5 Fungal Responses to Disturbance: Agriculture and Forestry

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CONTENTS

I. Introduction 65
II. Disturbance as a General Phenomenon 66
III. Fungi as Control Points in Management Practices 66
A. The Habitats of the Fungus 67
B. Effects of Disturbance on Fungi 68
C. Contributions of Fungi to Nutrient Cycling ... 68
D. Contributions of Fungi to Soil Aggregation ... 70
IV. Fungi and Agriculture 71
A. Tillage and Crop Rotation Effects on Fungi ... 71
B. Role of Fungi in Soil Restoration 73
V. Fungi and Forestry 75
A. Nutrient Additions in Forest Systems 75
B. Effects of Air Pollution and Fertilization on Fungi 76
C. Forestry Practices for Pulpwood and Lumber Production 77
D. Effect of Site Preparation on Fungi 77
E. Effects of Woody Debris on Ecosystem Processes 78
F. Effect of Opening the Canopy and Moisture Fluctuations on Fungi 79
VI. Conclusions 79
References 80

Introduction

In a comprehensive review of the effects of disturbance on fungal communities, Zak (1992) identified fungal responses to management practices as a neglected area of research. He pointed out that much of the past research on fungal responses to management practices has been descriptive, being concerned with the composition and richness of fungal species. Furthermore, Zak indicated that this approach contributes little to our understanding of the role of fungi in nutrient cycling and accumulation of organic matter. More recent studies using trophic structure and food-web approaches to understanding the effects of tillage and crop rotation on fungi and associated soil biota appear to be more informative (e.g., Beare et al. 1992; Wardle 1995); for example, by integrating fungal responses with tillage practices, particularly informative linkages of fungi to processes associated with the dynamics of soil organic matter (SOM) have been identified (e.g., Beare et al. 1992; Hendrix et al. 1986). Also, investigations have corroborated the importance of fungi in the hierarchical model of soil structure (Tisdall and Oades 1982; Oades 1984) by demonstrating the structural role of hyphae and the annealing properties of the polysaccharides that they exude to form and maintain a stable aggregate structure (e.g., Gupta and Germida 1988; Chenu 1989; Miller and Jastrow 1990 Cambardella and Elliott 1994).

Although there are many studies concerned with management practices in agriculture and forestry, a neglected area of research is the integration of fungal responses with these practices. especially as the responses relate to nutrient cycling and organic matter accumulation. One reason for this neglect is that plant and fungal responses and disturbance responses associated with land management practices are often studied at different spatial and temporal scales. Nevertheless, from a conceptual viewpoint, fungi do contribute to system processes and functions at various hierarchical organizational levels, indicating linkages and feedbacks between fungi and system responses (O'Neill et al. 1991; Miller and Jastrow 1994; Beare et al. 1995). The difficulty lies in our ability to focus questions and to measure responses or processes that function as control points.

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In this chapter, we will elaborate on the impacts of the various management practices associated with agriculture and forestry as they influence fungal structure and function. Contributions of fungi to nutrient cycling, organic matter accumulation, and the formation of soil structure will be discussed. Furthermore, we will discuss the hierarchical nature of soils and how this nature influences a systems response to disturbance. We will use examples from agroecosystems, soil restorations, and forest systems.

II. Disturbance as a General Phenomenon

Ubiquitous as the idea of "disturbance" is in ecology, it is not easily defined (DeAngelis et al. 1985). Disturbance is a common feature of many systems, occurring at all levels of ecological organization and at numerous temporal and spatial scales (Zak 1992). For our discussion, we mean by disturbance the physical or chemical phenomena that disrupt communities and ecosystems. Disturbances may be either anthropogenic or natural, but it is the biota and the variation in terms of disturbance severity, frequency, and scale that result in different pathways of ecosystem response (rather than being the source of the disturbance) (Waide and Lugo 1992). Some disturbances disrupt the physical structure of communities, such as soil tillage, clearcut harvesting, and storm damage; while other disturbances involve chemical additions, such as acid rain, fertilization, salinization, or addition of biocides. Fungal communities may be directly affected by these physical or chemical disturbances. Fungi also respond to the indirect effects of disturbance, such as the mortality of litter decomposers that results from the increased drying frequency of the forest floor following disturbance to forest canopies.

