment, modify the growth of other plants and fungi. Although we have shown a number of examples of these interactions, the actual effects of these chemicals, the occurrence of these effects in natural ecosystems, and the interactions with other organisms have not been clearly resolved. How important are these "allelopathic" chemicals in regulating ecosystem processes? How important are these chemicals in altering plant community composition? How important are they in affecting fungal community composition in all functional groups?

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6

Fungal Interactions with Humans

6.1 INTRODUCTION

As the world population increases (Meadows et al., 1992; Silver and DeFries, 1990; Brown, 1997) the effects of human activities on ecosystems escalates. The press has bombarded us with issues of climate change, acidifying pollutants (acid rain and nitrogen deposition), atmospheric carbon dioxide increase, stratospheric ozone depletion, and the threat of nuclear fallout. Major national and international discussions have taken place to decide the level of threat that these environmental changes may impose on human populations, their economies, and the environment. Much of the debate has been political or driven by economic factors, but the magnitude and effects of the actual threat are still very much in debate (Lomborg, 2001).

In the discussions of the effects of human activities on the environment, the role of fungi or the impacts of pollutants on fungi rarely hit the headlines in the popular press. As one of the concluding chapters in a book that explores the importance of fungi to ecosystem processes, it would be wrong not to have some discussion of the interactions among human influences and fungal diversity, activity, and function. In this chapter we will discuss a subset of the important interactions between human-induced changes in the environment and the processes mediated through fungi. I have chosen to discuss the effects of acidifying pollutants, heavy metals, radionuclides, and global carbon cycling in relation to elevated CO_2 levels in the atmosphere.

6.2 FUNGI AND ACIDIFYING POLLUTANTS

The interaction between acidifying pollutants (as they are known today) and fungi provides an interesting story in the evolution of thought within the scientific

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community. Following the industrial revolution in Europe, numerous industrially related changes in ecosystems and organisms were seen to be the result of pollution of one sort or another. For example, the emergence of a black race of the peppered moth (*Biston betularia*) and its evolution toward being a new species was attributed to its adoption of a more appropriate cryptic coloration for resting unobserved by predators on soot-coated tree bark than its lighter counterpart (Kettlewll, 1955). The decrease in the abundance of certain groups of organisms was identified as being a biological indicator of pollution. One such group is the lichens, whose decline in relation to increased atmospheric pollution was dramatic. Only recently have they been shown to be recovering in species abundance and diversity (Gilbert, 1992; Bates et al., 2001).

With the identification of a decline in the health of central European forests in the 1970s and the continued degradation of decorative limestone carvings on buildings and gravestones came the realization that acid rain was the culprit. This acid rain, consisting of sulfuric acid dissolved in rain droplets, was partly a by-product of the energy industry in Central Europe, where high sulfur-containing coal was used as the main fuel source. The sulfur dioxide released into the atmosphere as a result of combustion combines with water to form sulfuric acid. Observations of the declining tree canopies indicated damage to the cuticular waxes and a reduction in the photosynthetic capacity of the canopy, and thus a decline in tree performance (Bervaes et al., 1988; Oren et al., 1988). It was only in the late 1970s that soil ecologists became involved in the research on acid rain in relation to the "Waldsturben" effect of the forest dieback in Bavarian forests (Sobotka, 1964). It was the observations of Ulrich et al. (1979), Hütterman (1982), and Blaschke et al. (1985) that alerted researchers to the fact that acid rain was affecting both root growth and the mycorrhizal status of trees. Führer (1990), however, cautioned that forest decline in Europe was exacerbated by other "natural" stressors, including soil nutrient depletion, harvest management practice, and drought. Subsequently, research moved toward the study of the primary pollutant, sulfur dioxide, rather than its solubility products. A new wave of research based on both laboratory and field fumigation experiments emerged (McLeod, 1995). Again it was the plant physiologists, looking at above-ground components, who initiated this work. The soil ecologists followed. At that time, it was being recognized that the increase in ozone concentration of the lower atmosphere (rather than the loss of stratospheric ozone caused by chlorofluorocarbons; CFCs) could also play a major role in damage to cuticular waxes and the photosynthetic capacity of leaves of plants. As a result, cofumigation experiments of ozone and sulfur dioxide were conducted. Finally, NO_x was recognized as another major source of pollution derived from the combustion of fossil fuels. Nitrogen deposition and the problems of nitrogen fertilization and forest soil saturation with N emerged as the most recent line of investigation (Aber et al., 1989; Aber, 1992a,b; Tietema et al., 1993; McNulty and Aber, 1993;

Reynolds et al., 1998; Gundersen et al., 1998). It is now obvious that none of these pollutants operates alone and the reality is that there is some combination of all acidifying pollutants that influences ecosystem processes and the role of fungi within these processes. The logistics of teasing out the relative contribution of each pollutant is not simple, however, especially where they may have contrasting effects of damage to plant structure and reduction or increase in the availability of nutrients in soil.

6.2.1 Acidifying Pollutants, Mycorrhizae, and Plant Nutrient Uptake

In order to assess "critical loads" of pollutants, the degree to which the pollutant exceeds a threshold level can often be assessedby chemical analysis, changes in abundance, or changes in the physiology of a biological indicator. In Europe, the changes in the composition and abundance of macrofungal fruit bodies, particularly ectomycorrhizal Basidiomycotina, have been used as a biological indicator for terrestrial forested ecosystems (Fellner, 1988; Colpaert and Van Tichelen, 1996). Work emanating from the Waldsturben effect of the forest dieback in Bavarian forests suggested that part of the reason for forest tree decline was the damage caused to roots and their ectomycorrhizae by acidifying pollutants (Sobotka, 1964; Ulrich et al., 1979; Hütterman, 1982; Hütterman, 1985; Blaschke et al., 1985; Stroo and Alexander, 1985). Based on the idea that mycorrhizal formation was affected by both carbohydrate supply and nutrient levels in soil, which in turn influence hormone levels in roots (Nylund, 1989), Dighton and Jansen (1991) proposed a two-directional impact model of acidifying pollutants on the development of mycorrhizae (Fig. 6.1). In this model, they suggest that two mechanisms lead to the reduction of mycorrhizal associations of the plant roots: (1) via a reduction in photosynthesis in the tree canopy, reducing the energy supply to roots, and (2) acid-induced increase in the availability of toxic metal ions in soil, resulting in root damage. In the first scenario, pollutant-induced reduction in the photosynthetic capacity of the tree canopy reduces the allocation of photosynthate to roots and their mycorrhizae. Reduced energy supply both reduces the overall mycorrhizal colonization of roots and favors those fungal species that can survive on low carbohydrate supplies. In the second scenario, the acidifying pollutants reduce the soil pH and make toxic metals (aluminum, manganese, and magnesium) more soluble, and hence, more plant-available (Van Breemen and Van Dijk, 1988; Skeffington and Brown, 1986; Tyler et al., 1987; Ruark et al., 1991). This increased toxicity leads to reduced root growth, root dieback, and reduced mycorrhizal fungal growth and root colonization. The overall results of the work on the effects of acid rain on mycorrhizae are reviewed in Jansen et al. (1988), Jansen and Dighton (1990), and Dighton and Jansen (1991).

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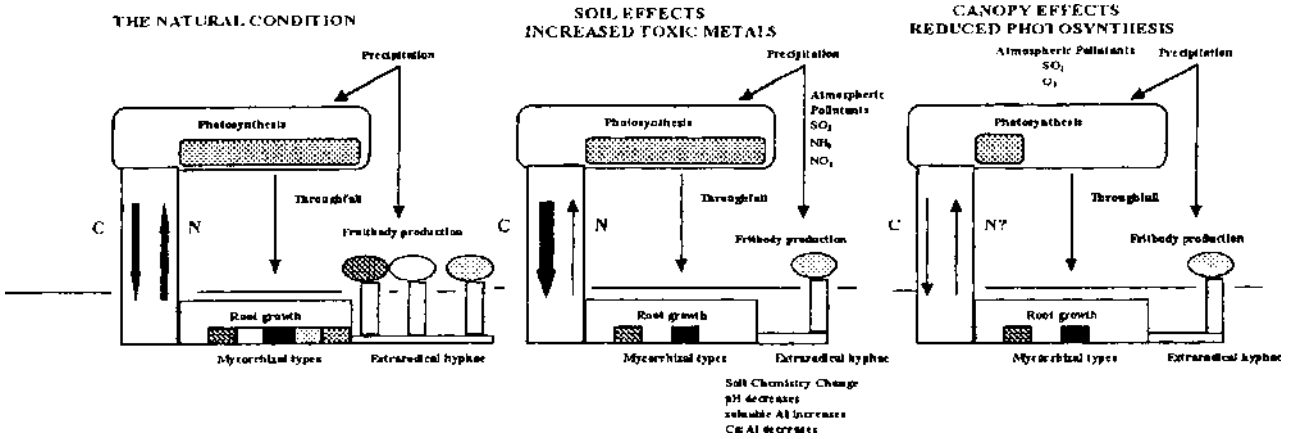

FIGURE 6.1 Schematic representation of the interactions among trees, their ectomycorrhizal symbionts, and environmental factors altered by atmospheric deposition of acidifying pollutants. The first model represents the "natural," situation, in which the trees is dependent on mycorrhizal diversity and its associated function to acquire nutrients and the mycorrhizal dependency on the host tree for the supply of carbohydrates for metabolic maintenance of the symbiosis. The second model indicates the effects of pollutants on soil, which increase toxic metal availability, leading to root and mycorrhizal damage and increased fertility from nitrogen sources, reducing the dependency of the plant on mycorrhizae. The third model represents damage to foliage and loss of photosynthetic capacity. This reduces the carbohydrate flux to roots, resulting in a loss of mycorrhizal diversity and function. *Source*: After Dighton and Jansen (1991).

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Evidence of a decline in the mycorrhizal formation on the roots of trees and reduced root vigor in forests come from the works of Sobotka (1964), Liss et al. (1984), Meyer (1987), and Blaschke (1988), among others. Evidence for the reduction in ectomycorrhizal fruit body production comes from researchers such as Arnolds (1985, 1988), Jansen and Van Dobben (1987), and Fellner (1988). Although the effect of the acidifying pollutants was different among ectomycorrhizal fungal species, there was a general trend of greater effect on mycorrhizal fungal species than on saprotrophic fungal species. Arnolds (1988) reported that in most healthy forest ecosystems fruit bodies of mycorrhizal fungi formed between 45–50% of all fruit bodies found. In polluted stands, however, only about 10% on the fruit bodies were of mycorrhizal origin. The stages of forest decline have been identified according to the macrofungal ratio of saprotrophic to mycorrhizal forms by Fellner and Pesková (1995), and are shown in Table 6.1.

Changes in soil chemistry, resulting on acidifying pollutants and leading to increased solubility of heavy metal ions into the rooting zone, were shown by Van Breemen and Van Dijk (1988), Skeffington and Brown (1986), and Tyler et al. (1987). The effect of these soil chemical changes on the ectomycorrhizal community structure of trees roots was shown in Finland by Markkola and Ohtonen (1988), who found that *Piloderma, Dermocybe*, *Hebeloma*, and a "type 03" ectomycorrhizal were significantly reduced in the presence of acidifying pollutants, whereas *Cenococcum* was found to increase. Similarly, Dighton and Skeffmgton (1987) found that simulated acid rain applied to *Pinus sylvestris* trees in lysimeters caused a change in the ectomycorrhizal community structure by reducing the occurrence of mycorrhizal morphotypes that were multibranched

TABLE 6.1 Relationship Between Saprotrophic and Ectomycorrhizal Fungal Abundance in Declining Forests

Levels of disturbance	Ectotrophic forest stability
Latent	Ectomycorrhizal fungi decreasing to 40%, while lignicolous species increase to more than 30%
Acute	Ectomycorrhizal species decreasing to less than 40%, lignicolous species increase to more than 40%
Lethal	Ectomycorrhizal species decrease to less than 20%, while lignicolous species rise to more than 55%

Source: As described by Fellner and Pesková (1995).

and that were associated with large amounts of extrardical hyphae. It appeared that the effect of the pollutant was greatest on fungal hyphal growth rather than on the actual mycorrhizal structure. This theory is supported by research on the effects of aluminum toxicity to fungal hyphae in culture. In addition to tree roots being damaged by increased availability of Al in soil solution (Schier, 1985), Thompson and Medve (1984) showed that a concentration of 146 μM aluminum suppressed growth of hyphae of *Cenococcum*, *Pisolithus*, and *Thelephora*, but that *Suillus* showed no growth reduction below 1000 μM concentration. Furthermore, the Al:Ca, Al:Mg, and Al:PO_4 ratios were found to be important determinants of fungal growth (Jongbloed and Borst Pauwels, 1988; 1989; Kottke and Oberwinkler, 1990). The improved growth of a variety of ectomycorrhizal fungal species at low Al:PO_4 ratios, even at high levels of Al concentration (Jansen et al., 1990), was explained by the absorption and thus immobilization of Al into polyphosphate droplets in the fungal hyphae (Kottke and Oberwinkler, 1990).

In a field fumigation experiment (McLeod et al., 1992) in which SO_2 and O_3 were released over circular plots containing monospecific stands of Scots pine, Sitka spruce, and Norway spruce, multivariate analysis of the ectomycorrhizal community structure on the root systems of the trees revealed that the only trend in change of mycorrhizal community structure was as a result of SO_2 fumigation on Scots Pine, where a reduction in the occurrence of *Paxillus involutus* mycorrhizae occurred (Shaw et al., 1992; 1993). In an analysis of the fruit bodies found in the plots, however, *Paxillus involutus* fruited more abundantly in Scots pine plots that received high SO_2 loading the converse of the root colonization. The influence of combined pollutants on mycorrhizal formation is dependent on the resistance of the plant species to the pollutant. In a study of the effects of acid rain and ozone on two provenances of Loblolly pine (*Pinus taeda*), Qui et al. (1993) showed that the ozone-tolerant provenance had less reduction in root surface area, less change in the amount of ectomycorrhizal root colonization, and less change in the species composition of these mycorrhizal fungal species than the ozone-intolerant provenance. The effect of ozone alone appeared to alter the nature (not the degree) of root colonization of the arbuscular mycorrhizal structure of sugar maple (*Acer saccharum*) by reducing the number of arbuscules but increasing the number of vesicles and hyphal coils within the cortex of the root (Duckmanton and Widden, 1994) (Fig. 6.2). Duckmanton and Widden suggest that this is a response to reduced photosynthesis of ozone-treated plants, in which the production of vesicles and hyphal coils is less energy-demanding than the production of arbuscules. As vesicles are thought to be storage structures, it is possible that their production is a stress response.

In the terrestrial, forested ecosystem, atmospheric deposition to the forest floor and the tree root system can be by direct deposition (bulk deposition) or via

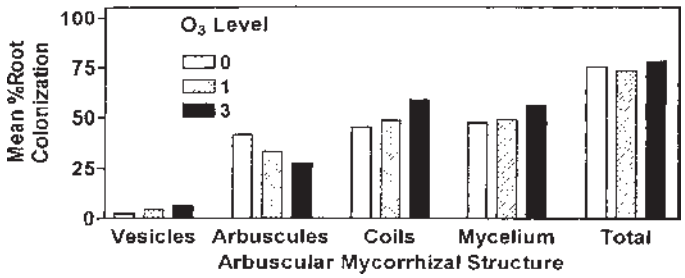

FIGURE 6.2 Arbuscular mycorrhizal development in sugar maple under the influence of elevated atmospheric ozone. Ozone level 1 = X, 1 = Y, 3 = Z. *Source*: After Duckmanton and Widden (1994).

throughfall through the tree canopy. Modifications to the actual rate of deposition can occur in throughfall precipitation. Higher than expected levels of deposition can results, as the surface area of the leaves in the canopy is frequently greater than the soil surface area over which they spread. N deposition onto this large surface area can then be washed off onto the soil below. Foliar uptake of N deposited on leaf surfaces, however, can result in less than expected forest floor N deposition. In contrast to sulfuric acid, nitrogen is a nutrient that is in demand by plants and is often a limiting nutrient in many ecosystems. The resultant N reaching the forest floor thus can be immobilized into plant and/or microbial biomass (with different biological half-lives), and that which is in excess to plant demand may leach down the soil profile or through lateral flow into watercourses. The degree of N leaching is in part dependent upon the limitation of other major nutrient elements (Harrison et al., 1995). This change in nutrient balance (net excess of N) leads to changes in biotic components of both terrestrial and aquatic systems when the level of N reaches a critical threshold.

Arnolds (1989a,b; 1991; 1997) suggested that the decline in the appearance of ectomycorrhizal fruit bodies and the increase in saprotrophic and pathogenic fungal fruit bodies in The Netherlands is associated with a combination of acidifying pollutants, and in particular, nitrogen deposition (Termorshuizen and Schaffers, 1987; 1991; Kårén and Nylund, 1997). Although there is little experimental evidence showing the effects of acidifying pollutants on saprotrophic mushroom-forming fungi, Kuyper (1989) gives evidence that nitrogen addition and the effects of liming, (to offset the effects of acidifying pollutants) stimulate saprotrophic fungi and leaf litter decomposition where nitrogen levels in the leaf litter are low, but suppress saprotrophic activity where leaf litter nitrogen content is high. He also shows that the effect of liming on mycoflora is very similar to that of nitrogen fertilization. Although they did not observe significant changes in the ectomycorrhizal species composition, Antibus

and Linkins (1992) showed that the effect of liming reduced the acid phosphatase activity of the mycorrhizal community in the litter layer of the forest floor. They did not explore how the relative availabilities of nitrogen and phosphorus in soil played a part in this, but it could be surmised that there is a synergistic activity of liming on increasing both N and P availability, thus reducing phosphatase activity by negative feedback mechanism.

Changes in phosphorus availability were implicated in the forest decline in the Vosges region of France (Estivalet et al., 1990). The responses of tree seedling growth to added phosphorus show that P availability was reduced in declining forest soils. Estivalet et al. (1990) attribute this to the change in the balance of rhizospheric microbial community, which in part suppressed the ectomycorrhizal development in declining forest soils. They showed that the fungal species *Penicillium*, *Trichoderma*, *Acremonium*, and *Cylindrocarpon* were more regularly isolated from declining soils than soils from healthy forests. They suggest that there may be some antagonistic—but not pathogenic—effect between these soil fungi and the ectomycorrhizal fungi of Norway spruce.

Arnolds (1989b,c) lists the changes over time of fungal and plant species in a nutrient-poor acidic-soil Dutch pasture in the presence of long-term inorganic and organic fertilizer application. He reports changes in the plant community toward plants that tolerate high levels of nitrogen. In the fungal community, the number of species found in 1974 and 1980 did not change, but the species structure did. Arnolds showed the loss of a number of fungal species, including *Hygrocybe ceracea*, *Entoloma confereendum*, *Mycena cinerella*, and *Geoglossum, glutinosum*, whereas other species, including *Marasmius oreades*, *Panaeolina foenescii*, *Clitocybe amarescens*, and *Panaeolus acuminatus*, increased between six- and 400-fold between 1974 and 1980. In addition, he showed increases in coprophytic fungal species. Although this study concentrates on the agricultural inputs of fertilizers, it suggests trends of response of the fungal communities to long-term atmospheric inputs of fertilizing pollutants, such as nitrogen. In contrast to the studies by Arnolds (1989a,b,c,d), Termorshuizen and Schaffers (1987), and Rühling and Tyler (1991), who showed a decrease in mycorrhizal fungal species compared to saprotrophic fungal species (Sasted and Jenssen, 1993), showed a decrease in saprotrophic species richness and an increase in the dominance of some ectomycorrhizal fungal species in response to simulated acid rain at two localities in Norway. They suggested that this difference may be due to local condition (soils, climate) and cautioned against the broad generalizations that have been made regarding the effects of acidifying pollutants. Arnold's observations have led to the adoption of "red data" lists for the conservation of fungal species (Arnolds, 1989b; 1997). Recently, a call for inclusion of fungi and nonvascular plants in the lists of species for conservation has been adopted in the United Kingdom (Watling, 1999). This action results from the fear of loss of fungal species due to anthropogenic influences.

Many of the studies on changes in mycorrhizal community structure have been made using fruit body appearance and comparative abundance as the measure of fungal response to changes in the environment. There is evidence to show that the appearance or nonappearance of fruit bodies of ectomycorrhizal fungi may bear little relation to the abundance of that mycorrhizal morphotype on the root system of the tree (Termorshuizen and Schaffers, 1989; Egli et al., 1993). This finding therefore adds a further complication to the interpretation of data and understandings of the complexities of interactions between environmental variables and fungal communities.

Concentrating on the below-ground component of the forest mycorrhizal system, it was shown that the addition of ammonium sulfate to Norway spruce forests decreased the fine root biomass but not the degree of ectomycorrhizal colonization of roots (Kårén and Nylund, 1997). Kårén and Nylund suggest, there however, that there may be changes in the structure of the ectomycorrhizal community. Termorshuizen (1990) showed that the addition of nitrogen to the forest floor significantly reduced the number of fruit bodies of basidiomycete ectomycorrhizal fungal species. This was not reflected in a change in the mycorrhizal formation on roots, however. Arnebrant and Söderström (1992) showed that the total mycorrhizal colonization of roots was reduced from 70–55% in Scots pine forest fertilized with 1700 and 950 kg N ha^{-1} over a period of 13 years. In contrast, in a Norway spruce forest nitrogen-addition experiment (NITREX) in Sweden, Brandrud (1995) compared the macrofungal flora of a control plot receiving natural N deposition, a plot receiving an additional 35 kg h^{-1} y^{-1} N, and a roofed plot to exude N deposition. He showed that there were changes in the ectomycorrhizal fungal flora due to the treatments (represented as a PCA analysis in Fig. 6.3). He showed that the dominant genera, *Cortinarius* and *Russula*, were reduced in abundance by additional N, *Lactarius* showed little change, and a few specific species, notably *Paxillus involutus* and *Lactarius rufus*, showed increased abundance with added N. Overall the species diversity, number of fruiting fungi, and total number of fruit bodies did not differ significantly among treatment. Jonsson (1998) showed that there was poor correspondence between the fruit bodies observed and the ectomycorrhizae on roots in both control plots and those receiving additions of nitrogen in the same NITREX experiment. Using molecular analysis of the ectomycorrhizal community structure on roots, she demonstrated about 1–4% correspondence between the species of fruit bodies and mycorrhizae. The occurrence of fruit bodies, however, showed a more dramatic shift in species composition than did the mycorrhizae on roots (Fig. 6.3). The addition of the equivalent of three times ambient N deposition (65 and 198 kg N ha^{-1} y^{-1} as ammonium nitrate) in beech woodlands caused an almost complete cessation of mycorrhizal fungal fruiting (Rühling and Tyler, 1991). Many leaf litter inhabiting, saprotrophic fungal species increased fruiting, however, including species of the general *Mycena*,

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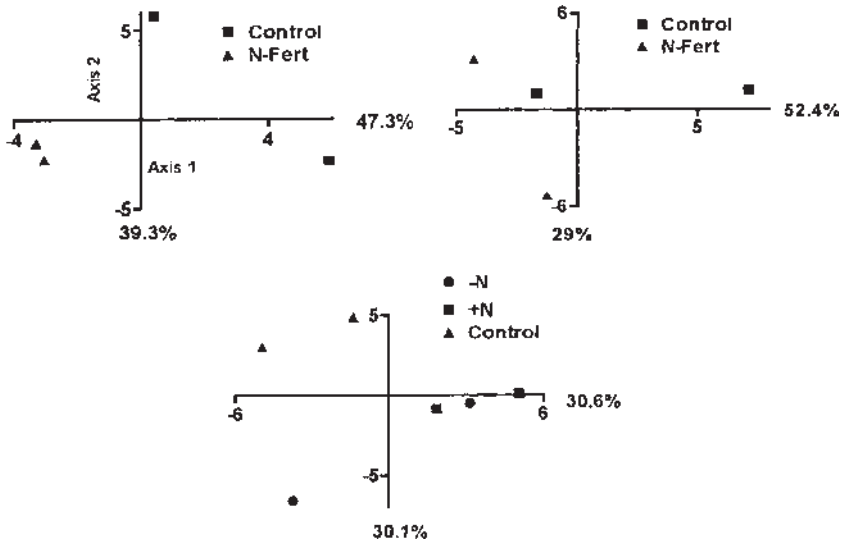

FIGURE 6.3 PC analysis of the effects of added nitrogen fertilizer, simulating atmospheric nitrogen deposition in a NITREX experiment in Sweden. The top two analyses are treatment plots in ectomycorrhizal fruit body species space, showing the nitrogen-treated plots having a different community structure than the untreated control plots. The third analysis is similar, but uses mycorrhizal community structure based on molecular identification of root tips. This latter analysis shows less difference in mycorrhizal community structure between unfertilized and fertilized plots. *Source*: Data compiled from Brandrud (1995) and Jonsson (1998).

Clitocybe, *Lepista*, *Agaricus*, and *Lycoperdon* (Fig. 6.4). A possible explanation for this is the increased availability of N to stimulate the decomposition of a recalcitrant leaf litter species.

From these results we can infer that the addition of nitrogen has a greater effect on the ability of basidiomycete fungi to produce fruiting structures than it has on changes in soil chemistry and consequent changes in mycorrhizal fungal colonization of root tips. The function of the ectomycorrhizal community (enzyme production, rate of nutrient uptake, degree of protection of host plant to root pathogens, fungal hyphal growth, etc.) as a result of altered soil conditions has not been fully investigated, however.