Fungi that are favored by disturbance generally have ruderal characteristics, including effective dispersal, rapid uptake of nutrients, and rapid extension for resource capture; they may also be stress-tolerant (Pugh and Boddy 1988). In contrast, fungi that are favored by relatively nonstressed undisturbed conditions are often combative or highly competent in competition with other species (Pugh and Boddy 1988). These patterns in fungi are similar to those identified in higher plants (e.g., Grime 1979); however, major differences exist between plants and fungi (Pugh 1980).

Substrates for decomposition can be viewed as discrete or continuous. Fungi of continuous substrates inhabit a niche which continually receives new resources, whereas fungi of discrete substrates inhabit the substrate. In his classical study on ecological groupings of soil fungi, Garrett (1951) states that the succession of fungi on a substrate causes a progressive deterioration in the capacity of the substrate to support further growth. He further states that the substrate comes directly to the soil microorganism, i.e., roots grow through soil and die in it; dead leaves fall upon the soil. The first example views a substrate as discrete, whereas the last example views a substrate as being continuous. Accordingly, disturbance can be a perturbation to both substrate and fungus. For a substrate, disturbance disrupts its delivery rate, its quality and its accessibility, whereas for the fungus, disturbance represents the physical or chemical disruption of the mycelial network.

III. Fungi as Control Points in Management Practices

Other than bacteria, fungi are the most numerically abundant organisms in the terrestrial ecosystem and are the primary decomposers of organic residues in soil. Although fungi may be numerically less abundant than bacteria, fungi can account for as much as 70 to 80% by weight of the soil microbial biomass (Shields et al. 1973; Lynch 1983). These fungi may be free-living or in mycorrhizal associations with plant roots. Studies of agricultural soils indicate that fungal biomass typically outweighs bacterial biomass (Anderson and Domsch 1978; Jenkinson and Ladd 1981; Beare et al. 1992). although studies to the contrary exist (Holland and Coleman 1987; Hunt et al. 1987; Hassink et al. 1993). It has been suggested that the size and composition of microbial communities upon and in soils are primarily controlled by the quality, quantity. and distribution of substrates, all of which are influenced by land management practices (Anderson and Domsch 1985; Schnürer et al. 1985). Differences in fungal; bacterial ratios most likely reflect changes in the composition in response to management effects on the retention of litter and its quality, e.g., fungi typically dominate under no-till conditions (e.g.,

Hendrix et al. 1986; Holland and Coleman 1987; Beare et al. 1992). Furthermore, many of the discrepancies reported in the literature may be explained by where bacteria and fungi tend to live in soil; e.g., a primary reason for fungal biomass being larger than bacterial biomass in surface litter is related to the ability of fungal hyphae to traverse the gap between surface litter and soil more readily than bacteria (Holland and Coleman 1987; Beare et al. 1992).

A. The Habitats of the Fungus

In an attempt to better conceptualize soil systems into biologically relevant regions on the basis of their spatial and temporal heterogeneity, the concept of "sphere of influence" has been proposed (Coleman et al. 1994; Beare et al. 1995). Figure 1 presents the five areas of concentrated activity in soils; the areas include: (1) the detritusphere, composed of the litter, fermentation, and humification layers above the soil surface, which have considerable root, mycorrhizal, and saprophytic fungal activity, and grazing by the soil fauna; (2) the drilosphere, or that portion of the soil that is influenced by the activities of earthworms and their casts; (3) the porosphere. which is a region of water films occupied by bacteria, protozoa. and nematodes and of channels between aggregates occupied by microarthropod and the aerial hyphae of fungi; (4) the aggregatusphere, the region where the activity of microbes and fauna is concentrated in the voids between microaggregates and even macroaggregates; and (5) the rhizosphere, or the zone of soil influenced by roots. associated mycorrhizal hyphae, and their products. The spheres are formed and maintained by biological influences that operate at different spatial and temporal scales. Moreover, each sphere has distinct properties that regulate interactions among organisms and the biogeochemical proper-