Some changes have been shown to occur in the growth and physiology of the mycelium of fungi in the presence of elevated N levels. Arnebrant (1994) showed that the addition of ammonium sulfate and ammonium nitrate at between 1 and 4 mg g^{-1} peat significantly reduced mycelial growth of *Paxillus involutus* and *Suillus bovinus* in mycorrhizae synthesized on roots of lodgepole pine

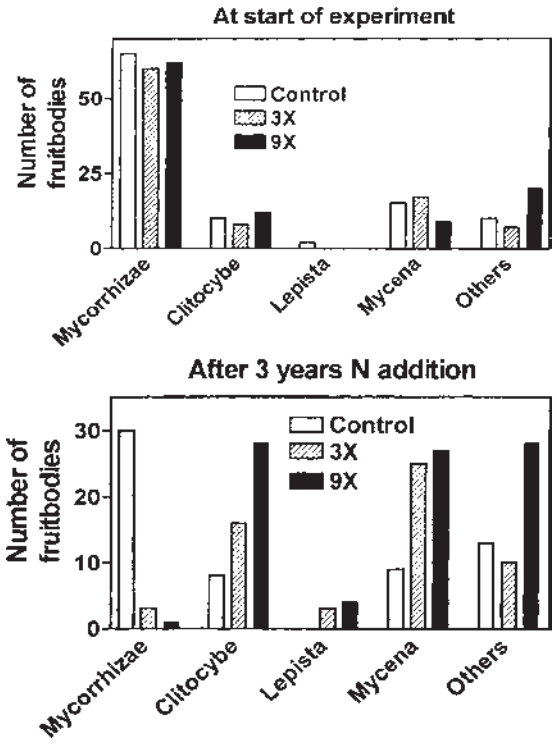

FIGURE 6.4 Mean number of mycorrhizal and saprotrophic fungal fruit bodies in experimentally N-fertilized beech forest plots at zero (control), 260 kg h^{-1} N (3x) and 790 kg ha^{-1}N (9x) at the start of the N addition (top) and 3 years later (bottom). *Source*: After Rühling and Tyler (1991).

seedlings. In contrast, Kieliszewska-Rokicka (1992) found that the addition of small amounts (0.17 to 19 mM N) of NH_4-N increased both the growth and acid phosphatase activity of *Paxillus involutus* mycelia in agar culture. This may be a synergistic effect of the additional nitrogen causing a temporary deficiency of phosphate in the plant and stimulating phosphatase enzyme production by a positive feedback mechanism. It has been shown that the imbalance of nutrients in soil by the addition of chronic levels of N can induce limitations of other nutrients. Potassium and phosphorus were shown to become increasingly limiting for growth of Sitka spruce forests in the United Kingdom with increased addition of N (Harrison et al., 1995), which supports the hypothesis of Leibig's "Law of the Minimum" (Read, 1991). The change in relative availabilities of inorganic and organic forms of phosphorus in soil, along with the relative availabilities of N and

P in an N-saturated situation, may strongly influence the mycorrhizal community structure by promoting fungal species with high phosphatase-producing potential and suppressing those species that are capable of acquiring nitrogen from organic sources. Considering the close association between ericaceous plants and their ericoid mycorrhizae, and the dependence of this association on the extraction of nitrogen from organic sources in the soil, it would be expected that the addition of readily available nitrogen would have significant effects on heathland ecosystems. The heathlands of The Netherlands have suffered considerable decline as a result of nitrogen deposition. In her study of the effects of adding ammonium nitrate at between 0 and 75 $kg\,ha^{-1}\,y^{-1}$ N to heather (*Calluna vulgaris*), however, Johansson (2000) found no significant effects of additional N on root production or mycorrhizal colonization of the roots. She concludes that the decline of heather under the influence of elevated nitrogen deposition is unlikely to be caused by a direct impact on the ericoid mycorrhizae.

As suggested earlier, plants are able to acquire nitrogen from that deposited on leaf surfaces as well as through roots. The deposition of nitrogen onto leaf surfaces can result in the foliar uptake of the equivalent of 2–8% of the total N demand of spruce trees (Boyce et al., 1996). This change in the root demand for N may significantly alter the physiology of roots and their ectomycorrhizae with aspect to the acquisition of other nutrients. Some adaptation of ectomycorrhizal fungal species may adapt them for coping with high rates of nitrogen addition. In an experiment to demonstrate the effects of added nitrogen on mycorrhizal N uptake, Wallander et al. (1999) showed that where fungal isolates exhibited inherently high NH_4 uptake affinity, N uptake rates by these fungi were inhibited to a greater extent than fungal isolates exhibiting inherently low rates of ammonium uptake. Isolates having high uptake rates translocate a greater proportion of the assimilated N to shoots. They thus conclude that low uptake rates may enable ectomycorrhizal fungi to avoid the stress of elevated nitrogen loading to the ecosystem.

Experiments have been conducted to study the interactions between misting tree canopies with a combination of sulfuric acid and ammonium nitrate that simulates occult deposition of pollutants. Using these methods, changes in soil chemistry were explored by Carreira et al. (2000). They showed that acidifying pollutants alter the inorganic P subcycle in soil by increasing P sorption capacity and decreasing the concentration of labile P. In addition, acid phosphatase activity in soil decreased (263 $\mu g\,pNP\,h^{-1}\,g^{-1}$, acid-misted, and 382 $\mu g\,pNP\,h^{-1}\,g^{-1}$, nonmisted), thus increasing the organic P component of the soil. They proposed that the addition of nitrogen to the point of nitrogen saturation also leads to a reduction in the availability of P in soil (Fig. 6.5). Although they did not invoke any fungal role in this process, we can speculate that the reduction in phosphatase activity could be due to a reduction in fungal biomass and activity. Phosphatase activity generally increases in the presence of

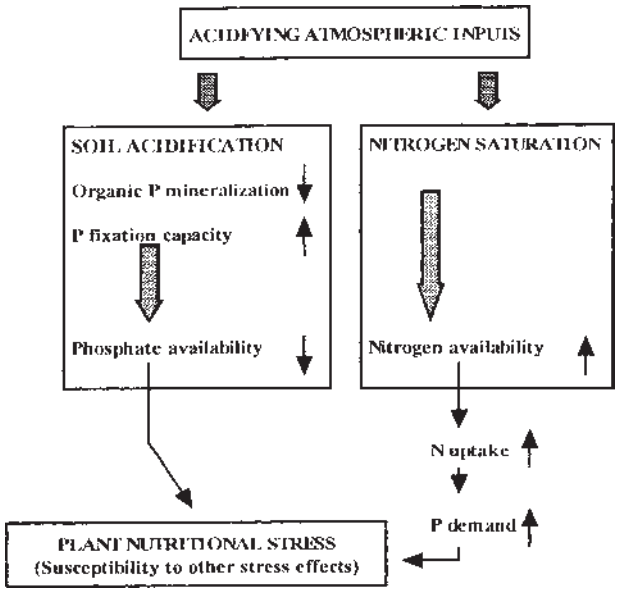

FIGURE 6.5 Hypothesized methods of acidifying pollutant effects to induce phosphate nutritional stress by (1) changes in soil acidity affecting inorganic and organic P cycling, and (2) increased P demand induced by N saturation. *Source*: After Carreira et al. (2000).

greater amounts of organic phosphate (Dighton, 1983; Dighton, 1991; Sinsabaugh et al., 1993; Antibus et al., 1997), however. The addition of N to forests will have differing effects, depending upon the initial nitrogen status of the forest soil. In N-limited ecosystems, additional nitrogen will act as a fertilizer and increase plant growth (McNulty and Aber, 1993). In contrast, in N-rich and saturating N conditions, the effect can be negative. Excess nitrate leaches from the soil into water courses, causing harm to aquatic organisms and reducing water quality for human consumption. At extreme levels of saturation there is increased N_2O and CH_4 production, leading to increased atmospheric concentrations of these greenhouse gases (Tietema et al., 1993; Aber, 1992a,b).

Despite the problems of trying to tease out the effects of single and mixed pollutants, it is fair to say that a number of environmental variables, either pollutants or natural edaphic factors (Conn and Dighton, 2000; Dighton et al., 2000), result in the alteration of ectomycorrhizal community structure on root systems. In their discussion of the effects of atmospheric pollutants on ectomycorrhizae, Dighton and Jansen (1991) suggested that two aspects were lacking from the studies at that time. One of those factors was a clear understanding of the changes in ectomycorrhizal community structure. This has

been addressed more recently by the combination of fruit body, mycorrhizal morphology, and molecular analyses of these communities (Kårén and Nylund, 1997; Jonsson, 1998; Jonsson et al., 1999a,b). The second area requiring further understanding was the function of the ectomycorrhizal community and the effect of this community function on the ecosystem as a whole; that is, what are the ecophysiological consequences of community change? There are many suggestions that all ectomycorrhizae do not function in the same manner or the same degree of efficiency in any one physiological process (Dighton, 1983; Abuzinadah and Read, 1986; 1989; Dighton et al., 1990). It is only recently that the debate on the role of species diversity per se or the composition of the species assemblage and function has received considerable investigation using controlled experimentation (Tilman et al., 1996). The diversity/function debate regarding mycorrhizal fungi is in its infancy. Van der Heijden et al. (1998) suggested that plant productivity is at its highest when arbuscular mycorrhizal diversity is highest. Using ectomycorrhizal diversity manipulation experiments in the laboratory, in which communities of one, two, or four species assemblages were constructed, Baxter and Dighton (2001) have shown that ectomycorrhizal diversity per se was a better determinant of improved birch seedling nutrient content than actual species composition or colonization rates. The effect of mycorrhizal diversity was for P than for N uptake into plant tissues. Much more work has yet to be done to fully explain the consequences of changes in both mycorrhizal and saprotrophic fungal community structure on ecosystem-level processes.

6.2.2 Effects of Acidifying Pollutants on Saprotrophic Fungal Activity

Part of the effect of sulfur-containing pollutants on fungi is the toxic solubility product sulfurous acid (H_2SO_3). At low soil pH (2 to 7), bisulfite (HSO_3^-) is the main toxic product, and in soils of pH 7 and higher, sulfite (SO_3^{2-}) predominates (Dursun et al., 1996a). Sulfur solubility products are used in the brewing and food industries for sterilization, so it is no surprise that they have a negative effect on fungi in natural ecosystems in the presence of atmospheric deposition of acidifying pollutants. Dursun et al. (1996a) and Boddy et al. (1996) showed that sulfite at the environmentally realistic levels of between 12.5 and 100 μM had negative effects on the growth of mycelia and germination of spores of *Mycena galopus*, *Phoma exigua*, *Cladosporium cladosporioides*, and *Aureobasidium pullulans*. The effects of sulfite were greatest on mycelia in terms of both growth and respiration, but spores were found to be more resistant to sulfites. The decomposition of Sitka spruce leaf litter in the presence of pure cultures of these fungi was also significantly reduced in the presence of sulfite. In a continuation of

this work on sulfur dioxide fumigation of leaf litters incubated with each fungal species, Dursun et al. (1996b) showed that 40 nl l^{-1} SO_2 had differential effects of the respiration of different fungal species and that this effect differed between leaf litter species. Although SO_2 reduced respiration of *Mycena galopus* on leaf litters, this reduction was only statistically significant for Sitka spruce (*Picea sitchensis*), and after 10 weeks for hazel (*Corylus avellana*). There was effectively little reduction in respiration on Scots pine (*Pinus sylvestris*) and beach (*Fraxinus excelsior*). The greatest effect of SO_2 was on Sitka spruce litter decomposition, in which respiration was reduced by over one-half. Respiration of the other fungal species (*Phoma exigua*, *Cladosporium cladosporioides*, and *Aureobasidium pullulans*) was unaffected by this concentration of SO_2 on any of the leaf litter species.

As a remediation treatment for acidifying pollutants, experimental, field-scale, liming experiments have been carried out. In one of these studies, Veerkamp et al. (1997) identified the community structure of lignicolous fungal fruit bodies in a Scots pine forest on acidic soils. They discovered that the effect of liming increased the number of fungal species but that the resultant community was more similar to those fungi found in deciduous woodlands than in coniferous woodlands. Species including *Amphinema byssoides*, *Hyphodontia breviseta*, *Hypochnicium geogenium*, and *Sitotrema octosporum* increased in abundance, and *Trechyspora farinacea* decreased in abundance. The rationale for the fungal community in limed sites to resemble that of deciduous woodland ecosystems was suggested to be due to the elevated pH of the soil increasing nitrogen availability and stimulating the decomposition of the high C:N ratio woody material. This would make the coniferous wood, which is of low resource quality, become more similar to the higher resource quality wood of angiosperms.

Previously, Newsham et al. (1992a,b) had investigated the effects of SO_2 fumigation at 10 to 30 nl l^{-1} SO_2 on the saprotrophic fungal community structure on ash (*Fraxinus excelsior*), birch (*Betula* spp.), hazel (*Corylus avellana*), oak (*Quercus robur* and *Q. petraea*), and sycamore (*Acer pseudoplatanus*) leaf litters. They showed that *Cladosporium* spp., *Epicoccum nigrum*, *Fusarium* spp., and *Phoma exigua* were less common in fumigated litters, whereas *Coniothyrium quercinum*, *Cylindrocarpon ortosporum*, and *Penicillium* spp. were more frequent on fumigated litter. They suggest, however, that there is no change in the leaf litter niches occupied by fungi. This is probably due to the fact that the resource utilization between these fungi is similar. The fact that reduction in litter decomposition had been shown to result from sulfur dioxide fumigation in other studies (Prescott and Parkinson, 1985; Wookey and Ineson, 1991a,b) suggests that the effects of fumigation may differ significantly among physiological groups of fungi. Similarly, evidence from the work of Wookey et al. (1991), and Newshman et al. (1992a,b) have shown that the community composition can be altered and decomposition potential of fungal communities in soil reduced in

the presence of sulfur dioxide and acid precipitation. In an experimental mesocosm study (an artificial representation of the "real world" constructed at a size that can represent complex interactions) (Odum, 1984) in which plants and leaf litter were exposed to an ozone and acid mist (2:1 mixture of H_2SO_4:HNO_3), Shaw (1996) showed that the amount of fluorescein diacetate-stained (i.e., metabolically active) fungal hyphae in two leaf litters was significantly greater in acid-misted than control systems. The stimulation in fungal activity of acid-misted leaf litter may have been attributable to the addition on nitrogen, which would help in the decomposition of high C:N litter resources (Garett, 1963; Killham et al., 1983; Shaw and Johnston, 1993). Given the varied response of different fungi to sulfur dioxide, the differential response of the same fungal species on different leaf litters, and the effects of combined pollutants, it is not easy to make a generalized statement of the negative impacts of acidifying pollutants on the rates of fungal decomposition of leaf litter and its impact on nutrient cycling within the ecosystem.

In aquatic ecosystems, the impact of acidifying pollutants appears to have little effect on aquatic fungal communities and their activity (Bärlocher, 1992a,b), probably because of the large dilution factor involved. Despite this, Bärlocher (1992a,b) states that a reduction in the pH of water from 6 to 4 decreases fungal growth on alder leaves.

6.2.3 Effects of Acidifying Pollutants on Fungal–Faunal Interactions

We have seen that acidifying pollutants alter the growth and probably the competitive abilities and physiology of fungi. It is therefore not surprising that changes in the fungal community structure or fungal biomass will influence the faunal communities that graze them. In a 2-year study of the effects of acid precipitation (pH 4.3 and 3.6 in throughfall) in pine forests in the southern United States, Esher et al. (1992) showed no effects of acidifying rain on saprotrophic microbial communities (using dilution plate counts), numbers of nematodes, or number of spores of arbuscular mycorrhizal fungi. They showed a significant reduction in the length and dry mass of fine roots and the number of short roots of both loblolly pine (*Pinus taeda*) and longleaf pine (*Pinus palustris*) that were ectomycorrhizal, however. They did not describe changes in the ectomycorrhizal species composition. Numbers of oribatid, prostigmatid, and astgmatid mites increased with increasing soil acidity, but the authors no speculation of the response of these populations with aspect to possible changes in fungal food resources. It is possible that the change in the balance between saprotrophic and ectomycorrhizal fungi in the fungal community alters the feeding preference of some of these faunal groups if the saprotrophic fungi are more palatable

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(Shaw, 1988; 1992), or provide a higher nutrient level than mycorrhizal fungi. Ruess et al. (1993) correlated the changes in nematode trophic groups (bacterial feeders and root and fungal feeders) to the changes in the bacteria:fungi ratio of forest soils subjected to experimental applications of sulfuric, nitric, and oxalic acids. Using the maturity index (Bongers, 1990), they showed a shift from bacterial feeders to fungal feeders with the addition of acidifying pollutants. This information suggests that bacteria are more sensitive to changes in soil pH and associated nutrient and toxic metal availability than fungi. The same general result was obtained from a 3-year acid precipitation experiment of the addition of equimolar sulfuric acid and ammonium nitrate on a Sitka spruce plantation forest in Scotland. Here, Ruess et al. (1996) showed that the soil acidity increased from pH 5.0 to 4.0 in the upper 2 cm of soil as a result of the acid rain treatment. This induced a significant increase in fungal biomass (measured by soil ergosterol content) and ectyomycorrhizal colonization of roots, which supported an elevated population of nematodes. As in her other study, there was a significant change in nematode trophic groups, where there was a reduction in omnivorous and predatory nematodes (*Filenchus* spp. and *Aporcelaimellus obtusicaudatus*) in the acidified soil and an increase in the fungal feeders (particularly *Aphelenchoides* spp.). The trophic interactions between forest floor fungi and fungiverous fauna require more research to understand the implication of changing fungal community under anthropogenic stress.

6.2.4 Effects of Acidifying Pollutants on Phylloplane Fungi

Live leaf surfaces are a resource available for fungal colonization. Many of these fungi are saprotrophs, deriving their nutrition from the wax cuticle and surface structure of the leaf, utilizing leaf exudates or the nutrients, water, and carbon arriving on the leaf surface as wet or dry deposition. In addition to the saprotrophs, endophytic fungi (pathogens and nonpathogens) may spend part of their existence on the leaf surface. As the leaf surface presents a large surface area to the environment, it not only intercepts nutrients and carbon-containing material from the atmosphere, it also captures atmospheric pollutants. Using the open-air fumigation system (McLeod et al., 1992; McLeod, 1995), Magan et al. (1995) investigated the effects of SO_2 and O_3 on the phylloplane fungal community of Scots pine, Sitka spruce, and Norway spruce trees over a 3-year period. Low levels of SO_2 markedly reduced the total phylloplane fungal population on Sitka spruce needles, but O_3 caused an increase in fungi on Scots pine. This increase in fungal biomass was recorded as increased fluorescein diacetate staining hyphae in the O_3 treatment only for Scots pine and Sitka spruce. It was hypothesized that both pollutants would increase fungal

TABLE 6.2 Trends of Fungal Species Occurrence on Needle Surfaces of Scots Pine, Sitka Spruce, and Norway Spruce in Relation to Pollutant and Isolation Method

Pollutant	Scots pine	Sitka spruce	Norway spruce
SO_2		Pink yeast $^{dil}\downarrow$	*Sclerophoma pythiohila* $^{dp}\uparrow$
O_3	*Epicoccum nigrum* $^{dil}\downarrow$	Sclerophoma pythiohila$^{dil}\uparrow$	*Aureobasidium pullulans* $^{dp}\uparrow$
	Cladosprium spp.$^{dil}\downarrow$	*Rhizosphaera kalkhoffii* $^{dp}\uparrow$	

Note: ^{dil} refers to dilution plating technique and ^{pd} refers to direct plating.
Source: Data from Magan et al. (1995).

colonization by causing damage to the leaf surface and allowing more resources to become available to the fungal community. Community changes as a result of pollutants were slight and differed among tree species, pollutants, and method (serial dilution and direct plating). A summary of the results is given in Table 6.2. Again, we can see that there is no consistent trend in fungal response to pollutants and that responses are dependent on other biological factors (host tree species) and the nature of the methodology used to measure the response. In cereal crops, however, Magan and McLeod (1991) demonstrated significant reduction in the number of pink and white yeasts on the flag leaves of barley in the presence of elevated SO_2, whereas *Cladosporium* spp., which are weakly parasitic, were found to increase. This suggests that in leaves with less surface waxes, the impact of SO_2 may increase susceptibility to the invasion of pathogenic fungi and weaken the plant.

6.2.5 Effects of Acidifying Pollutants on Lichens

Lichens have been known to be sensitive to pollutants and use has been made of them as indicators of industrial effluent. In a review of human impacts on lichens, Brown (1996) outlines the ways in which lichen communities have been reported to respond to a variety of pollutants. Lichen species can vary in their tolerance to pollutant loading (Richardson, 1988) (Table 6.3). Distribution maps in the United Kingdom of selected lichen species show apparent spatial relationships with areas of high industrialization and thus sulfur dioxide levels. There is evidence from experimental studies, however, that the response of lichens to SO_2 may be less than at first thought and that some distributions are related more to intensity of collection than pollutants. There are strong correlations, however, between the air pollutant loading and epiphytic lichen community classifications as shown by De Wit (1976). The degree of sensitivity of epiphytic lichens to acidifying

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TABLE 6.3 Variation in Lichen Tolerance of Atmospheric Sulfur Dioxide

Lichen species	Maximum SO_2 tolerance ($\mu g\, m^{-3}$)
Lecanora conizaeoides	150
Parmelia caperat	40
Usnea spp.	30
Ramalina fastigiata	10

Source: After Richardson (1988).

pollutants is modified by the substrate on which they are found. De Wit (1976) showed that *Evernia prunastri* and *Parmelia physoides* were less sensitive to pollutants on stems of oak than poplar or elm, whereas *Pyscia tenella* was least sensitive on elm. Especially sensitive to "acid rain" are cyanobacterial lichens (Gilbert, 1992). Such lichens are more tolerant than others to heavy metals, however, and can often be found as the sole inhabitants of abandoned heavy metal-contaminated mire sites.

Lichens have also been reported as good bioindicators of ozone pollution. Hur and Kim (2000), show a hierarchy of sensitivity of lichen species to ozone in the order of *Pharmotrema austrosinesnse* > *P. tinctorum* > *Certrekua braunsiana* > *Ramalina yasudae*.

Recently the recovery of lichen communities has been observed where industrializations in the greater London area has declined and pollution controls have been implemented (Bates et al., 2001). They have recorded revivial of communities of the macrolichen *Hypogymna physoides* and the crustose lichen *Lepraria incana* that is due to the reduction of SO_2 in a 70-km transect study from central London. The change in the range of distribution of the crustone lichen *Lecanora conizaeoides*, however, suggests that this species needs a low level of SO_2 in the environment and is now found in the only remaining sites that have above-ambient levels of pollution.

6.3 FUNGI AND HEAVY METALS

The central position of fungi in the control of pollutants in terrestrial ecosystems in shown in Fig. 6.6 (Wainwright and Gadd, 1997). Heavy metal pollutants can have negative effects on the survival, fitness, and physiology of fungi, such as hyphal growth and the ability to both produce extracellular enzymes and perform their function in the ecosystem. Where the metal concentration is sublethal, however, fungi are able to play a role in modifying the spatial and temporal availability of

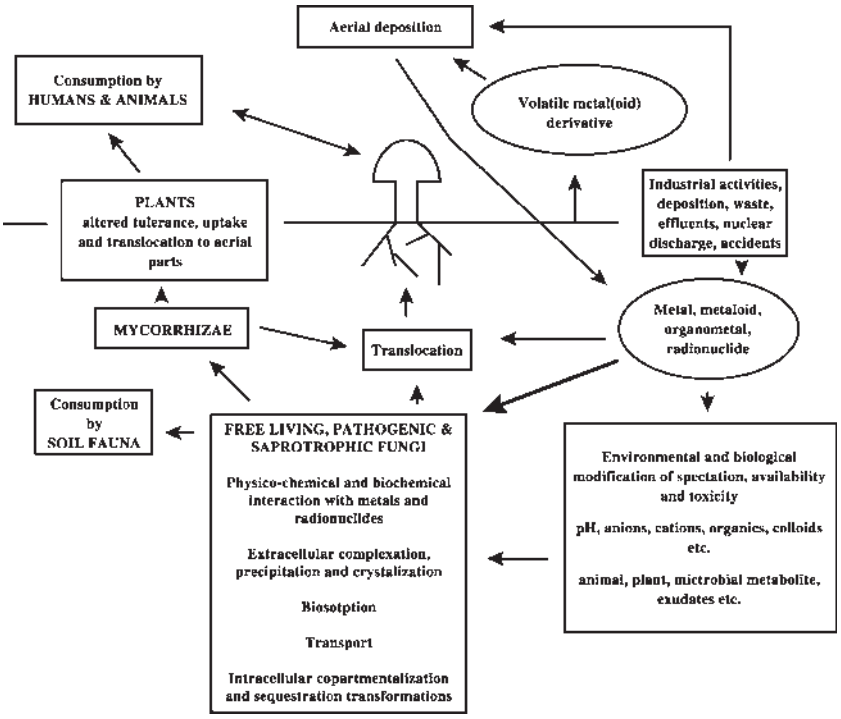

FIGURE 6.6 Diagrammatic representation of the interactions between pollutant metals and fungi in a terrestrial environment. Darkly shaded boxes represent the fungal components, and lighter shaded boxes the other biotic components. Open boxes represent the environmental factors that alter pollutant availability, whereas the ovals represent the pollutants and their chemical states. Thin arrows show the interactions of pollutant movement among components, but the thick arrow represents a direct effect of the pollutant on the fungi. *Source*: After Wainwright and Gadd (1997).

heavy metals to other components in the ecosystem. Fungi can exert a strong influence on the fate of heavy metals in the environment by virtue of the ability of fungi to immobilize heavy metals within their biomass, translocate those metals to other parts of the ecosystem, and then release heavy metals at other locations. Additionally, during these processes fungi may change the chemical state of pollutant. The activities of saprotrophic fungal species can be reduced by a pollutant chemical that suppresses the expression of enzymes or chemically interferes with the activity of an enzyme, but the tolerance of a specific fungal species to a pollutant chemical can be manifested in its survival or its rate of growth.

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Within the mycorrhizal symbiosis, the fungus may either alter the rate at which the pollutant enters the host plant or reduce the degree to which mycorrhizal fungi can colonization roots. In pathogenic fungi, the effect of the pollutant can increase host susceptibility to the fungus or alter the competitive ability of the fungal pathogen within the mixture of fungal pathogens that could infect the host. The presence of a pollutant chemical within the mycelium of the fungus can lead to changes in the chemical and physical state of the pollutant, making it more or less toxic to fungal consumers. The pollutant can be transferred up the food web by grazing of the mycelium or fruiting structure, or the pollutant may be released through death or leakiness of the fungal mycelium.

The fact that fungi are able to accumulate heavy metals into their biomass provides them with a potential role in biodegradation. All the factors outlined above regarding the impact of heavy metals on fungi and fungi on heavy metals to be taken into account when considering the potential role of fungi in the bioremediation of contaminated soil (Skladany and Metting, 1992). In the relative confines of industrial processes, however, the biosorptive properties of both live and dead fungal mycelium can be put into effect in the same way that ion exchange resins can be used for the cleanup of effluent solutions (Tobin et al., 1984; Singleton and Tobin, 1996). Biosorption of metals by fungi relies on the ion exchange between the metal and reactive groups of the cell wall. Some examples of the degree of metal binding by a range of microfungi and yeasts suitable for industrial metal retrieval from effluent are given in Table 6.4. The interaction between live fungal biomass and the relative availability of carbon, nitrogen, and phosphorus, however, may be of importance in influencing the solubility of heavy metals in the environment (Dixon-Hardy et al., 1998), showing that the role of fungi in metal binding is greatly influenced by environmental conditions.

TABLE 6.4 Ranges of Metal Uptake Capacities of a Variety of Microfungal Mycelial and Yeast Species that Could be Used in Industrial Processes

Metal	Uptake capacity (mmol metal g^{-1} biomass)
Copper	0.25 to 1.9
Silver	0.004 to 0.46
Zinc	0.12 to 15.3
Uranium	0.12 to 1.3
Cobalt	0.15 to 0.52
Thorium	0.27 to 0.84

Source: Data adapted from Singleton and Tobin (1996).

6.3.1 Influences of Heavy Metals on Saprotrophy in Terrestrial Ecosystems

If heavy metals reduce the efficacy of fungal hyphal activity, it is reasonable to assume that the ecosystem-level functions carried out by fungi will be impacted. In terms of the role of fungi in decomposition and nutrient mineralization, Bardgett et al. (1994) investigated the effects of chromium, copper, and arsenic wood preservatives on soil microbial and nematode communities. They found that increasing levels of each preservative had little effect on the biomass of the prokaryotic microbial community but a significant negative effect on the eukaryotic (presumed fungal) biomass as measured by substrate-induced respiration. This suggests that fungi are more sensitive to heavy metals than bacteria. Indeed, although Jordan and Lechevalier (1975), and Nordgren et al. (1986) found the reverse to be true, they showed that the decomposition of cotton strips (cellulose) was significantly reduced at higher heavy metal concentrations. As cellulose decomposition in soil is mainly effected by fungi, it is probable that heavy metals had an effect on fungal metabolism, if not on biomass. Kuperman and Carreiro (1997), however, showed that total and fluorescein diacetate active (FDA) fungal biomass and enzyme activity was reduced in heavy metal-contaminated (As, Cd, Cr, Cu, Ni, Pb, and Zn) soils of the Aberdeen Proving Grounds in Maryland. The presence of heavy metals reduced the activity of the enzymes N-acetylglucosaminease, β-glucosaminease, endocellulase, and acid and alkaline phosphatase by ten- to 50-fold. Nitrogen mineralization by both fungi and bacteria has been shown to be reduced by the presence of heavy metals in forests soils (Necker and Kunze, 1986) because of the maintenance of high levels of soluble Zn, Cd, and Ni in acidic soils. Lead, on the other hand, was the only metal to be less available under these soil-acidifying conditions, because of its being complexed onto humic materials in soil and thus becoming less available to other organisms.

Byrne et al. (1979) listed values of accumulation of nine metal elements in fruit bodies of 32 basidiomycete fungal species. Accumulations of silver, cadmium, copper, and zinc in basidiocarps of *Agaricus* species are given in Fig. 6.7. It can be seen from these figures that the accumulation of each element is not the same in each species and that the pattern of accumulation in the same species may differ markedly between individual basidiocarps. It is therefore difficult to make generalizations about fungi as a whole in their ability to concentrate metal ions.

Rizzo et al. (1992) showed that despite the fact that rhizomorphs of *Armillaria* spp. have a melanized outer cortex, they are able to take up heavy metals from the environment. Some elements were 50 to 100 times more concentrated in fungus than in surrounding soil. For example, concentrations of Al, Zn, Fe, Cu, and Pb in rhizomorphs reached up to 3440, 1930, 1890, 15, and

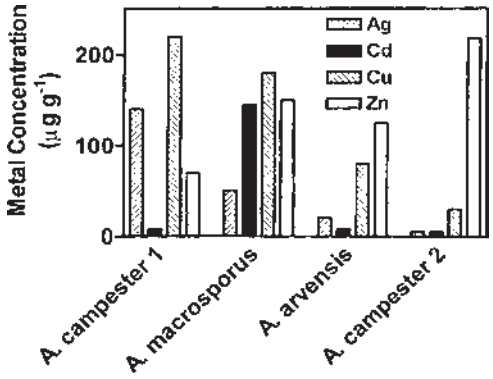

FIGURE 6.7 Concentrations of heavy metals accumulated in the fruit bodies of a variety of *Agaricus* species. *Source*: Data from Byrne et al. (1979).

680 $\mu g\, g^{-1}$, respectively. X-ray dispersal electron microscopy (EDAX) showed that the ions were accumulated in the outer portion of the rhizomorph and not concentrated in the interior. It was also suggested that a coating of metal ions in the outer layers of the rhizomorphs may play a key role in the longevity and survival of rhizomorphs in soil, where the heavy metals act as antagonists for other micro-organisms or grazing fauna.

Byrne et al. (1997) reviewed earlier work on heavy metal accumulation in fungi that had shown that numerous basidiomycete fungi accumulated arsenic in their fruit bodies (Byrne et al., 1979; Byrne and Tusek-Znidaric, 1983). Their discovery of dimethylarsenic acid (DMA) in the ectomycorrhizal basidiomycete *Laccaria amethystine*, however, led them to investigate other forms of arsenic in fungal fruit bodies and to determine the chemical transformations, including methylation, that could take place in fungal tissues. They discovered methylarsonic acid (MA) in *Sarcosphaera coronaria*, inorganic arsenic in *Entoloma lividum*, and a mixture of inorganic arsenic, MA, DMA, and arsenobetaine (AB) in *Sarcodon imbricatus*, *Agaricus placomyces*, and *A. haemorrhoides* (Byrne et al., 1995). By laboratory experimentation, they demonstrated that *Agaricus placomyces* effected methylation of arsenic when grown on malt extract agar in the presence of DMA and that arsenochlorine was accumulated by some species, such as *Sparassis crispa* (Slejkovec et al., 1997). Other metal transformation mechanisms have been identified in fungi (Morley et al., 1996), including the reduction of Ag and Co using NADPH and NADH as electron donors as well as methylation and dealkylation of organometallic compounds by enzymes or facilitating abiotic degradation. Fischer et al. (1995) showed that the amount of methyl mercury in a fungal fruit bodies ranged from 0.2 to 8 $\mu g\, Hg\, g^{-1}$ dry weight, depending on the fungal species.

As demonstration of the importance of mercury transformation in fungi, it was shown that in comparison with the levels in soil, bioaccumulation factors for methyl mercury were on the order of between 3 and 199, whereas those for total mercury were usually below 1 (Table 6.5). The process of methylation thus increases the concentration factor in the fungal tissue. Changes in the chemical states of heavy metals can significantly affect the toxicity of the metal to other organisms in the ecosystem. The presence of a methylation process in fungi in nature could have important implications in the movement and toxicity of arsenic and mercury in the environment and its transfer within food chains.

Heavy metals have been shown to be absorbed onto microbial tissue. Tobin et al. (1984) demonstrated that dead mycelium of *Rhizopus arrhizys* was efficient at adsorbing a range of metal ions, but not alkali metals (Table 6.6). Uptake and accumulation of metals by living fungi, however, is proving to be of considerable importance. In living tissue, however, metal ion accumulation results from both metabolic uptake and cation exchange on appropriate binding sites. McKnight et al. (1990) showed that the concentration of Mg, in particular, was positively related to the cation-exchange capacity of stipe tissue of 18 basidiomycete fungal species. Starling and Ross (1991) discussed the uptake of zinc fungus *Penicillum notatum*, showing that it was an essential element with different uptake kinetics at low- and high-solution concentrations. Zinc uptake is competitively inhibited by Cd and noncompetitively by Cu, indicating different interactions between metals and the fungal physiology. The wood-decaying fungus *Phanerochaete chrysosporium* has shown the ability in field trials to degrade toxic organic compounds by converting chlorine bound in an organic form to harmless inorganic forms and to degrade aromatic hydrocarbons to CO_2 and water (Coghlan, 1994). From both the aspects of metal ion accumulation and enzymatic competence of fungi, it is likely that fungi could be used to detoxify contaminated land.

6.3.2 Influences of Heavy Metals on Mycorrhizae and Primary Productivity in Terrestrial Ecosystems

The effects of heavy metals in the reduction of physiological activity of saprotrophs and the accumulation characteristics in their fruit bodies is of interest in terms of the movement and immobilization of heavy metals in the environment. Interest in the effects of heavy metals on mycorrhizae, however, and more particularly, the role of mycorrhizae in heavy metal resistance, has attracted interest because of its potential application for contaminated site restoration. Research has thus been directed to understanding the interrelationships among metal availability, mycorrhizal infection, mycorrhizal function, and plant performance.

TABLE 6.5 Relative Accumulation of Mercury in Fungal Fruit Bodies in Relation to Soil Humus Concentrations

	MeHg in fungus ($\mu g\,Hg\,g^{-1}$ dry wt)	MeHg in humus ($\mu g\,Hg\,g^{-1}$ dry wt)	Concentration factor MeHg	Total Hg in fungus ($\mu g\,Hg\,g^{-1}$ dry wt)	Total Hg in humus ($\mu g\,Hg\,g^{-1}$ dry wt)	Concentration factor total Hg
Xercomus badius	0.16	0.01	12.3	14.7	64.4	0.23
Xercomus badius	0.19	0.02	10.0	27.0	15.8	1.70
Xercomus badius	0.24	0.03	9.6	35.0	80.5	0.40
Leccinum scabrum	0.08	0.01	10.0	6.2	35.5	0.17
Amanita muscaria	0.55	0.05	10.4	67.5	140.2	0.48
Amanita musacria	0.71			82.0		
Amanita musacria	0.27	0.09	3.0	64.0	61.9	1.03
Hygrophoropsis aurantica	0.41	0.02	19.5	11.2	29.0	0.39
Vascellum pratense	1.56	0.04	38.0	8.2		
Coprinus comatus	7.94	0.04	198.5	144	82.7	1.70

Source: After Fischer et al. (1995).

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TABLE 6.6 Adsorption of Metal Ions onto Dried Mycelium of *Rhizopus arrhizus*

Metal ion	Uptake ($\mu M\, g^{-1}$)
Cr^{3+}	590
La^{3+}	350
Mn^{2+}	220
Cu^{2+}	250
Zn^{2+}	300
Cd^{2+}	270
Ba^{2+}	410
Hg^{2+}	290
Pb^{2+}	500
UO_2^{2+}	820
Na^{+}	0
K^{+}	0
Rb^{+}	0
Ag^{+}	500
Cs^{+}	0

Source: Data from Tobin et al. (1984).

The ability of ectomycorrhizal fungal species to tolerate high levels of heavy metals in the environment was shown in a survey of mushrooms along a pollution transect in Sweden by Rühling and Söderström (1990) in which the dominant contaminants in the humic soil horizon were As, Cu, Cd, Pb, and Zn. They showed that the abundance and diversity of fungi decreased with increasing pollutant loading, but that the ectomycorrhizal species were more tolerant of high metal concentrations than saprotrophs. Indeed, Rühling et al. (1984) showed that the ectomycorrhizal fungus *Laccaria laccata* was the most tolerant fungus to heavy metal pollutants, but that the number of microfungi isolated onto agar from soil did not decrease with increasing metal loading. Common species, such as *Penicillium* and *Oidiodendron*, did decrease, but some species, such as *Paecilomyces* and several sterile mycelial forms, were only found in the most polluted sites.

It is not the tolerance of heavy metals that is of the greatest interest, however; rather, it is the ability of ectomycorrhizae to continue to function in their presence. Many of the initial findings suggesting the importance of ectomycorrhizae in protecting host plants from heavy metal loadings come from the studies of Marx (1975; 1980). His observations of the survival of pine trees in mine spoil soils showed that inoculating tree seedlings with

ectomycorrhizal fungi improved both tree survival and growth. Of particular interest was the fungal species *Pisolithus tinctorius*, which appeared to be more frequent in these polluted sites than in other habitats. The effect of inoculation with *P. tinctorius* resulted in tree volumes 250% greater than those trees assuming natural inoculum from the site or inoculation with *Thelephora terrestris* (Table 6.7). These trees also had higher foliar phosphate levels, but reduced levels of Ca, S, Fe, Mn, Zn, Cu, and Al, suggesting that the effect of this mycorrhizal fungus may reduce the uptake of heavy metals into the host tree. The prevention of heavy metal toxicity to host plants afforded by mycorrhization of the roots is not limited to ectomycorrhizae. Indeed, Bradley et al. (1982) showed that ericaceous plants of the genera *Calluna*, *Vaccinium*, and *Rhododendron* showed evidence of growth in the presence of copper and zinc at concentrations of between 0 and 150 $\mathrm{mg\,l^{-1}}$ in sand culture only if their roots were colonized by ericoid mycorrhizae. Indeed, the production of enzymes, such as polygalacturonase, which degrades pectin, has been shown to increase in the ericoid mycorrhiza *Oidiodendron maius* in the presence of increasing concentrations of Zn and Cd (Martino et al., 2000a), which coincides with their greater growth rate at higher levels of heavy metal (Martino et al., 2000b). The effect of heavy metal availability in soil not only affects the growth of trees, however, it also affects the growth, colonizing ability, and physiology of the fungal associate within this symbiosis. Endophytic (mycorrhizal) fungi isolated from these ericoid plant roots showed significantly reduced growth at 100 $\mathrm{mg\,l^{-1}}$ Cu and 500 $\mathrm{mg\,l^{-1}}$ zinc, indicating that although the mycorrhizal fungi appeared to be exerting a positive effect on plant growth in the presence of heavy metals, the fungi to were being inhibited. In similar studies, with manganese as the heavy metal, Hashem (1995) showed that mycorrhizal cranberry (*Vaccinium macrocarpon*) produced significantly larger plants than nonmycorrhizal plants in the presence of Mn at concentrations ranging from 0 to 1000 $\mu\mathrm{g\,ml^{-1}}$.

TABLE 6.7 Mean Survival and Growth of Transplants of Loblolly and Pitch Pine and Their Hybrids When Inoculated with the Ectomycorrhizal Fungus *Pisolithus tinctorius* (*Pt*) After Two Growing Seasons Growth in Tennessee and Alabama Mine Spoil Soils

	Mycorrhizae at planting	Survival (%)	Height (cm)	Stem diameter (cm)	PVI ($\times 10^2$)
Tennessee	*Pt*	85	79	30	133
(overall mean)	Natural	81	53	2.0	43
Alabama	*Pt*	66	67	3.0	96
(overall mean)	Natural	56	43	1.6	20

Source: Data from Marx (1975).

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The mechanism of plant protection in the ectomycorrhizal system was elucidated by Denny and Wilkins (1987a,b). Using electron microscopy coupled with X-ray diffraction (EDAX), they identified adsorption of heavy metals onto fungal hyphae in the extraradical hyphal network, fungal sheath, and Hartig net, preventing translocation of the metal into the host cortex, and particularly preventing movement into the vascular tissue. More recently, Denny and Ridge (1995) have identified high zinc binding capacity of extracellular slime formed by the hyphae of the ectomycorrhizal fungus *Pisolithus tinctorius*. Using energy-dispersive X-ray spectroscopy, a variety of heavy metal binding sites have been reported in ectomycorrhizal fungal mycelia (Tam, 1995) (Table 6.8). Mycelia of the fungi *Hymenogaster* sp., *Scleroderma* sp., and *Pisolithus tinctorius* were tolerant of high concentrations of Al, Fe, Cu, and Zn (Table 6.9). It was observed that both Cu and Zn were linked to polyphosphate granules, and hence were metabolically inactive within the fungal hyphae. Indeed, Kottke et al. (1998) showed that in Norway spruce from contaminated sites in Germany, concentrations of phosphate-bound Zn were consistently higher in the fungal sheath ectomycorrhizae formed by the fungus *Xercomus badius* than other fungal species. This fungal species was found to contain higher concentrations of a range of elements, including nitrogen, phosphorus, potassium, magnesium, and iron. Leyval et al. (1997), however, suggest that this observation could be an artifact of sample preparation. Nevertheless, there is good evidence to suggest that phosphates play a role in the complexing of heavy metals in the vacuoles of ectomycorrhizal fungal hyphae (Turneau et al., 1993) and that metal become complexed to polysaccharides and cyctine-rich proteins in the outer pigmented layer of the cell wall of *Pisolithus tinctorius* (Turneau et al., 1994). Cadmium was also seen in abundance in the vacuoles of fungal hyphae, suggesting to Turneau et al. (1993) that the fungus was actively involved in the detoxification of heavy metals for the host plant.

TABLE 6.8 Protective Effect of *Paxillus involutus* Mycorrhizae on Birch Grown in 23 mM Zn as Expressed by Concentration (μmol g^{-1} Fresh Weight) of Zn in Various Root/Mycorrhizal Components

Region	− Mycorrhizae	+ Mycorrhizae
Stele	26	15
Cortex	50	20
Mantle	—	24
Extraradical hyphae	—	192

Source: Data from Denny and Wilkins (1987); Wilkins (1991).

TABLE 6.9 The 50% Inhibition Concentration (mg l^{-1}) of a Variety of Heavy Metals Exhibited by Five Ectomycorrhizal Fungal Species Grown in Mycelial Culture

	Ectomycorrhizal fungal species				
Metal	*Pisolithus tinctorius*	*Thelephora terrestris*	*Cencoccum geophilum*	*Hymeogaster* sp.	*Scleroderma* sp.
Al	200	10	10	200	200
Fe	400	100	200	200	100
Cu	200	10	10	10	100
Zn	200	10	10	100	100
Ni	10	1	1	1	10
Cd	10	1	1	0.1	10
Cr	10	10	10	10	10
Pb	200	200	200	200	200
Hg	1	1	1	1	1

Source: Data from Tam (1995).

The effects of heavy metals on mycorrhizae and their physiology have recently been reviewed by Leyval et al. (1997). Metals may be present in soils as free metal ions, complexed onto organic matter, or chemically precipitated into insoluble compounds, such as oxalates, carbonates, or hydroxides. The degree of toxicity of the metal to organisms depends upon its relative availability (solubility) within the soil solution. This availability is dependent upon a number of edaphic factors, such as soil pH, Eh, organic matter, and clay content, as well as biological factors, including solubilization, biosorption, and bioaccumulation (Berthelin et al., 1995). Leyval et al. (1997) suggest that there are two possible evolutionary routes that mycorrhizal fungi have taken to cope with heavy metals. One mechanism operates at low metal concentrations and is relatively metal-specific, whereby siderophores such as ferricrocin or fusigen are produced. The second method operates at higher external concentrations of heavy metals and is not metal species-specific. Siderophore production is suppressed, but the host plant is still protected against the heavy metal. Wilkins (1991) reports the findings of Jones and Hutchinson (1986), and Jones et al. (1988), who suggest that the protective effect of root colonization by the ectomycorrhizal fungus *Scleroderma flavidum* was provided by the exclusion of Ni by a nonmetabolic process. In nonmycorrhizal roots, and probably in *Laccaria laccata*, *Lactarius rufus*, and *Lactarius hibbardiae* mycorrhizas, metabolic uptake of the heavy metal occurred in the roots and protection was lost.

Heavy metals can have a direct and negative effect on the development and competitive abilities of ectomycorrhizal fungi, as has been seen by the effects of acidifying pollutants on the increased availability of Al in soil. Ectomycorrhizal

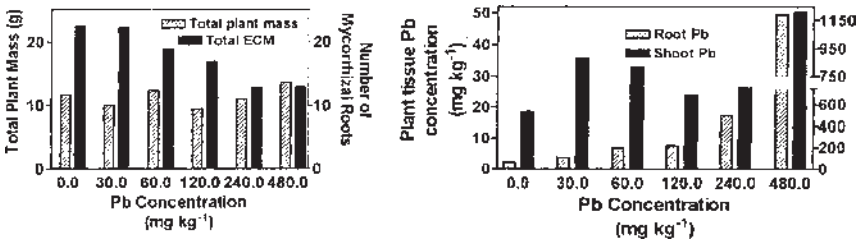

FIGURE 6.8 Loblolly pine biomass (hatched bars) and ectomycorrhizal colonization (solid bars); left graph and right graph: plant tissue concentration of lead in mycorrhizal plants at varying external concentrations of lead. *Source*: After Chappelka et al. (1991).

colonization (total number of mycorrhizal root tips) of Loblolly pine is reduced by increasing concentrations of Pb in soil (Chappelka et al., 1991), but total plant biomass was unaffected (Fig. 6.8). Different mycorrhizal types respond differently to the heavy metal (0 to 480 mg kg^{-1} soil), with some species being unaffected while others decline in abundance. Hartley et al. (1999b) showed that Cd was the most toxic of five metals (Cd, Pb, Zn, Sb, Cu) to ectomycorrhizal Scots pine tree seedlings. When metals were combined, the toxicity of heavy metal interactions on plant growth and ectomycorrhizal colonization could not be predicted from the results of single metal applications. The authors suggest that there are unknown complex interactions among the metals, which may reduce the overall effect of multiple metal contamination of soil. The heavy metals also have an effect on both the performance of pine seedlings and the ability of ectomycorrhizal fungi to colonize from one plant to another, previously uncolonized seedling (Hartley et al., 1999a). A general decrease in ectomycorrhizal colonization of previously uncolonized roots of Scots pine was also found in Cd- and Zn-contaminated soils (Hartley-Whitaker et al., 2000a). This did not affect the growth rate of tree seedlings, however, which were similar in metal-contaminated or uncontaminated soils. A significant change in the ectomycorrhizal community structure of trees between contaminated and control soils could have ecophysiological consequences that were not apparent in the short-term experiments. From an ecosystem restoration perspective, these studies suggest that the effect of heavy metals within soil will reduce the effectiveness of ectomycorrhizal inoculation to form associations with tree seedlings and reduce the degree of cross-plant colonization. Effective concentrations reducing root colonization by 50% were recorded for cadmium as 3.7 $\mu g\, g^{-1}$ for *Paxillus involutus* and 2.3 $\mu g\, g^{-1}$ for *Suillus variegates* (Hartley-Whitaker et al., 2000b), thus to be effective, all planted trees should be previously inoculated rather than allowing a few inoculated trees to act as a mycorrhizal source for others in the community. Colonization by mycorrhizal

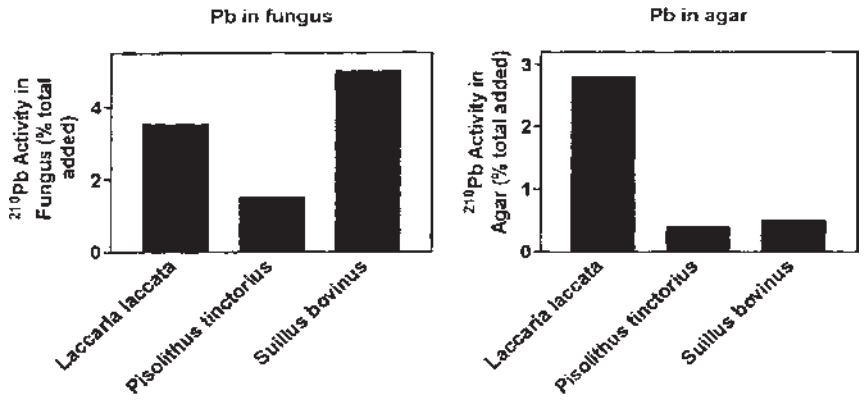

FIGURE 6.9 Lead accumulation in mycelial cultures of three ectomycorrhizal fungi (left) and the proportion of lead translocated to agar, distant from the site of lead addition, through the fungal mycelium. *Source*: Data from Vodnik et al. (1998).

fungi, however, reduced the toxicity of heavy metals by preventing translocation of plant toxic levels into the host plant tissue (Hartley-Whitaker et al., 2000b).

In an experimental system, Vodnik et al. (1998) investigated the movement of lead through the mycelia of four ectomycorrhizal fungi, each having a different tolerance to lead as a pollutant. They showed that lead uptake by *Pisolithus tinctorius* (1.1% of the total lead added to the experimental system) was much less than uptake by *Laccaria laccata* and *Suillus bovinus* (6.2% and 5.4%, respectively). Internal translocation of lead and its release into the environment at a distance from the site of uptake was also different between species. Some 45% of the lead taken up by *Laccaria laccata* was released in a different part of the mycelium, whereas only 10% was released by *Suillius bovines*, showing a greater

TABLE 6.10 EC_{50} Levels of Heavy Metals Cd^{2+}, Pb^{2+}, Zn^{2+}, and Sb^{2+} to Five Ectomycorrhizal Fungal Species

	EC_{50} (mmol m^{-3})			
	Cd	Pb	Zn	Sb
Lactarius deliciosus	0.79	45	100	0.66
Paxillus involutus	2.3	25	188	50
Suillus variegatus	0.008	25	343	50
Suillus granulatus	12.6	2.5	336	5.0
Suillus luteus	0.42	25	284	50

Source: Data from Hartley et al. (1997a).

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binding of Pb in the mycelium of *S. bovinus*. Although the amount of lead moved in the mycelium was low (10–45% of the applied Pb after 30 days of incubation), the experiment showed that there could be considerable temporal and spatial redistribution of heavy metals within the fungus and redistribution of the metal in the environment by release from fungal tissue (Fig. 6.9). If fungi are to be of importance in remediation, a greater knowledge of the physiology of the movement of heavy metals and radio–nuclides in relation to source–sink gradients and source–release gradients needs to be generated to adequately model the degree, duration, and strength of the retention of pollutants in the fungal thallus.

Blaudez et al. (2000) looked at the variability in responses of ectomycorrhizal fungal mycelia to heavy metals. Using petri dish studies, they measured the mycelial growth of each of 39 fungal isolates, representing five fungal species, in the absence or presence of cadmium, copper, nickel, and zinc at three concentrations. They demonstrated that *Pisolithus tinctorius*, *Suillus luteus*, and *Suillus variegatus* were more tolerant of the heavy metals Cu, Cd, and Zn than *Paxillus involutus*. *Paxillus* was more resistant to Ni, however. There were significant differences in growth between levels of each metal and between the presence and absence of metal in the medium within each isolate. The authors show that there are differences in the degree of variation between isolates of the same species at each level of heavy metal. The authors could not detect significant correlations between the resistance to heavy metals in culture and the level of pollutant in soil at the site of origin of the isolate, probably due to a small sample size. Similarly, Hartley et al. (1997a) published effective concentraions of heavy metals that caused 50% inhibition of growth (EC_{50}) of ectomycorrhizal isolates in pure culture. Again, they showed that there was significant variation among species for tolerance of different heavy metals and among metals within the same species (Table 6.10). In addition, they showed that there were significant interactions between metals on the growth of fungi in that in metal combination, one heavy metal may ameliorate the negative influence of another. Examples of this are that both Pb and Sb ameliorate the toxicity of Cd to *Suillis granualtus* and the combination of Cd + Pb + Zn was less toxic to *Lactarius deliciosus* than the individual or paired metals. Hartley et al. (1997a) suggest two mechanisms that might cause this interaction. First, two elements with the same valency or size may compete between each other for ion transporters across the plasma membrane and second, there could be an induced physiological response to the presence of Zn that decreases sensitivity to both Zn and Cd. In their review paper, Hartley et al. (1997b) suggest that there could be some evolution of resistance to heavy metal toxicity based on prior exposure. Some suggestions for this come from the survey of aluminum tolerance of *Pisolithus tinctorius* isolated from contaminated sites (Egerton-Warburton and Griffin, 1995). No relationship was found, however, between metal resistance and prior exposure

to fungi by Denny and Wilkins (1987a,b) or Colpaert and Van Assche (1992, 1993). They suggest, however, that in environments in which heavy metals are common, such as in acidic, peaty soils, the plant species may have coevolved with their mycorrhizal fungal endophyte to develop resistance. To substantiate this claim, they cite the ericoid mycorrhizal association of heathland species (*Calluna* and *Vaccinium*), which have been shown to have considerable tolerance to heavy metals (Bradley et al., 1981; 1982; Marrs and Bannister, 1978).

Leyval et al. (1997) cite examples in which the arbuscular mycorrhizal colonization of plant roots is high in heavily polluted spoil soils (863 mg kg^{-1} zinc, 456 mg kg^{-1} lead). They point out, however, that most of the studies did not relate the level of mycorrhizal colonization with measures of extractable (available) heavy metal in the soil. When such measures were made, there was no correlation between the degree of mycorrhizal colonization of roots or heavy metal content of maize plants and that available in soil solution (Weissenhorn et al., 1995a,b). As arbuscular mycorrhizal fungi are not easily grown in pure culture, there is relatively little information on the effects of heavy metals, or pollutants of any form, on the growth and physiology of the fungal mycelium. Using a compartmentalized soil system, however, Joner and Leyval (1997) were able to determine the relative contribution of clover roots and their associated arbuscular mycorrhizae in the uptake of cadmium. They concluded that the presence of arbuscular mycorrhizae enhanced Cd uptake into the plant through the fungal hyphae, but also that transfer from the fungus to the plant is reduced, retaining Cd in the fungal component of the root, thus detoxifying the system. Similar findings have been made by Tonín et al. (2001) for Cd and Zn in mycorrhizal clover. Heavy metals (Zn, Cu, Cd, Ni) from a contaminated soil delay the invasion of arbuscular mycorrhizal fungi into clover roots (Koomen and McGrath, 1990), although Joner and Leyval (1997) found no reduction of arbuscular mycorrhizal hyphal extension into soil with up to 20 mg extractable Cd kg^{-1} soil. Not withstanding the susceptibility of arbuscular mycorrhizal functioning in the presence of heavy metals, Call and Davies (1988) showed that the inoculation of three grass species by arbuscular mycorrhizae significantly increased grass survival, growth, and nutrient content in their attempts to restore the overburden of a surface lignite mine (Table 6.11).

Senior et al. (1993), and Donnelley and Fletcher (1994) reviewed the potential role of mycorrhizal fungi in restoration and reclamation. The ability of the mycorrhizal fungal partner to protect its host plant from toxic levels of heavy metal is one of the advantages of this symbiotic association. It is also possible that the host plant may confer some enhanced survival traits for the fungus, fitting it to survive better in a metal-contaminated environment. The ability of many ectomycorrhizal fungi to produce enzymes that degrade aromatic compounds may be advantageous in a restoration scenario. For example, both ericoid and ectomycorrhizal fungi produce enzymes allowing them to decompose lignin

TABLE 6.11 Survival and Growth of Three Grass Species Planted in a Restoration Project on Lignite Overburden as Influenced by the Presence of Inoculum with the Arbuscular Mycorrhizal Fungi *Glomus fasciculatum* (G. f) and *Gigaspora marginata* (G. m) or uninoculated (NM) After 3 Years of Plant Establishment

Grass species	Inoculum	Survival (%)	Biomass (g plant $^{-1}$)	N content (%)	P content (%)
Sideoats grama	G. f	97	25	0.82	0.14
	G. m	94	21	0.80	0.10
	NM	86	15	0.72	0.07
Indian grass	G. f	92	36	1.12	0.12
	G. m	81	30	1.09	0.10
	NM	72	21	0.90	0.07
Klein grass	G. f	61	19	0.75	0.14
	G. m	67	17	0.74	0.13
	NM	47	10	0.65	0.08

Source: Data from Call and Davies (1988).

(a polymer of phenolic compounds). As some fungi, such as the mat-forming *Hysterangium setchellii*, may account for up to 45–55% of the total soil organic biomass (Cromack et al., 1979; Fogel and Hunt, 1983), they have potential to exert a major influence on pollutant hydrocarbons in the environment. For example, 2,4-D and atrazine can be incorporated into the biomass of the ectomycorrhizal fungus *Rhizopogon vinicolor* and the ericoid mycorrhiza *Hymenoscyphus ericae.* Donnelley and Fletcher (1994) screened 21 mycorrhizal fungi for PCB decomposition and demonstrated that 14 species could metabolize some of the PCBs by at least 20%. The ectomycorrhizal fungi *Radiigera atrogleba* and *Hysterangium gardneri* were able to degrade 80% of 2,2′-dichlorobiphenyl, and two ericoid mycorrhizae, *Hymenoscyphus ericae* and *Oidiodendron griseum*, were less effective than the ectomycorrhizal species. In landfill restoration, Senior et al. (1993), and Tosh et al. (1993) showed that the survival of the ectomycorrhizal fungi was dependent on their abilities to survive reduced oxygen tension. They showed that both *Laccaria proxima* and *Hebeloma crustuliniforme* were able to survive the low redox potentials, but *Paxillus involutus* could not survive. A balance must be achieved in restoration projects between the applications of fertilizer to potentially promote plant growth and the beneficial effects of mycorrhizal fungi in detoxifying the soil N.C. Johnson (1998) cautioned against high applications of inorganic fertilizers in taconite mine tailing restoration with *Salsola kali* and *Panicum virgatum*. She demonstrated that the addition of arbuscular mycorrhizal inoculum and organic soil amendment (papermill sludge) was more beneficial in the survival and growth of the late successional plant species (*Panicum virgatum*), and may be more cost-effective.

We have seen that fungi are important contributors to the movement, immobilization, and chemical transformations of pollutant metals in the environment. In these examples of the effects of pollutant metals on mycorrhizae, we have been able to see that the function of the mycorrhizal unit (root plus fungus) has been altered. The extraradical hyphae see the heavy metal first, however. They are thus of prime importance in effecting initial adsorption, complexation, and translocation of the heavy metals in the fungal–plant association. Our knowledge of the growth, behavior, and physiology of the extraradical hyphae needs to be enhanced in order for us to understand the complex interactions that occur distal to the plant root surface and where there may be maximal interaction between the mycorrhizal component and other soil organisms. For example, without the work of Byrne et al. (1997), it was commonly regarded that methylation of mercury occurred in anaerobic conditions under the control of bacteria. What are the interactions owing mycorrhizal extraradical hyphae, rhizospheric bacterial communities, the distribution of anaerobic pockets in soil, and the mercury methylation process? It appears also that mycorrhizae may also alter partitioning of nutrients and heavy metals within the host plant outside the direct fungal component. More research is needed to fully understand the changes in the host plant biochemistry, signaling systems between the fungus and host plant, and within the host plant itself, that dictate such internal reallocation of elements.

6.3.3 Impact of Heavy Metals in Aquatic Ecosystems

Maltby and Booth (1991) state that there is little information about the influence of pollutants on the functioning of aquatic fungi. Their study assessed the impact of coal mine effluent on the communities of fungi effecting leaf litter breakdown in stream systems. By comparing up- and downstream locations from an inflow drainage stream that emanated from a coal mine, they showed that the difference in reduction in species number downstream of the inflow was attributed mainly to a significant effect of pollutants on the hyphomycetes (Deuteromycotina) (Table 6.12). The rate of decomposition of leaves was significantly higher upstream than downstream, which was reflected in the more rapid decline in the C:N ratio of the leaf litter upstream.

Duddridge and Wainwright (1980) measured the uptake of heavy metals into the aquatic fungi *Pythium*, *Dictyuchus*, and *Scytalidium*, showing that uptake of metals generally followed the order Zn > Pb > Cd. Both Cd and Zn had stimulatory effects on fungal growth at low concentrations ($< 1\,\mathrm{mg\,l^{-1}}$ and $< 10\,\mathrm{mg\,l^{-1}}$, respectively), whereas lead had no effect on growth. They also demonstrated that there is considerable transfer of Cd from fungal hyphae to a grazing amphipod, *Gammarus pulex* (a shrimp), showing bioaccumulation and concentration through the food chain. No shrimps survived being fed on *Pythium* containing 150 to 170 $\mu\mathrm{g\,g^{-1}}$ cadmium after 13 days, whereas 60% of the shrimp

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TABLE 6.12 Presence and Absence of Hyphomycete Fungal Species Upstream and Downstream of a Coal Mine Effluent Source

Aquatic deteromycotina	Upstream	Downstream
Anguillospora longissima	+	+
Articulospora tetracladia	+	−
Centrospora aquatica	+	−
Clavatospora longibrachiata	+	−
Flagellospora curvula	−	−
Helicodendron	+	+
Heliscus lugdenensis	+	+
Tetracaetum elegans	+	+
Tricladium	+	−
Total number of species	8	4

Source: Data from Maltby and Booth (1991).

survived to 21 days when fed on control hyphae. These dead animals contained $22\,\mu g\,g^{-1}$ Cd, demonstrating the transfer of lethal levels of heavy metal up the food chain. Bärlocher (1992a,b) cites his earlier work showing that heavy metals can be detrimental to the growth of aquatic hyphomycetes and reduce sporulation. The effects of high levels of metals, such as Cd and Zn, however, were reduced by the presence of calcium ions in water. This Bärlocher attributes to ion complexation and suggests as a mechanism for greater heavy metal tolerance of fungi in hard water.

We saw earlier that aquatic fungi can play a significant role in determining the decomposition of autochthonous and allocthonous materials in streams, rivers, and lakes. The activity of these organisms helps to regulate the net export of nutrients from terrestrial to marine ecosystems. The impact of pollutant metals on the fungal organisms and the processes they regulate requires further understanding, as more of our aquatic ecosystems are being affected by industrial and agricultural effluents.

6.3.4 Impact of Heavy Metals in Marine Ecosystems

In contrast to some of the example of negative effects of heavy metals on fungi in terrestrial ecosystem, Newell and Wall (1998) did not see any decline in fungal activity, but rather an increase in activity in salt marsh communities contaminated by high levels of mercury ($71\,\mu g\,g^{-1}$ dry weight of sediment Hg) and methylmercury ($190\,ng\,g^{-1}$). Both fungal biomass, measured as ergosterol content of decaying leaf mass, and ascospore production were higher than in a less contaminated location.

6.3.5 Impact of Heavy Metals on Lichens

In his review of pollution effects on lichens, Richardson (1988) highlights a property of lichens, which is their ability to accumulate heavy metals with little sign of determent to growth and survival. This accumulation is not infinite, however, so lichens lave been used to map pollutant plumes. This mapping has been especially useful for the determination of sulfur dioxide levels in the atmosphere, because different lichen species have different tolerances. Despite the fact that acidifying pollutant loading an increase in heavy metal availability are often co-occurring problems, neither Richardson (1988) nor Bates et al. (2001) considered that the changes in heavy metal availability could be contributing to the patterns of lichen distribution they associate with atmospheric SO_2 levels.

Fritze et al. (1989) measured soil microbial parameters along a 20,000-m transect away from a copper and nickel smelter in Finland. Within 500 m of the smelter there was an absence of epiphytic lichens and their place taken by an alga. *Hypogymnia physoides* and *Pseudevernia furfuracea* were more tolerant of heavy metal exposure than *Usnea hirta*, *Bryoria fuscescens*, and *Platismatia glauca*, demonstrating a differential tolerance within epiphytic lichens. Fungal hyphal length and soil respiration increased significantly at greater than 10 km from the smelter. The pattern of distribution of both lichens and mosses was found to correlate with levels of heavy metal loading in the environment (Kosta-Rick et al., 2001), where they found that the level of several heavy metals (Cd, Cu, Hg, Pb, Sb, Sn, and Zn) was significantly higher in lichens than in mosses. This is possibly attributable to the presence of fungal mycelia in the lichen, which may have a higher affinity for metals than moss tissue.

Current debate on climate change concentrates on the need for reduction in gaseous emissions of CO_2 and other potential greenhouse gases. Although there is a strong movement for the reduction in heavy metal loading in industrial effluents, however, heavy metals from previous industrial processes still exist in many ecosystems. There needs to be continued work applied to the potential role of fungi in the remediation of polluted sites in addition to the attention being paid to the role of genetically modified plant species in phytoremediation (Raskin and Ensley, 2000; Gleba et al., 1999; Zaurov et al., 1999) or the combination of plants and bacteria (Salt et al., 1999).

6.4 FUNGI AND RADIONUCLIDES

Following the development of nuclear weapons during the Second World War and the subsequent evolution of nuclear energy-generating industries, there has been considerable concern regarding the safe storage of radionuclide waste, together with the hazards of radiation pollution in the event of nuclear

detonations and release from atomic energy plants and reprocessing facilities. The ecological aspects of radionuclide release were discussed by Coughtree (1983) and were related to the recommendations of the International Commission on Radiological Protection. Within that publication, Heal and Horrill (1983) summarized element transfers within terrestrial ecosystem, highlighting the importance of organic soil horizons and the microbial communities within as potential accumulators of both nutrient elements and radionuclides.

More recently, as a result of the explosion of the Chernobyl Atomic Energy Station in the Ukraine in the 1986, attention was focused on the accumulation of radioactive fallout in a variety of biotic components in the terrestrial ecosystem. Much of this effort concerned measures of uptake and accumulation of radioisotopes into plants in Scandinavia, Russia, and central and western Europe. As some 90–95% of all plant species associate with mycorrhizal fungi for the uptake of nutrients, it is not surprising that mycorrhizae may be of importance in plant uptake of radionuclides. Additionally, as mushroom fruit bodies and lichens form a substantial part of the diet of animals and humans in many of the countries affected by the Chernobyl fallout (Horyna, 1991) (Table 6.13), interest arose in the potential accumulation into fungi and through the food chain, and hence the activity of radionuclides in fungal fruit bodies was measured by a number of research groups.

The renewed interest in fungi as radionuclide accumulators was based on earlier work of Witkamp (1968), and Witkamp and Barzansky (1968), who demonstrated that fungi were capable of storing radionuclides in mushrooms. Haselwandter (1978), Eckl et al. (1986), Haselwandter et al. (1988), and Byrne (1988) also showed that lichens and mushroom-forming fungi took up and

TABLE 6.13 Estimated Sources of Human Internal Radiocesium Contamination Due to Consumption of Foodstuffs and Fungi

	Annual intake (Bq)		
Source	1986	1987	1988
Milk	1000	550	70
Meat	1100	1100	120
Cereals	600	1900	100
Vegetables	310	200	70
Potatoes	160	340	60
Fruits	580	380	70
Mushrooms	1400	1500	1550

Source: Data from Horyna (1991).

accumulated radionuclides in their fruiting structures. Byrne (1988) paid special attention to members of the Cortinaraiacea, which are known to be Cs accumulators. The European Community set a limit of radioactivity in foodstuffs at 600 Bq kg^{-1}. Byrne found that the levels of $^{134,\ 137}$Cs radioactivity in fungi in Slovenia ranged between 0.5 kBq kg^{1} dry weight (*Cortinarius praestans*) to 43 and 44 kBq kg^{-1} (*Laccaria amethystine* and *Cortinarius armillatus*, respectively), up to 80 times the limit considered safe to consume. Byrne (1988) also showed elevated levels of the nuclide ^{110m}Ag, which has a half-life of 250 days, varying from 50 Bq kg^{-1} dry weight in *Agaricus campestris* to 565 Bq kg^{-1} in *Lycoperdon perlatum*. Genera of both Agaricaeae and Lycoperdaceae had been previously shown to be accumulators of silver (Byrne et al., 1979). Haselwandter, and Berreck (1994) reviewed the accumulation of radionuclides in fungal fruit bodies after the Chernobyl disaster. In addition to Cs, fungi have been shown to take up ^{7}Be, ^{60}Co, ^{90}Sr, ^{95}Zr, ^{95}Nb, ^{100}Ag, ^{125}Sb, ^{144}Ce, ^{226}Ra, and ^{238}U. Haselwandter and Berreck (1994) correctly point out that the level of radionuclide accumulation should be viewed as being over and above the contribution by the natural radioisotope of potassium (^{40}K), where potassium may be between 0.15–11.7% of the dry weight of fungal tissue. They cite values of ^{137}Cs from a variety of basidiomycete fungal species both before and after the Chernobyl explosion, which range between 266 and 25160 Bq kg^{-1} dry weight before and between 95 and 947400 Bq kg^{-1} following the explosion. Although a variety of radionuclides were released from Chernobyl, most of the surveys relate to the radiocesium content of mushrooms.

Data collected from a variety of sources show that there is considerable geographic variation in accumulation rates and considerable variation within and between fungal species. In their study of radiocesium accumulation into mushrooms at sites in the Ukraine, Grodzinskaya et al. (1995) divided up the country into regions of different levels of soil surface contamination. Of the 41 species of basidiomycete fruit bodies collected in this survey, activity of ^{137}Cs from the lowest surface-contaminated regions ($< 3.7 \times 10^{10}$ Bq km^{-2}) varied from zero to 33 kBq kg^{-1} dry weight to values between 1.4 and 3.7 MBq kg^{-1} dry weight for the heavily contaminated region (148×10^{10} Bq km^{-1} around Chernobyl and Prypyat). Within the ectomycorrhizai species *Suillus luteus* they showed a strong positive relationship between the accumulation of both ^{137}Cs and ^{134}Cs in fruit bodies and the level of soil surface contamination. Horyna and Randa (1988) showed concentration factors of between 0.4 and 99 (ratio of radiocesium content of mushroom to substrate) for radiocesium accumulation into basidiomycete fungal fruit bodies. The highest concentration values were found in the genera *Boletus*, *Paxillus*, *Tylopilus*, *Lactarius*, *Leccinum*, *Amanita Cortinarius*, and *Suillus* (mycorrhizal species), and the lowest in the genera *Scleroderma*, *Lepista*, and *Agaricus*, of which the latter two are saprotrophs (Horyna and Randa, 1988; Randa and Benada, 1990). The range of concentration factors varied considerably among species within the same genus

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(*Boletus*, between 5.4 and 99), however, and among isolates of the same species (7 to 99 within *Boletus badius*).

During a mapping effort of the distribution of radionuclides in mushrooms, similar wide ranges of activities of radiocesium were found in mushrooms from Poland (Mietelski et al., 1994), with 300 to 20,000 Bq kg^{-1} dry weight of ^{137}Cs between a sample of *Macrolepiota procera* and one of *Xercomius badius*. The greatest within-species variation for radiocesium was found in *Boletus edulis* (300 to 1800 Bq kg^{-1}), whereas the variation in activity of the α-emitting isotopes ^{90}Sr and $^{239+240}Pu$ ranged from 0.6 to 4 Bq kg^{-1} in *Leccinum* sp. for Sr and from undetectable to 90 MBq kg^{-1} for *Boletus edulis*. Wide ranges of accumulation of radiocesium (<3 to 1520 Bq kg^{-1}) were found in mushrooms collected in Japan (Muramatsu et al., 1991). The lowest levels of activity (<50 Bq kg^{-1}) were found in the edible species *Lentinus edodes*, *Flammulina velutipes*, *Pleurotus ostreatus*, and *Pholiota nameko*. Muramatsu et al. (1991) also suggested that cesium was taken up by *Sullius granulatus* and *Lactarius hatsudake* in preference to potassium, which is in contradiction to Olsen et al. (1990), who suggest that the affinity of fungi decreases in the order K > Rb > Cs > Na > Li, with a relative ratio of 100:42:7:4:0.5. Yoshida and Muramatsu (1994) published more figures of radiocesium levels in 81 species of fungi from six sites representing different ecosystems in Japan. Although the variability in radiocesium content was large between species, there was a trend that mycorrhizal basidiomycete species had higher radionuclide levels than saprotrophic species, a trend that was more pronounced for ^{134}Cs than ^{137}Cs. In addition, their analysis of the data suggested that the level of activity found in the mushroom was positively correlated with the level of activity in the substrate and depth in soil where the maximal mycelial biomass was found (Fig. 6.10). The level of radioactivity (mainly radiocesium) in mushrooms shows a positive correlation to the geographical distribution of level of radiation fallout from

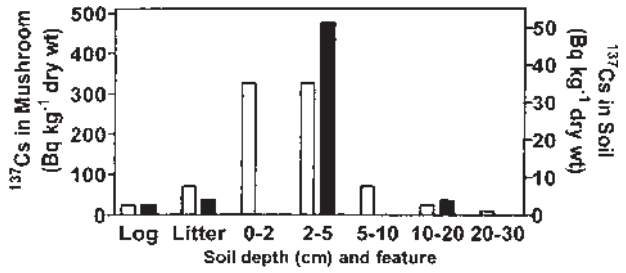

FIGURE 6.10 Relationship between radiocesium content in substrate and associated mushroom in relation to the location of the fungal mycelium producing the mushroom. *Source*: Data from Yoshida and Muramatsu (1994).

TABLE 6.14 Pre- and Post-Chernobyl Radiation Levels in the Environment and in Mushrooms

	Deposition ($Bq\,m^{-1}$)	Pre-Chernobyl ($Bq\,kg^{-1}$ dry weight)	Post-Chernobyl ($Bq\,kg^{-1}$ dry weight)
Netherlands	500 to 600	230 to 1000	1700 to 95000
United Kingdom	1000 to 9500		
Germany	10,000 to 40,000	3770[a]	25160 to 88700

[a] Calculated form fresh weight figure, assuming 70% water content.
Source: Date from Oolbekkink and Kuyper (1989).

Chernobyl (Oolbekkink and Kuyper, 1989) (Table 6.14). These fungi also accumulated more radioactivity than other organisms in the ecosystem, and can be considered to be good indicator species of radionuclide contamination (Fraiture et al., 1990; Giovani et al., 1990) (Table 6.15).

TABLE 6.15 Range of Radiocesium content of Ecosystem Components from the Same Ecosystem in Belgium in 1986 and 1987

Ecosystem component		Radiocesium content ($Bq\,kg^{-1}$)
Soil	Leaf litter	650 to 1060
	Organic horizon	240 to 265
Trees	Spruce	105
	Beech	180
	Birch	260
Fern	*Pteridium aquilinum*	137 to 146
Ericaceous herb	*Vaccinium myrtillus*	640
Mosses	*Rhytidiadelphus* sp.	5900
	Dicranium sp.	1070 to 2000
Lichen	*Hypogymnia physodes*	5300
Fungi	*Xercomus badius*	8000 to 18,800
	Cortinarius brunneus	7700 to 27,000
	Cortinarius armillatus	8200 to 24,300
	Russula ochroleuca	8300
	Boletus edulis	1350
	Clitocybe vibecina	630
	Hypholoma spp.	160 to 660
Roe deer	*Capreolus* sp.	350 to 2300
Wild boar	*Sus* sp.	20 to 600
Soil animal	Earthworms	600

Source: After Fraiture et al. (1990).

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By chance, the Chernobyl explosion turned into a large-scale experiment by virtue of the fact that among the radioisotopes released, the ratio of ^{137}Cs to ^{134}Cs was in a 2:1 ratio. As the two radioisotopes have different half-lives (^{134}Cs of 2.2 years and ^{137}Cs of 28 years), decay correction of ^{134}Cs in environmental samples can determine the proportion of the ^{137}Cs isotope that originated from Chernobyl. By analysis of the isotope ratio of radiocesium from Chernobyl (^{137}Cs:^{134}Cs) in fruit bodies of ectomycorrhizal basidomycete fungi, Dighton and Horrill (1988) showed that a large proportion (25–92%) of ^{137}Cs was accumulated that originated from sources occurring prior to the accident at Chernobyl (Table 6.16). Similar figures (13–69%) of pre-Chernobyl accumulation of radiocesium were calculated from the data presented by Byrne (1988) and Giovani et al. (1990) commented on the deviance from the from the 2:1 ratio and fungal accumulation of radiocesium from atmospheric nuclear tests. This information suggests that fungi could be long-term accumulators and retainers of radionuclides in the environment. Laboratory studies showed that there was a wide range of rates of uptake and incorporation of radiocesium into fungal mycelia grown in liquid culture, with the three saprotrophic basidiomycetes, *Mycena polygramna*, *Cystoderma amianthinum*, and *Mycena sanguinolenta*, having the highest rates of accumulation expressed on a biomass basis (Clint et al., 1991), compared to many ectomycorrhizal species. Differences in uptake among species, however, varied between about 100 to 250 nmol g^{-1} dry weight of fungus per h. If the uptake is expressed on a hyphal surface area basis, however, the ranking of species differs and the uptake values range from 0.1 to 2.5 nmol m^{-2} hyphal area per h. The uptake of radionuclides into plants is often regarded as root uptake phenomenon. Ertel and Ziegler (1991), however, suggested that the ranking of uptake of radiocesium

TABLE 6.16 Proportion of ^{137}Cs of Pre-Chernobyl Origin Found in Fruit Bodies of Two Ectomycorrhizal Fungal Species in Upland United Kingdom Based on Decay-Corrected Ratios of the Isotopes ^{137}Cs and ^{134}Cs

Fungal species	Location	Content of Pre-Chernobyl ^{137}Cs (%)
Lactarius rufus	MH86 peat under *Pinus contorta*	92
	MH86 peat under *Pinus contorta*	81
	St humic podsol under *Picea sitchensis*	74
	S2 peat under *Picea sitchensis*	67
	SB peat under *Picea sitchensis*	73
	B humic podsol under *Picea sitchensis*	25
Inocybe longicystis	SB peat under *Picea sitchensis*	75
	S4 peat under *Picea sitchensis*	83

Source: After Dighton and Horrill (1988).

by trees was related to the roughness of bark. They suggest that spruce and larch accumulated more radioactivity than sycamore due to a rougher bark and that root uptake accounted for 20% of the uptake in larch and 50% in sycamore. Their methodology, however, may have the underestimated the role of root uptake, and some of the differences could be explained by the differences in mycorrhizal association of these tree species; spruce and larch are ectomycorrhizal, whereas sycamore is arbuscular mycorrhizal, and, therefore may have reduced mycorrhizal uptake compared with the ectomycorrhizal species.

Haselwandter and Berreck (1994) reviewed the role of arbuscular mycorrhizae in plant uptake of radionuclides and found the information to be somewhat conflicting. They cite an example of arbuscular mycorrhizal inoculation of sweet clover and Sudan grass, which showed slight and statistically insignificant increases in uptake of ^{137}Cs and ^{60}Co by mycorrhizal plants. This is in line with the findings of Jackson et al. (1973), in which arbuscular mycorrhizal colonization of roots of soybeans by *Glomus mosseae* significantly increase ^{90}Sr uptake from soil. In contrast, they cite their own research that demonstrates that arbuscular mycorrhizal symbiosis in the grass *Festuca ovina* reduce the uptake of radiocesium into shoots.

Information suggesting a reduced plant uptake supports the findings of Clint and Dighton (1992), who showed that influx of radiocesium into mycorrhizal heather plants (*Calluna vulgaris*) with ericoid mycorrhizae was lower than that into nonmycorrhizal plants. The internal redistribution of Cs within mycorrhizal plants, however allowed a greater proportion of the Cs taken up to be translocated to shoots in mycorrhizal plants than in nonmycorrhizal plants, especially when incubated in a high potassium environment prior to radiocesium exposure (Fig. 6.2). Similar enhanced translocation of radiocesium into shoots of arbuscular mycorrhizal *Festuca ovina* were shown by Dighton and Terry (1996), but they did not observe enhanced shoot translocation in clover (*Trifolium repens*) (Fig. 6.11). In a more recent study, however, Berreck and Hasselwandter (2001) showed a decrease in the Cs translocated to the shoots of *Agrostis tenuis* in the presence of arbuscular mycorrhizae.

Elevated levels of radionuclide in roots compared to shoots in mycorrhizal plants suggests that the mycorrhizal fungi accumulate radiocesium in the fungal tissue in a similar manner to that shown for heavy metals and ectomycorrhizae (Denny and Wilkins, 1987a,b). This concept has been reviewed for arbuscular mycorrhizal symbiosis Berreck and Hasselwandter (2001), who investigated the impact of potassium fertilization as a method to reduce uptake of cesium by the mycorrhizal grass *Agrostis tenuis*. They showed that mycorrhizal development in plant roots reduced Cs uptake by the plant at moderate nutrient levels in the soil. They further suggested that the mechanism of protection is due to sequestration of Cs in the extraradical hyphae of the mycorrhizal fungus and a reduced

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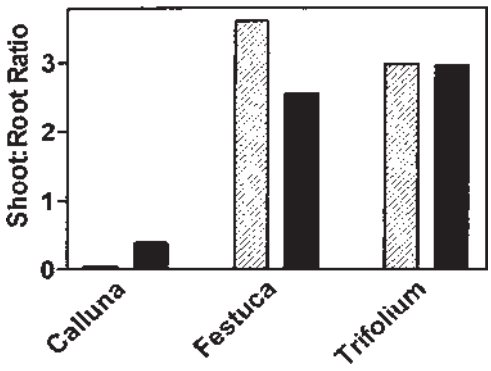

FIGURE 6.11 Histogram of shoot:root ratio of radiocaesium incorporation into the ericoid mycorrhizal plant heather (*Calluna vulgaris*) and the arbuscular mycorrhizal plants sheep grass (*Festuca ovina*) and clover (*Trifolium repens*) in the presence (solid bars) and absence (open bars) of mycorrhizae. *Source*: Data from Dighton and Terry (1996).

translocation into the host plant. They also demonstrated that there was no benefit of adding potassium to reduce Cs uptake for this fungal–plant interaction. Using a method of quantitative autoradiography, Gray et al. (1995, 1996) showed that translocation of radiocesium through a fungal thallus of *Armillaria* spp. and *Schizophyllum commune* was significantly reduced in comparison with a diffusion model of translocation. They also demonstrated preferential movement of radiocesium to developing fruit bodies, which were acting as nutrient sinks.

Saprotrophic fungi are involved with the decomposition of organic resources (dead plant and animal remains) in ecosystems. Grassland soil saprotrophic fungi have been shown to have great potential for uptake and immobilization of radioceaium fallout (Olsen et al., 1990; Dighton et al., 1991). Assuming an average influx rate of 134 nmol Cs g^{-1} dry weight of mycelium (determined from laboratory uptake studies) and an estimate of hyphal biomass of 6 g dry weight cm^{-3} of soil (determined by hyphal length measurements of field-collected samples), Dighton et al. (1991) estimated that the fungal compliment of two upland gas ecosystems in northern England would have been able to take up between 350 and 804 nmol Cs m^{-1} h^{-1}. Considering estimates of radiocesium concentration in pore water of these soils to be at the micromolar level (Oughton, 1989), these fungi have the potential to accumulate a large percentage of the total fallout.

Radionuclide uptake mechanisms in fungi have been related to cell-wall ion exchange sites and by potassium replacement. Potassium replacement is, however, species-specific, with suggestions that Rb and Cs replace K in

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the filamentous fungus *Fusarium solani* (Das, 1991), but only Rb, not Li, Na, or Cs could replace K in the yeast *Candida utilis* (Aiking and Tempest, 1977). Connolly et al. (1998) demonstrated that the wood decay fungus *Resinicium bicolor* could utilize strontium from strontianite sand, translocate it through mycelial cord systems, and deposit it in calcium oxalate crystals. This suggests that strontium behaves similarly to calcium in fungal metabolism, and although this work did not involve radiotracers, it suggests a pathway for translocation of the radionuclide ^{90}Sr within decomposer fungi.

Much effort has been invested in the potential and actual use of plants to accumulate pollutants (mainly heavy metals) in the process of phytoremediation (Raskin and Ensley, 2000). The accumulation of radionuclides by fungal mycelia could be a useful means to attempt to effect radionuclide cleanup from both industrial processes and from contamination of natural environments. The usefulness of fungal mycelia in environments cleanup has been suggested by White and Gadd (1990), developed air-lift bioreactor systems containing live cultures of fungi for biosorption of radiothorium. *Rhizopus arrhizus* and *Aspergillus niger* were found to be more efficient absorbers than *Penicilium italicum* and *P. acrysogenum*. These mycelial fungi were found to be of great use, as they can be palletized to make them physically similar to commercial ion-exchange materials. It is the potential use of fungi in the field that is of main interest to us in the context of ecosystem processes. The ability of ectomycorrhizal basidiomycete fungal species to accumulate radionuclides could in theory be an important component in the restoration of radionuclide-contaminated terrestrial ecosystems. The formation of large and harvestable fruiting structures (mushrooms) provides a potential means of removal of radionuclides that have been accumulated within. Mycorrhizal fungi have been shown to be a major component of the radionuclide accumulation (radiocesium concentration) in a boreal coniferous ecosystem in Sweden (Guillette et al., 1994) although its relative contribution to the total standing crop biomass is probably not large (Vogt et al., 1982; Fogel and Hunt, 1983) (Table 6.17). The distribution of fungal mycelia in upper soil horizons has been shown to correlate with the accumulation of radiocesium in the upper soil and reduced downward movement of the radionuclide by immobilization in fungal tissue (Rommelt et al., 1990; Guillette et al., 1990a,b). This attribute points to the potential utility of fungal mycelia in soil to prevent leaching loss of radionuclides and their accumulation in mushrooms, which could be harvested and removed from the site.

The method of translocation of ^{14}C and ^{32}P through hyphal systems of *Rhizopus*, *Trichoderma*, and *Stemphylium* was by diffusion (Olsson and Jennings, 1991). The rate of translocation of carbon within the fungal thallus has been shown to react in real time to provide directional flow to the building phases of the hyphae (Olsson, 1995). Jennings (1990) showed that the absorption of phosphorus by rhizomorphs of *Phallus impudicus* and *Mutinus canninus*

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TABLE 6.17 Radiocaesium Stores in a Boreal Coniferous Forest Ecosystem in Sweden with an Average Total Deposition of 220 kBq m^{-2}

Ecological component	^{137}Cs content (kBq kg^{-1} dry weight)
Leaf litter (A_o) horizon	26
A_1 soil horizon	14
Total organic horizon in soil	19
Facultative mycorrhizal species	230
Obligate mycorrhizal species	120
Saprotrophic fungi	140
Lichens	36
Mosses	19
Ferns	16
Angiosperms	8

Source: Data adapted from Guillette et al. (1994).

consisted of two transport systems. In contrast to the diffusion of C and P, translocation of ^{137}Cs through hyphae of *Schizophyllum commune*, however, has been shown to be slower than diffusion, suggesting a possible mechanism for accumulation (Gray et al., 1995). In addition, there is a suggestion from this work that there is the potential for preferential transport to sites of basidiocarp primordium production. This observation may support the finding of Dighton and Horrill (1988) and others (data from Yoshida and Muramatsu, 1994) that radiocesium accumulation in basidiomycete fungi could be high and long-lived. They found up to 92% of the radiocesium in mycorrhizal basidiocarps in the United Kingdom was derived from pre-Chernobyl sources of fallout. Measures of influx and accumulation of radiocesium into hyphae of a range of fungal species suggested that saprotrophic species had higher accumulation than mycorrhizal species (on a weight basis) (Clint et al., 1991). This rate of radiocesium immobilization in U.K. upland grassland saprotrophic fungal mycelia could have accounted for a high proportion of the immobilization of Chernobyl fallout radiocesium (Dighton et al., 1991).

Recent work from the remains of the Chernobyl Atomic Electric Station have shown that fungal communities in soil have been altered by intense radiation doses (Zhdanova et al., 1994), leading to simpler community structure and a dominance of melanin-containing (pigmented) fungal species at higher levels of radioactivity. Large numbers of fungal species can still be isolated from the walls of the reactor room (Zhdanova et al., 2000), although the effects of the intense and sustained radiation has led to a shift in the genetic composition within some

fungal species (Mironenko et al., 2000). Monitoring the fungal communities in the region around Chernobyl during the last 15 years has resulted in the isolation and culturing of about 2000 strains of 180 species of 92 genera. Zhdanova et al., (1994) showed that the microfungal community structure in soil around Chernobyl differed in relation to the degree of exposure to radionuclides. The complexity of the community was represented diagrammatically by pleiads (constellations of points representing fungal species and the distance between them indicating their degree of similarity of abundance within a location), in which the number of linear connections between points (representing fungal species) indicated the degree of linkage or complexity of the community. Additionally, they identified a number of fungal species that contained melanin pigment in their cell walls. This mathematical and diagrammatic representation of the fungal communities broadly suggested that the complexity of the fungal community (diversity) decreased with increasing radioactive dose, but that the proportion of melanized species within these communities increased with dose rate. This suggests that melanin may be involved in the protection of fungal tissue against damage by radionuclide emissions. This may be a protective mechanism similar to that seen in the melanin-containing lichen fungi that protect the fungal symbionts against ultraviolet light (Gauslaa and Solhaug, 2001).

Of these microfungi, many have been shown to be capable of growing into and decomposing carbon-based radioactive debris from the reactor (Zhdanova et al., 1991), called "hot particles." They showed that *Cladosporium cladosporioides* and *Penicillium roseo-purpureum* could overgrow these hot particles, which were of less than 1147 Bq of γ-activity, and destroy them within 50 to 150 days. Indeed, some of these fungi isolated in areas of high radioactivity have developed a form of radiotropsm (Vember et al., 1999; Zhdanova, 1994) in that they actively direct their growth toward sources of radioactivity. These fungi, isolated in areas of high radiation, have been shown to direct their growth toward collimated source of radioactivity in culture, whereas the same species isolated from areas of low levels of radioactivity do not. Ecological studies have characterized fungal bioindicator traits (melanization and species composition) of high, middle, and low levels of radioactive contamination (Zhdanova et al., 1990; 1991; 1994; 1995; 2000). Zhdanova et al. (1995) showed that both *Chaetomium aureum* and *Paeciliomyces lilacinus* were indicators of high levels of radionuclide contamination of soil in woodland ecosystems.

The ability of fungi to survive high levels of radioactivity has been shown by the isolation of microfungi from the walls of the nuclear reactor room at the Chernobyl Atomic Electric Station under conditions of 1.5 to 800 mR h^{-1} in the presence of alpha- and beta-emitting ^{239}Pu, $^{240+241}$Pu, ^{241}Am, and ^{244}Cm, and mainly the gamma-emitting ^{137}Cs (Zhdanova et al., 2001). Thirty-seven species of 19 genera were isolated, with the frequency of isolation being greater at higher levels of radioactivity (Table 6.18).

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TABLE 6.18 Frequency of Isolation (>10% of Isolates) of Microfungi from the Walls of the Reactor Room at Chernobyl in Relation to the Intensity of Radiation

	Frequency of isolation (%)	
Fungal species	$1.5-25\,mR\,h^{-1}$	$40-220\,mR\,h^{-1}$
Acremonium strictum	33.5	22.2
Alternaria alternata	40.2	44.4
Aspergillus niger	13.4	22.2
Aureobasidium pullulans	20.1	44.4
Aureobasidium versicolor	26.8	55.5
Botrytis cinerea	13.4	11.1
Cheatomium globosusm	20.1	22.2
Cladosporium cladosporioides	26.8	11.1
Cladosporium herbarum	20.1	44.1
Cladosporium sphaerospermum	73.7	99.9
Fusarium solani	13.4	11.1
Penicillium ingelheimense	13.4	—

Source: From Zhanova et al. (2000).

The fungal component of the lichen symbiosis is also responsible for the elevated radionuclide content of lichens in Austria following Chernobyl (Heinrich et al., 1999). Heinrich et al. (1999) report that levels of ^{137}Cs rose from about $0.4\,kBq\,kg^{-1}$ to over $50\,kBq\,kg^{-1}$ after the explosion at Chernobyl. The ^{137}Cs concentration of *Pseudovernia furfuracea* exceeded the natural ^{40}K activity by 430 times. Within this foliose arboreal lichen the biological half-life of Cs is approximately 1.3 years, and that for ^{90}Sr is 1.2 to 1.6 years. In contrast, the terricolous lichen *Cetraria islandica* had a biological half-life for ^{137}Cs of 2.5 years. Similar biological half-lives were obtained for radiocesium in the lichens *Evernia prunastris* and *Hypogymnia physoides* by Guillette et al. (1990a,b). This indicates that lichens are strong accumulators of radionuclides and that the long biological half-life allows for transfer to animal grazers over an extended period. Indeed, Gaare (1990) indicates that reindeer densities of about four per hectare are common in parts of Norway. Lichens form the greater part of their winter feed and account for about 40% of their annual food intake. In an analysis of the radionuclide content of lichens between 1986 and 1988, Gaare (1990) showed that mean activity ranged between 6,700 and $24{,}000\,Bq\,kg^{-1}$ (Table 6.19). High intake of radiocesium by roe deer during the autumn in Sweden was associated with a greater proportion of fungal fruit bodies in their diet. Johanson et al. (1990) give figures of fungal-derived intake of $3{,}000\,Bq\,d^{-1}$ in August and September and $2{,}500\,Bq\,d^{-1}$ in October. Similarly, Bohac et al.

TABLE 6.19 Radiocesium Content of Lichens in Norway Collected in 1986

Location	Lichen species	^{137}Cs content (Bq kg^{-1})
Species on soil	*Alectoria ochroleuca*	24005
	Coelocaulon divergens	16683
	Cetraria nivalis	24286
	Cladina mitis	12389
	Cladina stellaris	16572
	Sterocaulon pashale	17274
Species on rocks	*Pseudephebe pubescens*	54080
	Ramalina polymorpha	9315
	Umbilicia hyperborea	31767
	Umbilica deusta	34756

Source: Data from Gaare (1990).

(1989) demonstrated accumulation of radicesium and radiostrontium into ectomycorrhizal fungal fruit bodies. They suggested that fungi were important in transferring radionuclides into higher trophic levels, because of the observed accumulation of radionuclides in the organic horizon of steppe soils. They also state that there is significant accumulation of mercury in fungal-feeding beetles (17.5 mg kg^{-1} dry weight), compared to 2 to 2.5 mg kg^{-1} dry weight for saprophagous, phytophagous, and zoophagous genera. More recently, Barnett et al. (2001) estimated that as a result of fungal consumption, the radiocesium transfer to the average consumer in the United Kingdom is a radiation dose of less than one microsievert (one-millionth of the annual limit imposed by the IAEA). This figure may be higher in areas in which the practice of eating wild mushrooms is more widespread than in the United Kingdom and is dependent upon which fungal species are eaten.

In summary, fungi appear to be very resistant to radionuclides in the environment. It is possible that the presence of melanin pigment in the hyphae of mitosporic fungal species may provide some protection against ionizing radiation in the same way that it has been shown to protect against ultraviolet light. Due to the long-lived and extensive hyphal network, fungi appear to be very efficient in absorbing radionuclides from the environment. This is particularly true of radiocesium, which is reported to behave in a similar way to potassium in biochemical pathways. Internal translocation of radionuclides between sources and physiological sinks occurs in the same way as essential nutrients and can account for the long-term retention of radionuclides within the fungal biomass. Adsorption of radionuclides onto ion-exchange sites of fungal hyphal walls has been reported in the literature, this attribute has been used in industrial effluent

cleanup. Many questions regarding the interaction of fungi and radionuclides need further investigation. The intriguing concept of behavioral adaptations of fungi to evolve radiotropism needs further study to identify the triggers and the physiological mechanisms of the response. In terms of ecosystem processes, aquantitative measure of the potential immobilization of a range of radionuclides into fungal tissue, the rates of translocation into harvestable fruit bodies, and the potential to use fungi in environmental remediation projects needs to be evaluated. Indeed, Entry et al. (1993) compared the uptake of ^{137}Cs and ^{90}Sr by ponderosa and Monterey pine seedlings, as both are fast growing and potential candidates tree species for planting for site remediation. They showed that ponderosa and Monterey, respectively, accumulated 6.39 and 8.3% of the radiocesium present in the growth medium and 1.59 and 4.5% of the radiostrontium. The possibility of enhancing this uptake by the addition of ectomycorrhizal symbionts showed promise (Entry et al., 1994), with 3 to 5 times more ^{90}Sr taken up in the ectomycorrhizal seedlings (Table 6.20). In a realistic situation, the combination of mycorrhizal-enhanced uptake of radionuclides into trees together with the production of harvestable fruit bodies could prove an effective soil remediation technique.

TABLE 6.20 Accumulation of Radiostrontium by Ponderosa and Monterey Pine Seedlings with and without Ectomycorrhizal Symbiosis

	Monterey pine			Ponderosa pine		
Mycorrhiza	Total tree uptake (Bq)	(%) Uptake	Concentration ratio	Total tree uptake (Bq)	(%) Uptake	Concentration ratio
Pisolithus tinctorius 144	378	6.5	133	229	3.2	144
Pisolithus tinctorius 101	407	6.0	128	224	3.9	135
Laccaria laccata	386	6.6	128	348	6.0	162
Hebeloma crustuliniforme	393	6.9	127	228	3.9	148
Cenococcum geophilum	352	6.0	88	175	3.0	102
Uninoculated	47	0.7	27	31	0.6	28

Note: Concentration ratio is specific activity in plant/specific activity in soil.
Source: After Entry et al. (1994).

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6.5 FUNGI AND CLIMATE CHANGE

6.5.1 Interactions with Primary Production

As a result of industrialization, increased use of automobiles, consumption of fossil fuels, and reduction in land cover by carbon-sequestering plants, atmospheric carbon dioxide concentrations are continuing to increase. In an attempt to increase the terrestrial carbon sink, international protocols have suggested increasing plantations of forests, where the greater ground cover of rapidly growing plants could be utilized to fix carbon. Pacala et al. (2001) suggest that land-based carbon sinks for the United States are between 0.3 and 5.8×10^{15} g C. As an example, China has seen a mean annual accumulation of carbon of 0.021×10^{15} g C over the last 30 years (from 4.38 to 4.75×10^{15} g C between 1970 and 1989) as a result of increased forest production. Planted forests alone have sequestered 0.45×10^{15} g C in China (Fang et al., 2001). One of the questions to be asked is what the allocation of this carbon within the forest structure is and how fungi play a role either as mycorrhizae or as saprotrophs.

Potential changes in the geographical distribution of plant species along with their associated fauna and fungi will be a long-term and slow change as plants colonize new areas that have suitable climatic and edaphic quality allowing their successful competition with established plant species. As they invade marginal habitats or are eased out of formerly optimal habitats, the role of fungi as pathogens to reduce populations and individual plant fitness is likely to increase, whereas the role of mycorrhizal fungi in preventing pathogens, allowing access to scarce nutrients, will likely increase in importance.

Dighton and Jansen (1991) show the possible scenarios of climate change on the availability of nutrients for plant and mycorrhizal uptake and the changes in carbohydrate supply to support mycorrhizal symbiosis. Based on data of predicted patterns of changes in net primary productivity, which suggest that most increases in productivity will occur distant to the Equator (Leith, 1978) and that the greatest increase in active carbon pool size and rates of translocation will occur in cool, adapted plants (Potvin et al., 1984), Dighton and Jansen suggested that major climatic changes would affect ectomycorrhizal and ericoid mycorrhizal-dominated plant communities to a greater extent than arbuscular mycorrhizal-dominated plant communities. The suggested model for ectomycorrhizal plants (Fig. 6.12) shows an enhancement of photosynthetic activity with increased CO_2, which would provide a larger pool of carbohydrates to support mycorrhizal development, fruiting, community diversity and investment into extraradical hyphal exploitation of the soil. The effect of increased availability of CO_2 could increase the C:N ratio of plant litter, making the role of mycorrhizal fungi as saprotrophs more important. Mycorrhizal diversity thus will be maintained and favor those species capable of producing enzymes for the acquisition of major nutrients from organic sources. In contrast, however,

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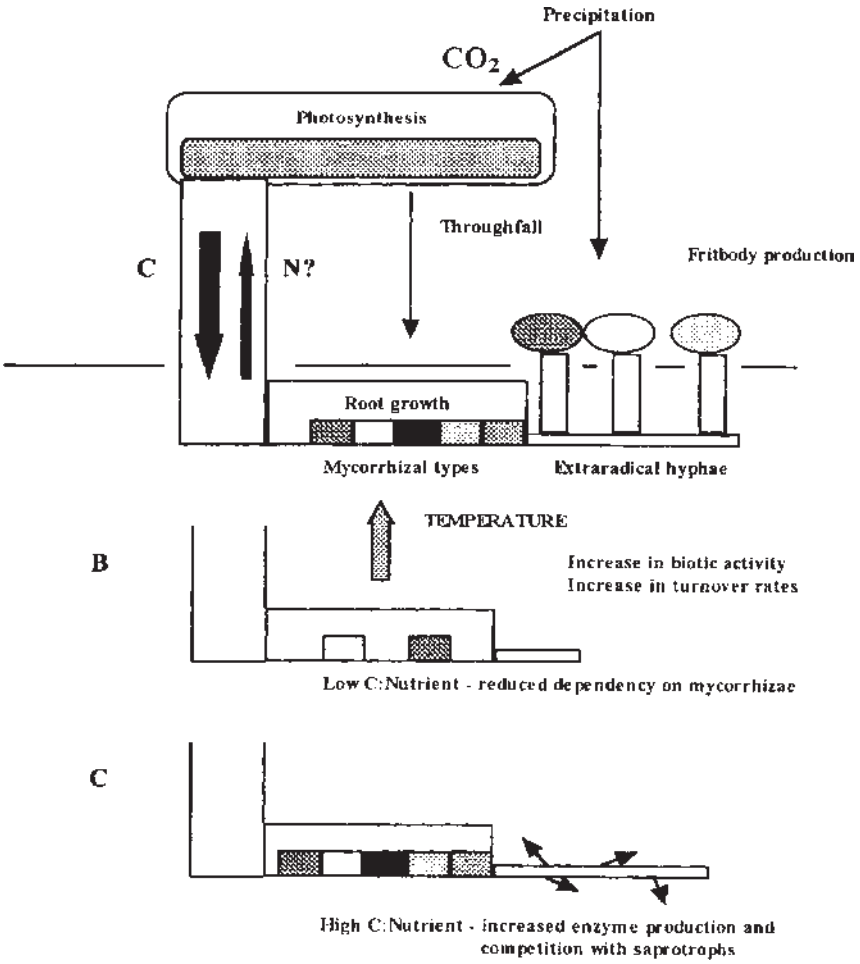

FIGURE 6.12 Model of the possible effects of increased atmospheric CO_2 and elevated temperature on the tree–ectomycorrhizal symbiosis. The top model indicated the diversity and function of mycorrhizae in an elevated CO_2 scenario. Increased photosynthesis leads to greater C supply to roots and fungi, which supports a greater access to nitrogen (in N-limiting systems). The effect of elevated temperature in scenario B suggests increased leaf litter decomposition and nutrient mineralization, leading to a reduced host dependency on the mycorrhizal symbiosis. In scenario C, the change in leaf litter chemistry (enhanced nitrogen content) increases resource quality, and the mycorrhizal fungi have to compete with the saprotrophic community for access to mineralized nutrients by increasing diversity and extraradical hyphal exploitation of soil. *Source*: Adapted from Dighton and Jansen (1991).

the consequential increase in atmospheric temperature with increased CO_2 will increase the rate of activity of saprotrophic microbial communities, increase the rate of plant litter decomposition and mineralization, and increase the size of available nutrient pools (Swift et al., 1979; Van Cleve and Yarie, 1986). This fertilizer effect is likely to reduce the dependence of a plant on its mycorrhizae, leading to a decline in mycorrhizal diversity and soil exploitation by extraradical hyphae. Subsequent to the publication of this model a number of research projects looked at the role of enhanced CO_2 and temperature on the mycorrhizal status of plants and the physiology of their association. How well do these studies fit or refute the model? Indeed, Vogt et al. (1993) and O'Neill (1994) discuss the importance of selecting appropriate below-ground indicators of environmental change, as soil organisms are sensitive to stress and may be influenced prior to any observable above-ground symptoms. They specifically suggest that fine root growth, turnover and mycorrhizal status, and function are among the potentially most useful measures of response to environmental change.

6.5.2 Soil Nutrients and Carbon Stores

A. Decomposition and Nutrient Availability

The effect of enriched atmospheric CO_2 on soil organisms is inconsistent (Kandeler et al., 1998; Bardgett et al., 1999). Increased carbon dioxide and elevated temperature increased microbial carbon, but decreased the metabolic quotient when temperature alone was increased. The increase in CO_2, however, led to an increase in root biomass and an increase in the C:N ratio, possibly because of a change in the balance between allocation of carbon to root growth and carbon storage. The inconsistency in the pattern of below-ground response to elevated CO_2 was echoed by Zak et al. (2000), who summarized the results of 47 publications on soil C and N cycling under elevated carbon dioxide. The basic generalities of these studies, spanning graminoid, herbaceous, and woody plant ecosystems, were that (1) there was greater plant growth under elevated CO_2, with more carbon entering the below-ground component, and (2) that there was greater metabolic activity of soil microbial communities under elevated CO_2. Changes in C and N cycling between life forms were significant, leading to coefficients of variation between 80–800%. The increase in plant biomass also corresponds to an increase in soil organic matter accumulation in temperature grassland ecosystems (Hunt et al., 1991), but the increased storage was not enough to keep pace with the rate of CO_2 buildup in the atmosphere.

In a review of the effects of enhanced atmospheric CO_2 concentrations on plant leaf chemistry, Gifford et al. (2000) showed that data were mixed and that there was little consensus about the changes in leaf chemistry. In general they suggest that there is a trend toward an increase in the C:N ratio to a level of about

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a 15% increase under a doubling of CO_2. The response of leaves in terms of C:P ratios are also very variable, and there is no consensus for a stable trend in the data.

De Angelis et al. (2000) showed that the effects of elevated CO_2 increased the C:N and lignin:N ratios of oak leaf litter in a Mediterranean forest ecosystem to such an extent that leaf litter decomposition was retarded. Decomposition constants for mixed leaf litter (*Quercus ilex*, *Phillyrea angustifolia*, and *Pisatcia lentiscus*) exhibited a drop of between 5–8% in k value for field experiments and a 12.5% drop in k value for microcosm decomposition experiments in elevated CO_2. Cotrufo et al. (1998) showed that the reduction in nitrogen content of leaves grown in enhanced CO_2 varied from 50% in sweet chestnut (*Castanea sativa*) to 19% for sycamore (*Acer platanoides*) and that this change in nitrogen content stimulated grazing of leaves by the isopods *Oniscus asellus* and *Porcellio scaber* (Hättenschwiler et al., 1999). The conclusion is that reduction in leaf litter resource quality in elevated CO_2 environments reduces the activity of the saprotrophic community, including fungi.

The significant increase in C:N and lignin: N ratios of beech twigs grown in elevated CO_2 (C:N ratio change from 45.6 to 72.7 and lignin:N ratio change from 16.3 to 22.4), however, did not change the rate decomposition of the twigs or the dynamics of nitrogen and lignin during decomposition on (Cotrufo and Inseon, 2000). Gorisen and Cotrufo (2000), however, cautioned that the changes in leaf chemistry may not be correlated to the rate of decomposition processes. Although they identified an increase in the C:N ratio of grassland leaf material (*Lolium perenne*, *Agrostis capillaries*, and *Festuca ovina*) with an increase in CO_2 from ambient (350 $\mu l l^{-1}$) to double, the respired CO_2 during decomposition could not be attributed to the labeled C that was accumulated under the elevated CO_2 treatment. Their data on the internal allocation of sequestered carbon in the elevated CO_2 condition indicated that this additionally available carbon was translocated to the plant roots. Leaves made a contribution of about 6% and roots about 26% to the carbon remaining during decomposition over 222 days (Fig. 6.13). This suggests the potential importance of plant root material to below-ground storage of carbon. This study did not separate the mycorrhizal compartment from the plant root component, so we can make no assumptions of the role of mycorrhizal immobilization of carbon from these data. In a modeling exercise, McMurtrie et al. (2000) suggest that the ability of forest systems to sequester carbon on a long-term basis is also limited by the availability of nitrogen. It may be here that mycorrhizae are of importance. Johnson et al. (2000) showed that under elevated CO_2 conditions, ponderosa pine forests accessed more nitrogen from either the surface soil horizons or from more recalcitrant forms of nitrogen in the soil to support their increased biomass. It is possible that the enzymatic capabilities of ectomycorrhizae and their ability to sequester nutrients from organic sources in soil could be of increased benefit in a high CO_2 world.

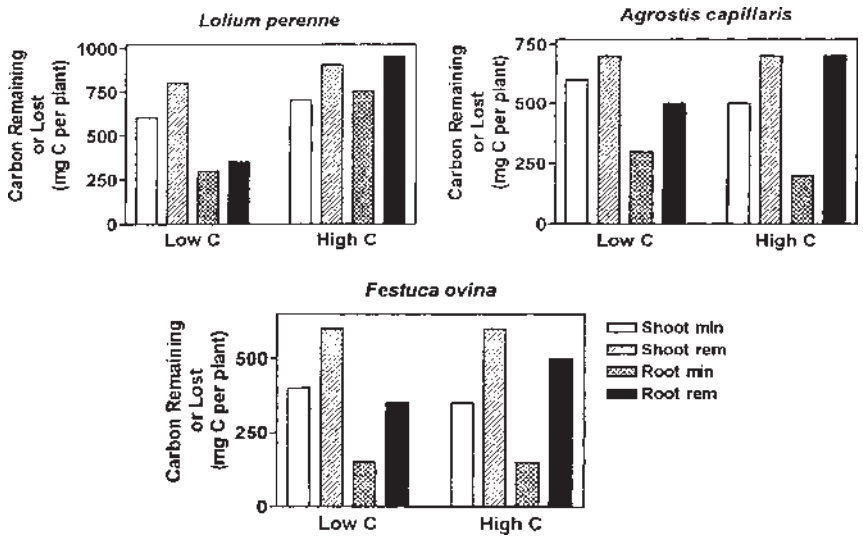

FIGURE 6.13 Amount of carbon mineralized from and remaining in leaf litter derived from three grass species grown under low ($350\,ml\,l^{-1}$) or high ($700\,ml\,l^{-1}$) atmospheric CO_2 in the presence of high nitrogen availibility after 222 days. *Source*: Data from Gorisen and Cotrufo (2000).

B. Carbon Stores

Roots and their mycorrhizal components are frequently overlooked as potential sources of carbon within ecosystems. Indeed, the modeling study of Wullschleger et al. (1994) showed that the lack of knowledge of the role of mycorrhizae in physiological response to elevated CO_2 leaves a void in the detail of the model. In forested ecosystems, Vogt (1991) gives comparisons of biomass allocation within the forest for a variety of tree species and locations. Of the 24 examples she cites, in only nine cases were there details of both the above- and below-ground biomass standing stock carbon. These examples represented only four tree species (three conifers and one deciduous). Below-ground biomass carbon accounts for between 16% in *Pinus menziesii* to 64% in *Pinus eliottii* of total tree biomass carbon. From these limited data sets we can extrapolate the potential role of aforestation and reforestation in enhancing carbon sequestration in a global change scenario. The below-ground input to the decomposer system under forested ecosystem can be considerable. Bowden et al. (1993) point out that nearly two-thirds of the soil respiration of a temperate mixed hardwood forest comes from root activity, and the decomposition of root litter contributes

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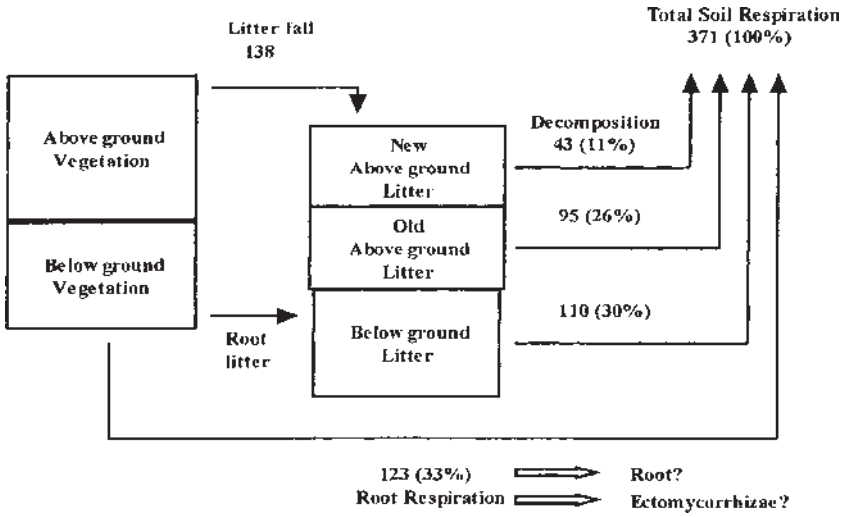

FIGURE 6.14 Soil respiration budget for a mixed hardwood forest in the eastern United States with carbon flux values ($g\,C\,m^{-2}\,y^{-1}$) and percentages of total soil respiration in parentheses. Root respiration is regarded as a "black box," and the relative contribution to respiration by root and mycorrhizal fungal tissue is not given. *Source*: After Bowden et al. (1993).

70–80% of total soil respiration in a range of forested ecosystems (Fig. 6.14). In heathland ecosystems *Molinia* root turnover contributes 67% of total litter production, 87% of litter nitrogen loss, and 84% of total litter phosphorus loss (Aerts et al., 1992). In contrast, *Calluna* and Deschampsia growing in the same ecosystem contributed two to three times lower percentage values. Root respiration values vary considerably, from an estimated 35% in tulip tree (*Liriodendron tulipifera*) (Edwards and Harris, 1977) to 62% of soil respiration in slash pine (*Pinus eliottii*) (Nakane et al., 1983). The data support the hypothesis of Bonan (1993) that coniferous trees allocate twice as much carbon to roots than do deciduous tree species. It is further suggested that this difference in carbon allocation to roots is a trade-off in terms of nitrogen acquisition, in which leaf litter quality of coniferous trees is characteristically low, leading to low rates of N mineralization and low N demand for tree growth. In mor soils, in which there are distinct surface organic horizons, Bradley and Fyles (1996) found that carbon investment in roots supported soil exploitation and nutrient uptake, as nitrogen was in ready supply. In mull soils, however, in which organic matter is more incorporated into the mineral horizons and nitrogen supply was limited, they suggested that photosynthates were being used to stimulate N mineralization

by increasing rhizodeposition of easily assimilated carbon to prime the microbial community to decompose organic forms of nitrogen (Hendricks et al., 1993).

The above studies did not go as far as to say that the dependence on ectomycorrhizae may be greater in coniferous trees than deciduous forests, in which carbon investment into mycorrhizal enzyme synthesis could be a mechanism of adaptation to nutrient-poor environments. In any case, these examples serve to show that the allocation of carbon to root systems is not trivial and the allocation to mycorrhizal components is rarely adequately quantified. These below-ground stores of carbon may be significant in a world of increasing atmospheric CO_2 concentration as a potential carbon sink.

Atmospheric temperatures are predicted to increase as a consequence of elevated atmospheric carbon dioxide. Increased soil temperatures raise the activity of saprotrophic microbial communities, including fungi, to such an extent that rates of decomposition are higher. In a forest simulation, Bonan and Van Cleve (1992) compared the consequences of a 5°C rise in temperature on the decomposition of forest floor residues in a variety of boreal forest ecosystems. It was concluded that the effect of a rise in air temperature would cause a soil temperature increase of between 300 degree days in white and black spruce forests to 500 degree days in birch forests. This would cause an increased soil respiration loss of 439 g C m^{-2} birch and 675 g C m^{-2} in black spruce, a considerable loss of soil carbon store. The total gain in carbon as a result of increased photosynthesis, however, was shown to effectively counteract the loss except for the white spruce ecosystems, in which decomposition loss exceeded carbon gain (Table 6.21).

In their review of root system adjustments to elevated atmospheric CO_2, BassiriRad et al. (2001) came to the conclusion that there was no consistent pattern in the literature for such compensatory adjustments as changes in root:shoot ratios and root architecture, root nutrient absorption capacity, and nutrient use efficiency. Numerous researchers, however, have shown responses of

TABLE 6.21 Predicted Changes in Carbon Loss and Gain in Boreal Forest Ecosystems as a Consequence of a 5°C Increase in Air Temperature After 25 Years

	Forest floor mass (kg m^{-2})		Tree biomass (kg m^{-2})		Ecosystem carbon flux (gC m^{-2})
	Control	Warning	Control	Warning	
Paper birch	2.5	2.0	12.1	12.6	+23
White spruce	5.4	5.1	12.6	13.6	−129
Black spruce	10.7	9.9	4.3	5.0	+46

Source: Data from Bonan and van Cleve (1992).

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both roots and their mycorrhizae to changes on atmospheric CO_2 concentrations (Diaz, 1996). For example, Dhillion et al. (1996) showed that a Mediterranean old field monoculture of *Bromus madritensis* responded to an increase in atmospheric CO_2 from 350 to 700 $\mu mol\, mol^{-1}$ by increasing root biomass by 31%, rot length by 88%, soil microbial biomass by 42%, soil fungal hyphal length by 20%, and total root colonization by arbuscular mycorrhizae by 57%. These increases in fungal biomass in soil are reflected by increases in fungal-feeding nematodes, suggesting a higher rate of energy transfer through the fungal-based food web at elevated CO_2 (Hungate et al., 2000). It is agreed that there is no clear pattern in response, and like many ecophysiological functions, each of these may be case-, plant-, or ecosystem-specific.

There is a positive drain of carbohydrates from plant shoots to roots to sustain their mycorrhizal associates. In arbuscular mycorrhizal symbiosis, Douds et al. (1988) showed that there was five to six times greater translocation of carbon to mycorrhizal root systems than nonmycorrhizal root Carrizo citrange seedlings. Similarly, Wang et al. (1989) showed that mycorrhizal roots in a split-pot experiment caused a 20% increase in the carbon exchange rate in *Panicum* plants, increased photosynthate storage in leaves by 45%, and more than doubled sink activity (movement to roots) in mycorrhizal-infected plants. The formation of different root architectures also has different demands on photosynthate translocation below ground. Wullschleger et al. (1994) showed that the enhanced investment in root growth under elevated CO_2 is rewarded by increased exploitation of N and P sources, but that the development of more branched root systems has a higher energy demand than less branched systems. The increase in energy demand is due to the greater amount of meristematic tissue in highly branched systems, in which the metabolic rate in meristems is higher than other root tissue.

It is known that one of the effects of ectomycorrhizal colonization of root systems is an increase in root branching, so it is reasonable to assume that part of the increased carbohydrate drain to support mycorrhizal root systems is due to in root branching. Seegmüller and Rennenberg (1994) showed that in oak, elevated CO_2 increased stem height, stem diameter, total plant weight, and lateral root formation and that the effects of *Laccaria laccata* ectomycorrhizal association had more than an additive effect in the presence of elevated CO_2 (Fig. 6.15). Nylund and Wallander (1989) showed that photosynthesis was enhanced in mycorrhizal plants and that the translocation of photosynthate to roots was enhanced by the ectomycorrhizal fungus *Hebeloma crustuliniforme*, but not by *Laccaria laccata*. These studies were conducted in hydroponic culture systems, however, which are less conducive to true mycorrhizal function as soil culture. Species-dependent functional response among mycorrhizal species was shown by Gorisen and Kuyper (2000). In a comparison between *Laccaria Laccata*, an ectomycorrhizal fungus commonly found in nitrogen-rich environments, and

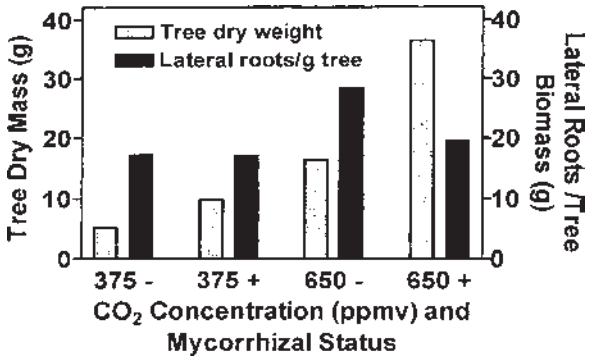

FIGURE 6.15 Effects of increasing atmospheric CO_2 on the growth and lateral root formation of oak trees in the presence (+) and absence (−) of *Laccaria laccata* mycorrhizae. *Source*: After Seegmüller and Rennenberg (1994) with kind permission of Kluwer Academic Publishers.

Suillus bovines, found in nitrogen-poor environments, Gorisen and Kuyper (2000) demonstrated a greater net accumulation of carbon in plants associated with both mycorrhizal species. That extra carbon, however, was translocated below ground and incorporated into root and fungal biomass in *Suillius* mycorrhizae, but the additional carbohydrate translocated into *Laccaria* colonized roots was respired. The plant return for the carbon investment in *Suillus*-colonized root biomass was an increase in nitrogen uptake, resulting in plant N contents twice as high as Laccaria-colonized trees, irrespective of CO_2 concentration. These results lend support to the concept that carbon use for nitrogen acquisition is more important in mycorrhizal symbiosis that are characteristic of N-limiting ecosystems.

The change in ectomycorrhizal community seen in Douglas fir seedlings in response to both elevated atmospheric CO_2 and elevated temperature (Rygiewicz et al. 2000) in a low-nitrogen soil could be a response to changes in carbon allocation to roots and nitrogen-use efficiency. This study indicated that the total number of mycorrhizae increased in elevated CO_2 conditions, but that an increase in ectomycorrhizal diversity resulted from an increase in temperature where *Rhizopogon* and *Cenococcum* morphotypes dominated. O'Neill et al. (1987) showed that seedling oak and pine trees produced an average of 66% (pine) and 56% (oak) increase in biomass because of the increased mycorrhizal colonization of seedlings growing in a CO_2-enriched environment (double ambient). It was suggested that increased photosynthesis offset the carbon drain imposed on the plant by the increased mycorrhizal colonization of the roots system.

Together with evidence of fruit body production of mycorrhizal fungi being a major part (15% of soil organic matter) of the forest floor biomass

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(Vogt et al., 1982; Vogt, 1991), it is probable that mycorrhizae form a significant carbon sink in soils. Fine roots of forest trees in the eastern United States have a mean age of 3 to 18 years (dead roots an age of 10 to 18 years) and composed of carbon fixed between 3 to 8 years earlier in organic soil horizons to 11 to 18 years earlier in the mineral soil horizon (Gaudinski et al., 2001), suggesting that root biomass and necromass carbon is a midterm carbon store in soils. Keeping carbon below ground and in the biomass of plants and fungi is also facilitated by ectomycorrhizal fungi. Finlay and Read (1986a) showed that there is significant between-plant transfer of carbon through interconnected plants via mycorrhizal bridges. This transfer is enhanced between source plants, optimizing photosynthesis and sink plants, which grow in the shade. This transfer of carbon, both within and between tree species in the field (Simard et al., 1997a,b), along with potential interplant transfer of nutrients (Finlay and Read, 1986b,c), implies that the root network acts as a resource for whole plant communities to conserve both carbon and nutrients within the forest system rather than the traditional concept of each plant and each plant species acting as a single unit in a field of competitive interactions.

In reviewing the effects of CO_2 on mycorrhizal growth and biomass, Treseder and Allen (2000) showed that there was some evidence suggesting that mycelial growth could be enhanced by elevated CO_2. For example, Sanders et al. (1998) found a five-fold increase in arbuscular mycorrhiza extraradical mycelium with elevated CO_2 (Fig. 6.16) in experimental conditions. In a long-term exposure study, Rillig et al. (2000) compared the arbuscular mycorrhizal status of New Zealand pastures in a transect away from cold CO_2 springs. They found that mycorrhizal root colonization and soil hyphal length increased linearly ($r^2 = 0.47$, $P = 0.0016$ and $r^2 = 0.76$, $P < 0.000$, respectively) along the increasing CO_2 gradient. Staddon et al. (1999), however, found that elevated CO_2 had similar growth-promoting effects on both mycorrhizal and

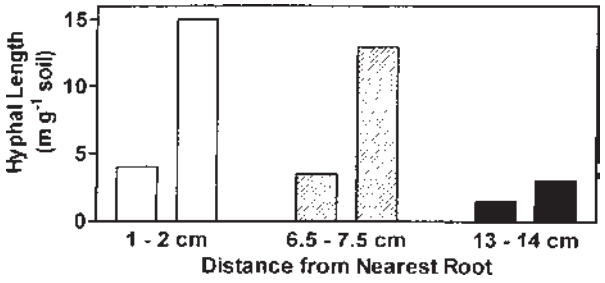

FIGURE 6.16 Arbuscular mycorrhizal extraradical hyphal length in the absence (left column of pair) and presence (right column of pair) of elevated CO_2 at different distances from the root surface. *Source*: Data from Sanders et al. (1998).

nonmycorrhizal *Plantago lanceolata*, but had no effect on carbon partitioning between roots and shoots of either mycorrhizal status. The increased flow of carbon through root systems in elevated CO_2 conditions resulted in a greater accumulation of soil organic matter rather than plant biomass. Fitter et al. (2000) suggest that it would not be expected that there would be direct effects of increased atmospheric CO_2 on mycorrhizal hyphal growth, as these fungi grow in a high CO_2 atmosphere in the soil anyway. They consider that the indirect effects via photosynthesis would be most likely, and suggest that a positive feedback loop could ensue, in which increased plant carbon fixation increased mycorrhizal growth and the ability to capture P (arbuscular mycorrhizae), as evidenced by Knight et al. (1989), and N (ectomycorrhizae), as discussed above, to alleviate the plant from nutritional stress and increase plant growth. In the arbuscular mycorrhizal case, they suggest that high turnover of extraradical hyphae would increase soil respiration and counter the enhanced C fixation. Sanders et al. (1998) did not find any increased uptake of P through the increased extension of arbuscular mycorrhizal hyphae due to increased CO_2. They inferred that the increase in hyphal mass would contribute to below-ground carbon stores and to the increase in soil aggregation. Estimates of arbuscular mycorrhizal hyphal biomass range from $0.02\,m\,g^{-1}$ soil in poplar, through $38\,m\,ml^{-1}$ soil in shrub steppe, to $111\,m\,ml^{-1}$ soil for prairie communities (Rillig and Allen, 1999), which amounts to a maximum of $457\,\mu g\,ml^{-1}$ soil of hyphal dry weight (approximately $500\,kg^2$). Treseder and Allen (2000), however, make a contrary argument for ectomycorrhizae, whose long-lived mycelium may be resistant to microbial attack and be incorporated into long-term carbon stores in soil by entering the "slow pool" of carbon. The effect of enhanced CO_2 differs considerably among mycorrhizal fungal species and may result in a shift in the mycorrhizal community structure (Cairney and Meharg, 1999). Klironomos et al. (1997, 1998) showed that infection and extraradical hyphal growth differed between two species of *Glomus—Acaulospora denticulata* and *Scutellospora calospora*—in the presence and absence of elevated CO_2. The two *Glomus* species only caused increased plant growth under elevated CO_2 conditions. The other two mycorrhizal genera caused no difference in plant growth, but only a difference in the form of the mycorrhizal association.

The potential increased development of extraradical hyphae in arbuscular mycorrhizal associations results in more fungal biomass for faunal consumption. For example, Lundquist et al. (1999) reported that the incorporation of fresh rye shoots into soil increased that number of bacterial and fungal-feeding nematodes, but that the FDA-active (live) fungal hyphal length did not increase significantly. There is thus probably a balance between a system being able to produce fungal biomass and the rate at which it is consumed by organisms in the next trophic level. The amount of overall accretion of soil carbon therefore is a balance between what carbon enters and is retained in a "slow" turnover pool and that

which enters a "fast" turnover pool. Klironomos and Kendrick (1996), Klironomos and Ursic (1998), and Klironomos et al. (1999), however, have evidence to suggest that these fungi are less favored food sources for soil fauna than saprotrophic fungi. As a number of these fungi produce the glycoprotein glomalin (Wright and Upadhyaya, 1996), Treseder and Allen (2000) calculate that glomalin could account for 30–60% of the carbon in undisturbed soils. An increase in the glomalin content of grassland soils under long-term exposure to elevated CO_2 (Rillig et al., 2000) suggests a secondary function of carbon storage in the increased development of soil stability due to aggregate formation. This carbon is somewhat protected in soil aggregates and could be regarded as a potential long-term carbon sink.

The role of ectomycorrhizae in below-ground carbon storage may be important only in ecosystems in which the tree species is native and the association between trees and mycorrhizal flora had coevolved. In the case of exotic tree plantations, the interaction may be the exact opposite. Despite the suggestions that plantation forestry may be an ideal sink for excess atmospheric CO_2 (Fang et al., 2001), the effects of plantation forests on soil carbon dynamics is often confounded with site preparation management, such as plowing and ripping, which causes massive soil disturbance and pulses of respiratory loss of stored carbon. In a study of radiata pine plantations in Ecuador in which there was no site preparation, Chapela et al. (2001) calculate that there is greater carbon loss from soil than there is gain from photosynthesis of the forest. Stable isotope studies of the soil carbon accreted under the former paramo grassland ecosystem show a 30% loss of this carbon during the first 20 years of forest rotation. Stable isotope values and carbon-dating figures show that a large proportion of this carbon is being incorporated into the three dominant species of ectomycorrhizal fungi associated with the exotic tree. The reduced ectomycorrhizal species diversity of *Suillus luteus*, *Thelephora terrestris*, and *Rhizopogon vulgaris* was identified by both fruit body and molecular analysis of root tips and compares to the 100 or so species normally encountered as mycorrhizal associates of this tree species in its natural range (Fig. 6.17). It is suggested that the prolific fruiting (1200 kg dry weight $ha^{-1}y^{-1}$ for all species), especially of the larger species (*Suillus luteus*), is a major contributor to respiratory carbon loss from the ecosystem, as these mycorrhizal fungi utilize organic forms of nutrient and nonhost carbon (Dighton et al., 1987; Durall et al., 1994; Zhu et al., 1994). The concept of plantation forestry as being our salvation in creating large atmospheric carbon sinks has to be viewed more skeptically in light of these findings.

The impact of land-use change may also be of significance to the total carbon store in soils. In part this may be due to the changes in plant communities, or lack thereof, resulting from both the land-use change and changes in decomposition rates, invoking changes in biomass and activity of fungal and

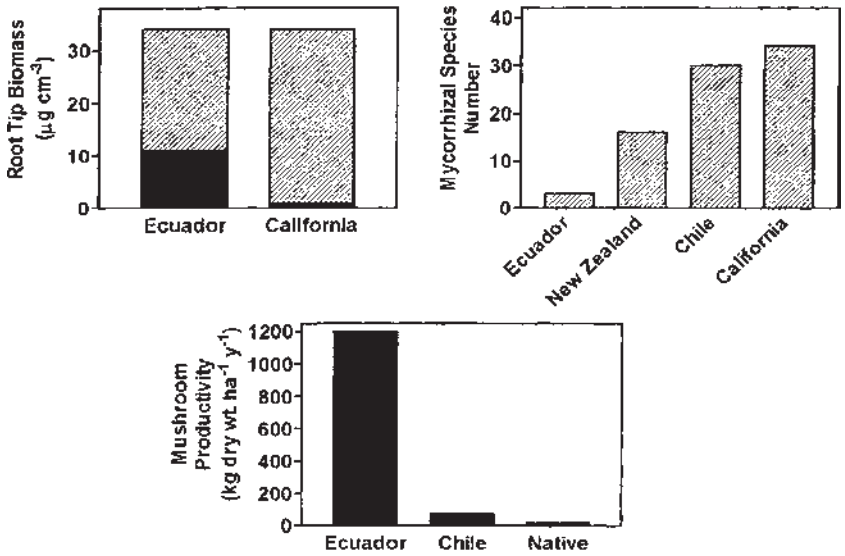

FIGURE 6.17 Comparison between the proportion of *Suillus* spp. and other ectomycorrhizal fruit bodies in radiata pine plantations in Ecuador and California, the overall diversity of mycorrhizal associations between countries and the carbon fixed in mushroom production. *Source*: Data from Chapela et al. (2001).

bacterial sparotrophs. Howard et al. (1995) document the changes that have occurred in land-use change in the 6 years from 1984 to 1990 in Great Britain. Using a conservative Markov modeling technique that assumes no change in the rate of land-use change, they predicted the change in soil carbon stores into the future, with a resultant net loss of some $151{,}000 \times 10^3$ t C to the atmosphere by the year 2044 (Table 6.22). The effect of the increase in CO_2 concentrations would increase atmospheric and soil temperatures, likely increasing greater soil respiration and the induction of a positive feedback mechanism to exacerbate global warming .

Jastrow (1996) suggests that the degradation of soil aggregates, as a result of soil management or mismanagement could result in the loss of soil carbon from protected fraction in aggregates. The development of stable soil aggregates can increase the carbon sink of soils, hence, fungi and bacteria are of great importance in the formation of and stability of aggregates. In a study of the restoration of prairie soils from agriculture the increase in the percentage of stable aggregates in the soil followed an exponential model. The rate constant k for aggregate formation was 35 times that for the accumulation of carbon into other parts of the soil, with the time to reach 99% of the equilibrium at 10.5 years

TABLE 6.22 Changes in Land Use in England and Wales During 6 Years (1984–1990), the Calculated Loss of Soil Carbon, and the Predicated Loss by the Year 2020

Cover type	Soil C ($t \times 10^3 km^{-2}$)	Area change (km^2)	Change as percentage of total area	Change in soil C ($t \times 10^3$)	Predicted change by 2020 ($t \times 10^3$)
Arable	16.9	+549	+0.36	+9293	−44137
Bog	107.4	−111	−0.07	−11921	−69434
Coniferous	31.8	+267	+0.18	+8499	+43790
Deciduous	26.1	+319	+0.21	+8340	+39553
Horticulture	19.0	−220	−0.14	−4171	−10681
Ley	19.3	−3099	−2.04	−59891	−74473
Lowland heath	24.8	+200	+0.13	+4964	+25434
Orchard	17.0	−200	−0.13	−3387	−8338
Permanent grass	23.6	+1854	+1.22	+43759	−8990
Recreation	21.3	+52	+0.03	+1104	+6259
Rough grazing	36.7	+136	+0.09	+4979	−28381
Scrub	28.8	−63	−0.04	−1798	−4610
Upland grass	60.2	−931	−0.61	−56057	−70653
Upland heath	69.9	+339	+0.22	+23646	+97914
Urban	0	+907	+0.60	0	0
Total				−32640	−106747

Source: Data from Howard et al. (1995).

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TABLE 6.23 Changes Over Time in the Carbon Sequestration of Different Soil Components

Carbon fraction	Soil under corn	Four season restoration	Ten season restoration	Virgin prairie
Mineral-associated macroaggregate C	1181	2548	3348	4692
Intramacroaggregate POM C	77	131	138	250
Mactoaggregate associated C	1258	2679	3485	4924
Total C in aggregates $<212\,\mu$m diam	1918	837	576	567
Total C in whole soil	3517	3996	4733	6106

Source: After Jastrow (1996).

for aggregates and 384 years for the whole soil. Analysis of the C:N ratio of the carbon in aggregates indicates that it is of very recent origin, suggesting that it is a derivative of bacterial and fungal biomass and not highly processed as some of the carbon in whole soil. Indeed, a significant fraction of this material is of fungal cell wall residues, which contribute to binding the microaggregates into macroaggregates. This carbon in aggregates is in a particulate or colloidal state and is physically protected from further rapid decay. The changes in partitioning of carbon over time within restored prairie soils are shown in Table 6.23. Under a CO_2-enriched environment, Jastrow et al. (2000) showed that soil carbon and nitrogen stocks increased under a tallgrass prairie ecosystem. They suggest that rootlike light particulate organic matter turns over more rapidly than more amorphous heavy particulate organic matter (POM), which accumulates over time under elevated CO_2. This they attribute to the influences in the nitrogen cycling, particularly mineralization, immobilization, and asymbiotic N fixation. The first two components are very much mediated by fungal activity in the soil.

As a result of agricultural practices, George and Boehm (2001) show that irrigation of sugar beet and maize rotation cropping resulted in a loss of $2.4\,\mathrm{t\,C\,ha^{-1}}$, whereas incorporation of all crop residues increased topsoil carbon content by $3.4\,\mathrm{t\,ha^{-1}}$ within 17 years. These arguments have been put forward to promote no-till and minimal-till agricultural practices (Beare et al., 1994a,b; 1989), which are shown to increase soil carbon stocks by 3.2 to $4.7\,\mathrm{t\,C\,ha^{-1}}$ in 10 years (George and Boehm, 2001). As some of this carbon is stored in soil aggregates, which are larger and more stable in no-till systems (Beare et al., 1994a,b), greater knowledge of the role of fungi in soil carbon sequestration in both aggregates and protected organic matter (organic matter that is less available for decomposition) would assist the evolution of more sustainable agricultural practices and increase global carbon fixation.

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6.6 CONCLUDING REMARKS

In this chapter a small selection of human impacts on ecosystems has been explored. This coverage is far from complete or exhaustive, but serves to show that human impacts affect the community structure of fungi in the environment and their functional activities. In addition, we have seen that fungi are phenotypically plastic, allowing adaptation to their environment. In this fashion, fungi are capable of surviving in adverse conditions and altering the environment for their own growth and for the growth of other organisms. This is particularly true for the role of fungi in heavy metal and radionuclide pollution, in which there is substantial evidence to show that fungi are able to accumulate, redistribute (in time and space), and alter the chemical state of elements. Industrial uses of fungi as metal accumulators have been shown to be feasible (Tobin et al., 1984), but the utility of these physiological attributes has not been fully explored in the context of the potential use of fungi in bioremediation (Singleton and Tobin, 1996).

The above discussion on the effects of atmospheric acidifying pollutants has highlighted the complexity of ecosystems. It has shown us that the effects of a single pollutant may not explain all the ecosystem and organism responses observed. Frequently human impacts are multifactoral and the synergistic and antagonistic interactions among the impacting factors are often difficult to tease apart when studies are performed with single factors. In addition, it is often not easy to represent all of the ecosystem components in an experiment. Frequently our information is gained from laboratory studies in highly controlled microcosms. Much more information can be gained from the study of more complex interactions among greater numbers of organisms in mesocosms (Odum, 1984), which more closely represent the natural ecosystem. The trade off here, however, is the balance between increased information and increased variation, which results in less accuracy in determining significant results. The use of multivariate statistics and trend analysis, however, allows us to make predictions from trends in the data, rather than relying entirely upon parametric statistics. Therefore, I see the challenge for the future as directing fungal ecology towards functional fungal ecology in a synecological setting as opposed to an autecological view.

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7

Synopsis and Outlook to the Future

7.1 INTRODUCTION

Previous chapters in this book have gone into some detail about the role that fungi play in specific ecosystems and in ecosystem processes in general. In Chap. 6 we encountered a number of anthropogenic impacts on ecosystems and saw how they have affected the fungal community and also how the fungi have been instrumental in moderating the effects of the perturbations on other organisms and processes. The intent of this final chapter is to step back and take a much broader and to some extent more philosophical and conceptual approach to the detail that has come before. In this chapter I will outline some areas that I believe warrant further investigation.

In recent years a large number of sophisticated techniques have become available to researchers. Many of these techniques have been devised for other areas of research and have been adopted by mycologists. Because of this, we currently see from the number of articles appearing in the mycological journals a movement away from the traditional observation and ecological approach to the subject, toward detailed physiological studies and molecular-based taxonomy. This is probably a necessary evolution of our communal thought processes and I think in the near future we will see a better integration of these new tools to address some of the broader, ecosystemwide questions. My feeling is that a number of these new techniques are highly relevant to the understanding of the role of fungi in ecosystem processes, but the application of the methods to this end is far from complete. In particular, when we are discussing the role of fungi in ecosystem processes, there are orders of magnitude of difference in the scale at which an individual fungal hyphum operates and at which the processes are

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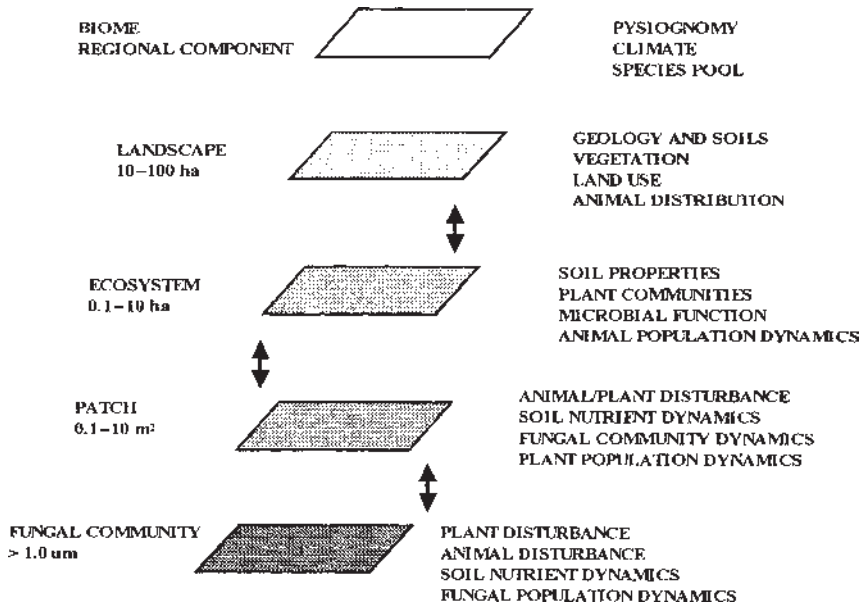

FIGURE 7.1 Concepts of hierarchy and scale in ecosystems. The relationship between scales (indicated by double-headed arrows) is important in assessing the impact of function at a lower scale on the processes at higher scales. *Source*: From Friese et al. (1997).

manifest in the ecosystem. The ability to measure and understand the processes at the microscale of resolution and then to translate them to the larger scale at which plant and larger animal communities operate is one of the big challenges of the future (Friese et al., 1997; Schimel and Gulledge, 1998). Friese et al. (1997) provide us with a conceptual framework on which we can start to effect the translation of information from the microscale to the ecosystem level of the impacts of fungi (Fig. 7.1). It is here that new methods, such as remote sensing and GIS (geographic information systems), will allow us to identify fungal effects and superimpose data and information on many levels (scales). This will assist our efforts to determine the magnitude of hyphal-scale events at landscape levels (Oudemans et al., 1998).

7.2 THE ECOSYSTEM

In a recent article, Pickett and Cadenasso (2002) discussed their ideas of what we think about the concept of an ecosystem. They started their discussion with the basic definition of Tansley, which states that an ecosystem consists of an assemblage of organisms (the biotic component) and the associated physical

environment in which the organisms live. They further suggest that the interaction among the component parts of an ecosystem, both among the organisms and between the organisms and the physical environment, is another important aspect of the ecosystem. These interactions provide a hierarchical structure through which material (energy and nutrients) flow. They further show that the evolution of the use of the term ecosystem incorporated the idea that ecosystems are scale-independent and are dynamic in nature (meaning that they are not static), and changes in time reflect changes in the complexity and degrees of divergence from equilibrium or stability.

As an ecosystem consists of component parts that are important in the movement of materials within the ecosystem, the system is ideally suited to modeling. These models are similar to the way that an industrial process can be simplified to supply and demand functions that are rate-limiting steps governing the rate of a process—the production of an end product. As Pickett and Cadenasso (2002) readily point out, however, the complexity of ecosystems is not as easily modeled, and indeed, many models may need to be developed to understand each of a variety of complex processes that occur simultaneously in the ecosystem. The level of sophistication of the model used depends of the nature of the question being asked, and may vary from a simple word model to a complex mathematical model that attempts to incorporate as many variables as possible. A complex model will need to identify and understand the contribution of each organism and abiotic component to the process being studied. Understanding the intermediate level of organization of an ecosystem by grouping organisms into functional groups or guilds may also provide a holistic understanding of the system without knowledge of the details of each contributing entity, however. This is referred to as an "averaging engine" by Andrén et al. (1999), and for a process modeler, requires only knowledge about the values of the stocks and fluxes between stocks within the ecosystem (Fig. 7.2).

It is the complexity of the interaction between component organisms in an ecosystem, however, and the interaction of the organisms with changing environmental conditions that leads to the evolution of diversity of organisms. As we become increasingly aware of the effects that humans have on environmental conditions, we become increasingly aware of the diversity of the organisms within ecosystems, their potential fragility, and the possible consequences of their loss (Tilman, 2000; Adams and Wall, 2000; Schwartz et al., 2000; Wolters et al., 2000). There is a philosophy that in order to understand how an ecosystem works it should be "kicked" and the nature of the response of the ecosystem processes and organisms will give an indication of the controls and feedbacks in the system and what major organisms effect these controls. Wolters et al. (2000) discuss the variable responses of different groups of organisms in soil to global warming. Not all organisms respond to the same degree or even in the same direction, thus to be able to understand what it is that determines the overall

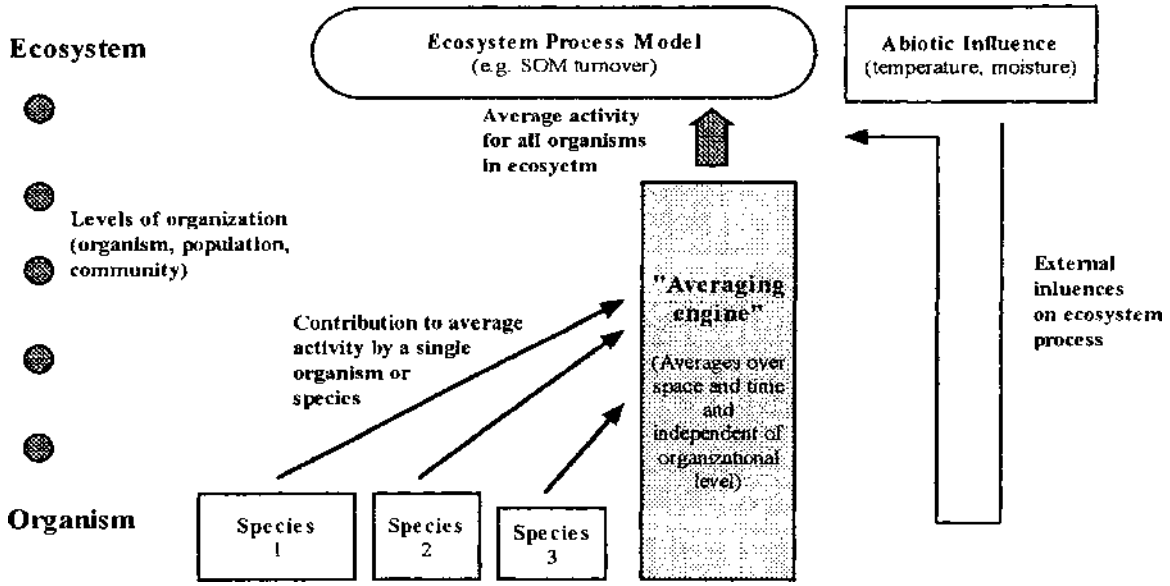

FIGURE 7.2 An ecosystem as seen from the point of view of a modeler. Here only the components of a system are necessary for explaining processes. Dots represent real or imaginary organisms. The large upward arrow represents the average activity value for all organisms in the ecosystem. Arrows from species indicate the contribution of each species to the whole ecosystem activity and represents functional groups, enzyme activity, etc. External environmental forces are represented by the box and arrow on the right. *Source*: Modified from Andrén et al. (1999).

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response of an ecosystem, it is often useful to understand the role of individual organisms or functional groups.

It is for this reason that we are attempting to understand the role of fungi in ecosystem processes. As was stated earlier in this book, however, we have limited knowledge of the taxonomic diversity of fungi in ecosystems and even less understanding of the physiology of these organisms. To give an idea of the magnitude of the problem that faces mycologists, Hawksworth (1991) estimates that we may have 3 million species of fungi on planet Earth. In their search for fungal species in tropical ecosystems for potential pharmaceutical use, Bills and Polishook (1994) made a total of 1709 fungal isolates from samples of leaf litter collected from four sites in Costa Rica. The number of isolates per sample ranged from 281 to 599, equivalent to 78 to 134 species per sample. Using rarefaction statistics, they determined that the number of species isolated per sample was considerably higher than was predicted from a random subsample of 200 isolates from each sample (Table 7.1).

What is the importance of this level of diversity of fungi in the ecosystem? It is logical to think that each fungal species had a unique function. In their analysis of 40 data sets that related ecosystem function to the diversity of organisms within the ecosystem, however, Schwartz et al. (2000) suggested that the majority of studies showed a Type B relationship between diversity and ecosystem function rather than a Type A response. A Type A response (Fig. 7.3) is one in which ecosystem function continues to increase as diversity increases. In a Type B response, however, the function within the ecosystem reaches a maximum before the maximum species diversity is attained (a saturation response). In this condition, it is thought that there is duplicity of function within the members of the community, and functional redundancy occurs. In the case of a Type B response, a loss of diversity is inconsequential to the function unless diversity is reduced below a threshold level or until a "keystone species" is removed (Paine, 1966). Schwartz et al. (2000) say that the response of different ecosystem functions

TABLE 7.1 Total Number of Fungal Species Isolated from Leaf Litter at Four Sites in Costa Rica in Relation to the Expected Number of Species as Determined by Rarefaction Analysis

Site code	Total number of fungal species	Expected number of fungal species
OS56	134	84
OS83	81	46
OS133	78	47
OS136	93	75

Source: Data from Bills and Polishook (1994).

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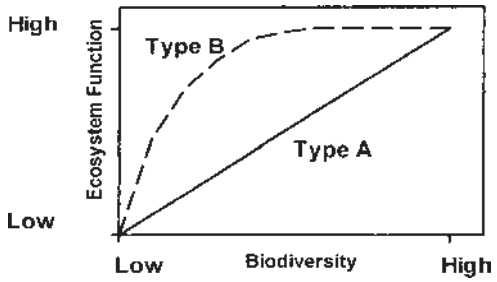

FIGURE 7.3 Hypothetical relationships between biodiversity and ecosystem function. Type A response shows a continued increase in ecosystem function as diversity increases. Type B response shows saturation of the ecosystem response before maximal species diversity is attained. *Source*: Adapted from Schwartz et al. (2000).

may vary in relation to a change of diversity of a functional group of organisms. They cite the results of van der Heijden et al. (1998), in which plant shoot biomass saturated at approximately 50% of the diversity of arbuscular mycorrhizae added to the roots of an old field plant community (a Type B response), whereas root biomass continued to increase as mycorrhizal diversity increased (a Type A response). At issue, however, is how representative shoot and root biomass are indicative ecosystem processes. A more global ecosystem function that could have been measured, however, would have been net primary productivity.

In terms of ecosystem components being organized in a hierarchical structure, O'Neill et al. (1991) have shown that with respect to the organization of communities of individual organisms, the levels at which different processes occur can be used to dissect out the functional contribution of individual species or groups of species. Using hierarchy theory, they maintain, hypothesis generation can be more accurately achieved. Within ecosystems, organisms of a variety of sizes coexist. We normally identify ecosystems by macroplant community assemblages, but the processes occurring in ecosystems are frequently modified by much smaller organisms. For example, decomposition and nutrient mineralization are carried out by bacteria, fungi, and micro- and mesoarthropods. The immediate effect of any one of these organisms is at the microscale of resolution; however, the combined effects of these organisms are seen at the local, landscape, and whole ecosystem level. One of the most challenging tasks that we face is to create the ability to seamlessly transcend the scales of resolution and convert the processes we observe and measure at one scale to that of the next level up or down. Ecologists thus have taken either a top-down or bottom-up approach to try to understand the complexities of interactions between scales (Parmelee, 1995; Friese et al., 1997; Anderson, 2000). Recently,

the idea of reducing ecosystem complexity to its minimum (microcosm approach) has been aided by the development of "mesocosms" (Odum, 1984), in which the degree of complexity of a controlled and contrived ecosystem becomes more analogous to the real world. Here the number of organisms in the ecosystem is relatively large, and complex interspecific interactions are allowed to develop. Concomitant with this comes a lack of control of changes in the ecosystem, but a more realistic set of dynamics is allowed to develop (Anderson, 1995; Lawton and Jones, 1995). Studying the processes occurring in microcosms, in which almost complete control of the system can be maintained, provides us with limited information. The use of mesocosms that are a nearer facsimile of the "real world" allows us to better understand interactions between organisms and their environment and the functional significance of these interactions. Increasing the complexity of the study system in this way allows us to increase in the functional diversity of the component organisms and to better predict the rate determining factors of environmental processes. As fungal hyphae act at the micrometer scale of resolution, their species and community effects may extend to the scale of meter and tens of meters, and there is much more use that can be made of studies of the same process at multiple levels of scale.

7.3 THE FUNGAL ORGANISM

The evolution of fungi in terrestrial ecosystems is still unclear. It is hypothesized that fungi were around in marine and aquatic ecosystems before plant emergence onto land; however, the fossil record for fungi is almost completely absent. It is only when plants emerged onto land that the fossil record of fungi was first noted, and here only where fungi were associated with plants and hence appeared in the plant fossils. Kidston and Lang (1921) documented the occurrence of fungi in primitive land plants, *Rhynia* and *Asteroxylon*, in the Silurian. The association between the fungal structures with plant has been interpreted by Pirozynski and Malloch (1975) as being a primitive mycorrhizal association. According to their hypothesis, it appears that land plants only evolved in conjunction with a mycorrhizal fungal partner. The detail of the pictures and descriptions in the original Kidston and Lang (1921) publication leave much doubt as to the actual function of the fungal/plant association seen, however. Are these fungi pathogens? Are these fungi endophytes other than mycorrhizae? How much of the plant kingdom not preserved in the fossil record had emerged onto land prior to *Rhynia* and *Asteroxylon* and were being decomposed by saprotrophic fungi? Were the plant fragments seen by Kidston and Lang actually dead and being colonized by saprotrophic fungi? Whatever the outcome of this debate, it is clear that fungi have a variety of functional groups and their associations with plants, and, presumably animals, have an ancient origin.

As we have seen from the previous chapters, fungi constitute an important component of the ecosystem. Fungi have been found in all the major ecosystems of the world and have been seen to play a large variety of roles. We have seen how fungi may be important in soil formation, soil fertility, decomposition, primary production, secondary production, and population regulation, and how they may influence plant community composition. The processes that are mediated by fungi are mediated by environmental conditions. An example of this is the influence of C:N and lignin:N ratios within plant residues (Melillo et al., 1982). This has been a dominant concept in the understanding of fungal succession and function during leaf litter decomposition and the rates of nutrient immobilization and mineralization (Frankland, 1992; 1998; Conn and Dighton, 2000). The changes in resources of the leaf litter during decomposition and the changes in fungal assemblages that effect the decomposition results in heterogeneity of resources and species assemblages in space and time (Morris and Boerner, 1999; Morris, 1999). Miller (1995) reviewed the relationship between taxonomic fungal diversity and function. In his review he lists some 21 ecosystem functions carried out by fungi (Table 7.2). He suggests, however, that we do not always have adequate tools and expertise to link these two factors together.

There are two aspects of diversity within fungi that require discussion. First, genetic diversity is important, as different fungal species may have different physiological traits. It is because of this fact that we see fungal successions on decomposing resources (Frankland, 1992; 1998; Ponge, 1990; 1991). As we saw earlier these resource successions occur where different fungal species have different enzyme capacities and thus are capable of using different components of the initial resource. At any one time, if a fungus does not possess the enzyme suite allowing resource utilization, this fungus is at a competitive disadvantage and is likely to be replaced by a species with the requisite enzyme competence. Fungi exist as a variety of functional groups (Miller, 1995), and are associated with a range of plant and animal species. They occur in a variety of environments, ranging from eutrophic agricultural and forest ecosystems, to highly oligotrophic systems in which they utilize silicon compounds as an energy source (Wainwright et al., 1997) (Fig. 7.4), to cold oligotrophic conditions in the high Arctic (Bergero et al., 1999), to man-made extreme environments, such as the former reactor room at Chernobyl, in which high levels of radiation have existed for a number of years (Zhdanova et al., 2000). Due to the number of associations between fungi and other organims, it is therefore not surprising that Hawksworth (1991) comes to estimate the potential diversity of fungi at 3 million. He came to this figure by extrapolating the number of fungi known in the United Kingdom as a percentage of the world, adding in the ratio of fungals plant associations with the predictions of the number of new plants yet to be discovered, and

TABLE 7.2 Ecosystem Functions Performed by Fungi

Physiological and metabolic	Decomposition of organic matter, volatilization of C, H, and O
	Mineralization of N, P, K, S, etc.
	Immobilization of nutrient elements
	Accumulation of toxic metals
	Synthesis of humic materials
Ecological	Energy exchange between below- and above-ground system
	Alteration of niche development
	Regulation of successional trajectory and velocity
Mediative and integrative	Transport of elements and water from soil to plant roots
	Interplant movement of nutrients and carbon
	Regulation of water and ion movement through plants
	Regulation of photosynthesis
	Regulation of below-ground C allocation
	Seedling survival
	Protection of roots from pathogens
	Modify soil aggregate formation and soil permeability
	Modify soil ion exchange and water-holding capacity
	Detoxification of soils
	Contribution to food webs
	Development of parasitic and mutualistic symbioses
	Production of secondary metabolites

Source: As presented by Miller (1995).

then doing the same for the number of insects likely to be found in the future (Table 7.3). Even at the more conservative estimate of 1.5 million fungal (Hawksworth, 2001) species (ignoring potential new insect species being found), Hawksworth points out that we now know about 4.6% of the fungi that could exist. "Where are the missing fungi?" asks Hyde (2001a,b). This question has triggered recent surveys to find the missing fungi in a variety of ecosystems and functional groups (Sipman and Aptroot, 2001; Watling, 2001; Zhou and Hyde, 2001; Yanna and Hyde, 2001; Dulymamode et al., 2001; Taylor, 2001; Wong and Hyde, 2001; Ho et al., 2001; Arnold, 2001; Photita et al., 2001).

As fungi are nondiscrete organisms, however, they exhibit a considerable degree of phenotypic plasticity. Such plasticity exhibited by an individual fungus

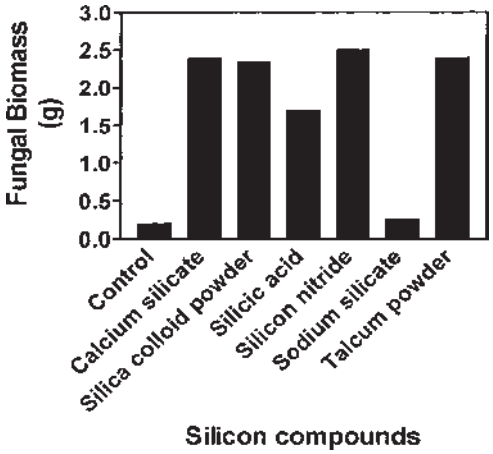

FIGURE 7.4 Effects of various silicon substrates added to Czapek Dox medium on the yield of mycelium of *Aspergillus oryzae*. *Source*: Data from Wainwright et al. (1997).

TABLE 7.3 Estimates of the Total Number of Fungi in the World

Estimate	Basis	Total number of species
A	British Isles	1,620,000
B	U.S. plants and plant products	270,000
C	Biological flora of British Isles	1,539,000
D	Alpine sedge community	1,620,000
E	Mean of above	1,262,250
F	Unstudied substrates	1,650,000
G	Anamorphs = teleomorphs	1,504,800
H	Assuming 30 million insects	3,004,800

Note: Predictions are made from the number of fungi already known (A), modified by the average number of fungi known to associate with plants (B), this value extrapolated for A using the plant species in the British Isles (C), modified for a figure from alpine communities (D), and then all these values are averaged (E). Conversions and extrapolations F to H are based on predicted unknown substrates for fungi yet to be discovered, the fact that some anamorphs and teleomorphs will be found to be the same species, and extrapolating to the potential number of insects yet to be discovered that will bear fungi.
Source: Data from Hawksworth (1991).

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can be seen in the response of the thallus of external nutrient conditions. In nutrient-poor environments, fungal hyphae adopt a searching strategy, forming fast effuse growth with a low hyphal density. On substrates with high nutrient availability the same fungus adopts a slow, dense pattern of hyphal growth as the hyphae utilize the resources available. These patterns of growth are highly distinctive (Das, 1991; Rayner, 1991; Ritz, 1995), and call for significant changes in the polarity of the hyphae and alterations of the hyphal-branching pattern. As Rayner (1991) points out, these hyphal aggregates possess emergent properties that provide functions of the fungi that cannot be achieved by the hyphal mycelium alone. The physiological function of a fungal thallus can therefore be markedly different in different parts of the same organism.

Differentiation of the thallus into functionally and physiologically diverse components (absorptive hyphae, exploratory hyphae, mycelial cords for water and nutrient translocation, etc.) permits multifunctionality of the same individual. The concept that "the mycelium of higher fungi is portrayed as a developmentally versatile collective in which an initially dendritic pattern of branching is converted, by hyphal anastomosis, into a communication network" (Rayner, 1991) highlights the role of fungi in nutrient and energy transport. This system of differentiated and specialized mycelia can convey "information" (nutrients and energy) at a faster rate than can be done via hyphae (Gray et al., 1995; 1996; Wells et al., 1999; Boddy, 1999). The ability to have multiple functions within the same individual is most obvious in higher fungi, and is probably more unusual in fungi than their nearest morphological counterparts, clonal plants. This ability of fungi provides them with the ability to exploit patchily distributed resources and withstand stress. The challenges posed by the utilization of heterogeneously distributed resources in an environment can either be met by the development of distinct microbial communities within each patch of resource (Morris and Boerner 1999; Morris, 1999), or particularly in the case of fungi, by the exploitation of all resource islands by the same species and differentiating physiological attributes within the same thallus in each of the resource islands (St. John et al., 1983; Andrews, 1992; Cairney, 1992; Rayner, 1991; Boddy, 1999). In either case, there is a need to be able to identify the physiological functional differences in the communities or the individual in the different resource units and translate that function to ecosystem-level processes. Using an adaptation of the BIOLOG microtitre plate enzyme analysis system devised for bacterial community functional analysis (Tunlid and White, 1992; Winding, 1994; Dobranic et al. 1999) were able to investigate the enzyme expression of fungal communities in a variety of microhabitats, providing an index of functional diversity (Zak, 1993). Microscale changes in the carbon substrates of decomposing leaves were measured by infrared microspectroscopy (Mascarenhas et al., 2000; Dighton

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et al, 2001), by which fungal activity could be measured at the scale seen by fungal hyphae. The use of these methods is necessary to the understanding of the function of fungi in the ecosystem in order to identify physiological activity at the mycelial level. The challenge is to translate the outcome of these processes up to higher scales of resolution.

The potential size of fungal individuals in the ecosystem (Smith et al. 1992), in which a persistent organism with different functionality linked by conductive connections may cover hectares of forest floor, leads one to regard fungi as true ecosystem engineers (Lawton and Jones, 1995), particularly in the role of plumbers (Rayner, 1998). In this way, we have seen that trees can be connected below ground by ectomycorrhizal connections among their roots (Amaranthus and Perry, 1994; Read, 1998; Rayner, 1998). With arbuscular mycorrhizal fungi, herbaceous plants can be similarly connected (Heap and Newman, 1980; Newman and Eason, 1989; Eason et al., 1991). This allows the movement of nutrients, energy, and water between plants in relation to changes in source–sink relationships, especially when they are stressed or perturbed. The more recent finding that plants of different species can be connected by these underground mycelial networks (Simard et al., 1997 a,b,c) alters our concepts regarding plant interspecific interactions. In contrast to the hypothesis that plant communities arise from competition among members of the plant assemblage, we must now start thinking in terms of the balance between competition and synergism among plants of different species. This ability of fungi to connect separate parts of the ecosystem together is not restricted to soil. In tree canopies and at the soil surface mycelial cords have been shown to connect dead leaves together and to effect decomposition (Hedger et al., 1993; Lodge and Asbury, 1988).

The fact that there is a large mycelial community of fungi in soil in many ecosystems is a benefit to both plant populations and communities. If the ecosystem suffers some disturbance, the continued presence of a mycorrhizal mycelial network enables recruitment of replacement individuals back into the community as they readily form new mycorrhizae that benefit the host plant growth (Amaranthus and Perry, 1989) and colonization of bare ground (Jumpponen et al. 1999; 2002). Indeed, Hart et al. (2001) suggest that it is fragmentation of the mycorrhizal hyphal network that facilitates invasion by exotic species into an existing ecosystem (Fig. 7.5). By the possible sharing of resources among plant species in the community, mycorrhizal fungi are likely to be able to facilitate recruitment of species into the plant community that are able to establish mycorrhizal connections with existing plants and derive carbon and nutrients from them (Simard et al., 1997b,c). In contrast, the effect of plant pathogens may influence the plant effect on the environment, thus enabling community changes to take place (Anderson et al., 2001).

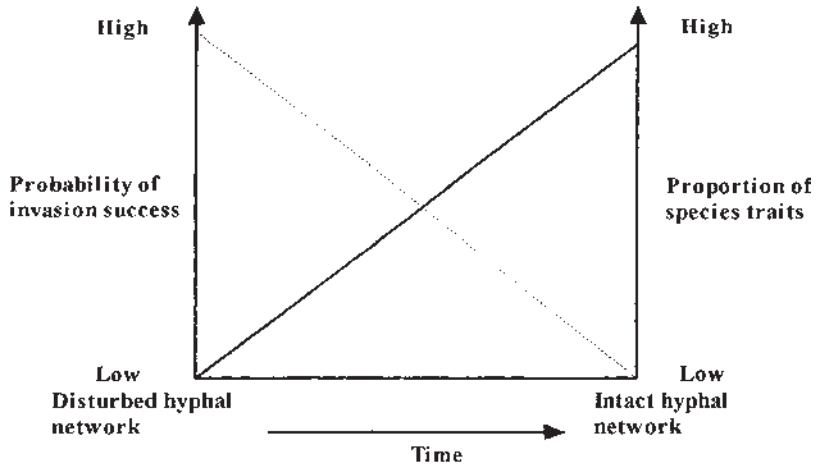

FIGURE 7.5 A life history framework for arbuscular mycorrhizal invasion success. In disturbed systems, only fungi with high colonization potential will succeed (dashed line). Over time a sustained, intact hyphal system will develop (solid line) with superior persistence traits. *Source*: From Hart et al. (2001).

The concept of fungi as being major ecosystem engineers is relatively new. Rayner (1993), however, suggests that fungi are the equivalent to the infrastructure seen in modern cities. He likens fungal networks in forests to the communication, power supply, plumbing, and sewage systems of cities. We know little about the actual extent of foraging of individual fungi, although molecular mapping tools are allowing us to do this with greater precision (Dahlberg and Stenlid, 1994; 1995; de la Bastide et al., 1994). Molecular methods for the identification of fungal species have helped us to know who is in the environment (Gardes et al., 1991; Horton et al., 1998; Hirsch et al. 2000; Pennanen et al., 2001), but we are not yet at the stage when we can easily use these techniques to tells us how much of each species coexists at any one point in space and time. The development of tools to allow us to do this and to integrate the information on species composition and their function will help us increase our understanding of the role of fungi in ecosystem processes.

7.4 THE FUNGAL COMMUNITY

How much do we know about assemblages of fungi? We have seen in earlier chapters of this book that there is replacement of fungal species by others during the colonization and utilization of specific resources in the environment. Such

successions of saprotrophic fungi are related to the relative abilities of each functional group of fungi to produce the appropriate degradative enzymes (Frankland, 1992). The competition among fungi is thought here to be mainly caused by resource competition. In a similar way, there have been suggestions of successions of ectomycorrhizae on trees during growth of the forest (Dighton et al., 1986; Jumpponen et al., 1999; 2002) as resources in the ecosystem change in relation to the functional properties of the mycorrhizal community. How much, however, do these assemblages exist due to (1) competition (leads to the dominance of the individual), or (2) synergism and mutualism (leads to cooperation and a true community)? We are aware that some bacterial communities around ectomycorrhizal roots have the ability to solubilize phosphates (Leyval and Berthelin, 1983) and facilitate the development of mycorrhizal associations as "helper bacteria" (Garbaye, 1994). How much have these synergistic associations evolved over time? At present we are quite ignorant of the close interactions among fungi and many other organisms in the ecosystem. Indeed, we think of fungal communities as being derived from competition events between individual species. How much are these species assemblages acting in synergism?

Within these fungal communities it is likely that there is overlap in function among different fungal species. The concept of functional redundancy has been explored to some degree in bacterial communities, but we have little idea of how important this concept may be to fungal communities. Ekschmitt and Griffiths (1998) show that the increase in diversity of soil biota can enhance synchronization of processes in the decomposition cycle and that the effect of species richness is more likely to be seen at larger spatial scales. In the same way, de Ruiter et al. (1998) suggest that the greater levels of diversity in soil ecosystems increases both the rate of energy flow through the system and the stability of the system. For example, why is it that we have hundreds of different ectomycorrhizal fungi that may associate with one tree species, whereas the number of fungal species per plant species is very much less in the arbuscular mycorrhizal association (Smith and Read, 1997)? Along with the concept of functional redundancy is the possibility of some organisms being "keystone" species (Paine, 1966). Are there examples of fungi acting as keystone species, in which their absence in the ecosystem leads to a significant decline in ecosystem properties? There are examples in which the presence of a single species of fungus, usually a plant pathogen, may have significant effects on ecosystem processes. See, for example, the effects of chestnut blight, oak decline, and Dutch elm disease cited in Chap. 3 (Anangostakis, 1987; Brasier, 1996). Most of these examples come from the effects of exotics, however, and not from native plants fungal interactions, initiating great concern regarding the worldwide movement of plants and micro-organisms on the future of our landscapes (Rossman, 2001; Brasier, 2001).

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7.5 PERTURBATIONS

One of the ways in which we can understand the functioning of ecosystems, the processes that occur within them, and particularly the feedback mechanisms that regulate processes and maintain stability is to "kick" the system. By effecting a perturbation, it is possible to see and measure the processes that are active in returning the system to stability or moving the system to a different state of equilibrium. One way in which to gain insight into the role of fungi in ecosystem processes is thus to investigate fungal communities and their function in disturbed ecosystem. In Chap. 6, I have thus selected a few examples of perturbed ecosystems, particularly in relation to pollution and climate change. We find that in these altered ecosystems, fungi are often as much affected by the disturbing influence as other organisms, but there are examples in which the physiological plasticity of fungi allow them not only to persist, but to play a major role in returning the ecosystem back to balance. For example, in the presence of heavy metal pollution, we have seen that some fungi are capable of immobilizing planttoxic heavy metals into fungal biomass (Byrne et al., 1979; 1997). In the mycorrhizal condition, this detoxification can ameliorate soil conditions to allow plants to grow where they would not be able to without the fungal intervention (Marx, 1975; 1980; Denny and Wilkins, 1987; Denny and Ridge, 1995; Leyval et al., 1997). Saprotrophic fungi are capable of changing the chemical state of some heavy metals to make them more or less toxic to other organisms in the ecosystem (Byrne, 1995; Slejkovec et al., 1997; Morley et al., 1996; Fischer et al., 1995).

The fact that fungi are capable of surviving and, indeed, thriving in extreme environments is an indication of their potential to withstand stresses imposed by perturbation in the environmental. For example, fungi have been found to grow in the most oligotrophic of environments (Wainwright et al., 1997; Bergero et al., 1999), and are being cultured from the walls of the former reactor room of the Chernobyl nuclear power plant some 13 years after the explosion. Levels of radiation have been significantly elevated here (Zhdanova et al., 2000; Zhdanova, (2002) pers. comm.). The effect of a stress on fungi may manifest itself as a change in species composition of the community (Zhdanova et al., 1995; Fritze et al., 1989; Brandrud 1995; Jonsson, 1998; Lilleskov et al., 2002) or a change in the physiology and activity of the fungi (Rühling and Tylor, 1991; Arnebrant, 1994; Blaudez, et al. 2000). Another effect of a stressor on fungi, however, is to increase its tolerance and persistence if the fungus can adapt to this stressor. These stress-tolerant (S strategist fungi of Grime, 1979) may add stability to the ecosystem. For example, in desert conditions, fungal mycelium is able to more readily respond to water than bacterial populations. As fungal mycelia are perpetual in soil, they can readily take up water when available and put their physiological functions into action. Bacterial populations, on the other hand, need to grow to a critical

abundance before the effect of the physiological process of each organism can make an impact on the ecosystem. It is the presence of fungal mycelia in dry soils that improves the stability of these stressed ecosystems and allows them to respond rapidly to pulsed improvements of edaphic conditions (Zak, 1993; Zak et al., 1995). In what other ways can the sustained presence of fungal mycelia in the ecosystem help in maintaining ecosystem stability?

7.6 FUNGI IN ECOSYSTEM PROCESSES: WHAT NEXT?

We have seen that we need further understanding of the physiology and function of individual species of fungi. We have seen too that although we are developing tools for the rapid identification of fungal species, we need to be able to do this in mixed-species assemblages in a quantitative, as well as a qualitative, way. By combining the two pieces of information, we will be able to get an idea of the ecological function of fungi. The measurements we make on the individual organism will usually be in controlled and artificial conditions, however. The fungus will not be in a state of interaction with other fungi or other organisms that would usually be found in the same ecosystem, thus there is a need for the integration of research between levels of scale form that of the individual hyphum (at the micrometer to millimeter scale), through the individual at the mycelial scale (millimeters to meters), to the individual and community at the scale of tens of meters, to a landscape level. In order to achieve this objective the researcher needs to adopt tools of the ecologists by using a combination of top-down and bottom-up approaches. Increasing the level of complexity of a system by moving form the petri plate (microcosm) through mesocosms (Odum, 1984), a greater understanding of the function of the community can be achieved than that gained form a study of either the intact ecosystem or a single component studied in isolation.

The development of in situ methods, such as fluorescent and molecular markers and radiotracer and natural abundance isotope methods, allows us to locate and measure functional attributes of organisms, both in the environment and in artificially created facsimiles of ecosystems. How can molecular techniques help us to understand the role of fungi in the support of plant and animal populations and communities (Ruess et al., 2002)? The judicial use of these methods, along with careful observation and design of experiments, is necessary to further the science of fungal ecophysiology. Specific, broad-based questions that need to be addressed are as follows:

What are the relationships between fungal diversity and ecosystem function? Based on the fact that there may be 1.5 million fungal species in the world, how much do we really know about the physiology and

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function of these organisms as species? Much of our knowledge base on fungal physiology is constructed from studies of a very few fungal species, which are either highly amenable to laboratory culture or are of economic significance.

What methods can we devise to culture those fungi, which we have not been able to before? Do these fungal species have particular traits that we do not see in other fungi that can be readily cultured? Many fungal species have yet to be brought into culture, where we can study their physiology. We can only guess at their function, but assume that they must possess attributes that are different from other species that are readily amenable to culture. What are these specific traits and how important are they in modulating ecosystem function?

Is there functional redundancy in fungal communities? This question obviously relates to the two above, but has implications regarding pollution, climate change, and other perturbations. How much of our fungal diversity can we afford to lose without compromising ecosystem functioning? Evidence from Europe suggests that pollution is significantly reducing the diversity and abundance of mycorrhizal fungi. How serious is this?

Do these concepts, as developed by plant and animal ecologists, hold true for a nondiscrete, clonal organism such as a fungus? There is relatively little literature on the behavior of clonal organisms compared to that of discrete organisms. Many of the concepts and theories of ecology are based on the observations of discrete organisms. How much do fungi follow the ecological rules already set out? How much do we misinterpret fungal behavior and activity because fungi do not follow these rules?

What is the ratio between competitive and synergistic interactions among fungi in the environment? Do fungal communities follow the pattern of competitive interactions for their sustainability, as we previously assumed plant communities did? Our understanding of ecosystems and community interactions is largely based on the premise that there is competition among species for resources in the environment. In particular, fungi are a group of organisms that form close or intimate associations with other organisms (mycorrhizae, endophytes, termite gardens, etc.). How much have synergistic relationships in ecosystems been overlooked? What are the real interactions among fungi and other biotic components of the ecosystem? It is thought that there is a continuum of plant–fungal interactions between mutualism and symbiosis at one end and pathogenicity at the other. Is this true? What factors alter the balance and lead to a trajectory of evolution of the relationship toward one extreme or another?

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Mutualistic interactions, such as mycorrhizal symbioses, may not show significant benefit to either partner. How much of this is an artefact of sampling and methodology and how much is a function of temporal change in the strength of the interaction? This is a subject for which some of the new methodologies can become important. The use of natural abundance isotope ratios, molecular markers, radioactive tracers, and in situ microanalysis methods will allow us to measure the flux of energy and nutrients in the ecosystem rather that having to rely on results from contrived experimental conditions. In the future we should thus be able to rationalize the differences that we see in the behavior of ecosystem components in laboratory experiments and our actual observations of the interactions among fungi and other ecosystem components in the real world.

How important is heterogeneity in space and time a factor influencing the expression of a function of fungi? Spatial and temporal heterogeneity and the differences in scale between that at which an individual fungal hyphum and the ecosystem as a whole operates lead to great problems in relating observed fungal activity and its consequences for ecosystem processes. This is a question I have raised frequently during the discussions above and I believe it is central to our abilities to accurately model the role of fungi in the ecosystem.

In many of my mycology classes at Rutgers University, I try to leave the students with the concept that "fungi rule the world." I say this with tongue in cheek, but I firmly believe the comments of Rayner (1992) that fungi are important in many if not most of the processes in terrestrial ecosystems. Their importance in aquatic and marine ecosystems is perhaps less strong, but I do not believe that these ecosystems have been thoroughly studied from a fungal perspective.

I hope that each chapter in this book has suggested some of the ways in which fungi are important, either as fungi alone or in their multifarious interactions with other organisms, in the processes of establishing soils and soil nutrients, allowing plants to grow, and modifying the rates of primary production by making nutrients and water available through decomposition and mycorrhizae. The negative effects of fungi on primary production are seen through regulation by plant-pathogenic fungi. Fungi are a food for animals. As such, they directly affect secondary production in ecosystems. Indirectly, they alter the quality and quantity of plant food available to herbivores. They directly influence secondary productivity by acting as pathogens of both vertebrates and invertebrates, and in so doing, they regulate the populations of animals. This, and the regulation of plant-pathogenic fungi by other fungal species, has led to a new science of biological control, which is starting to be applied to agricultural pests.

By altering plant and animal abundance and fitness, we have seen that fungi play a role in regulating community structure. Specially introduced plant-pathogenic fungi can have a highly significant impact on the landscape by altering competition among plant species. As perennial organisms, fungi are able to connect patches of different resources in the ecosystem and effect translocation of nutrients and energy among ecosystem components. This smoothing of environmental heterogeneity and connectivity among components allows fungi to be effective in imparting stability to the ecosystem, thus when we have seen the impacts of pollutants and perturbations on the ecosystem, we not only see an effect of the disturbance on the growth and function of the fungal community, but also an effect of the fungi in remediating the effects of the disturbance factor.

We have come a long way since Harley (1971) gave his opinion on the role of fungi in ecosystems. With the new ecological, physiological, and remote sensing tools that are available to us today, I believe that our understanding of the role of these inconspicuous organisms in ecosystem processes could be enhanced at a more rapid rate than that between 1971 and now. We are aware that fungi do not work alone in the ecosystem, and further understanding of where and how they fit into the complexities of ecosystems will require both bottom-up and top-down approaches. Central to all of these studies will be the ability to model the effects seen at one spatial scale to the scales above and below it. This I see as one of the many challenges before us.

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