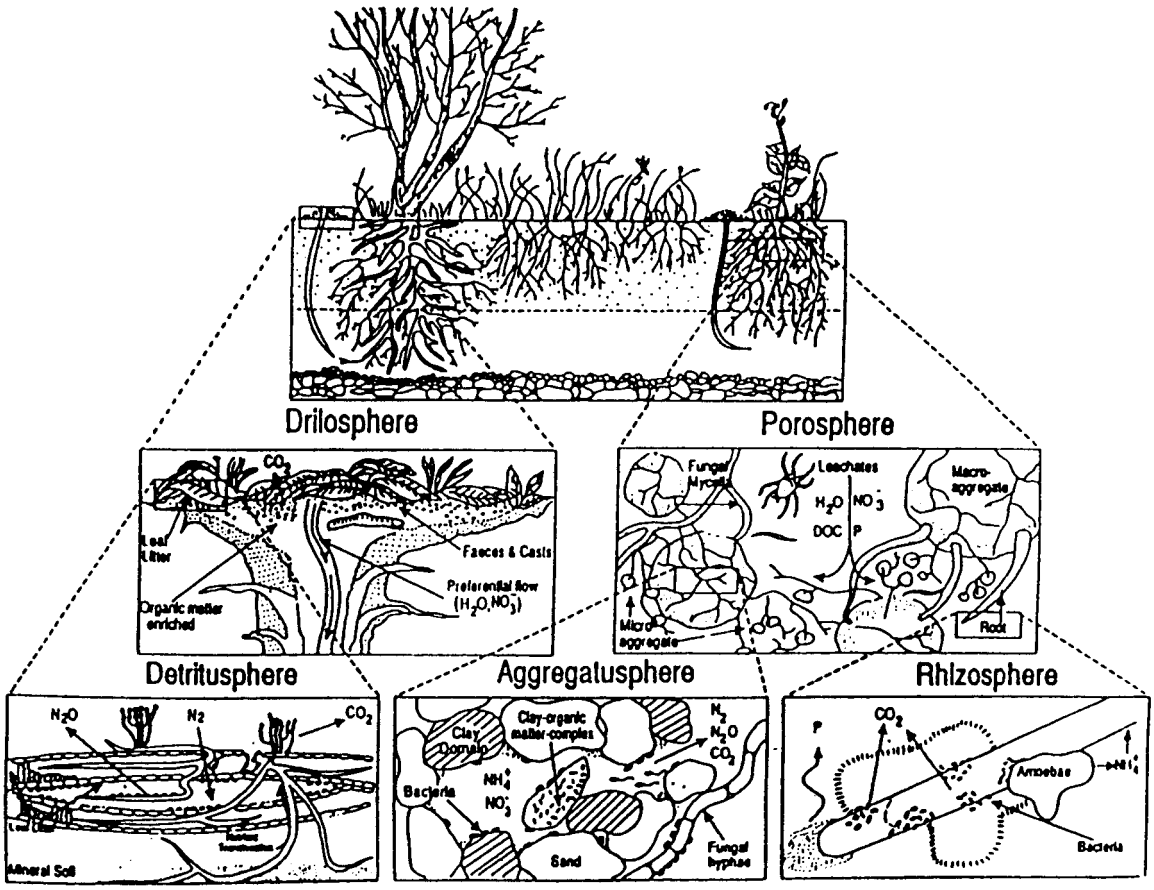

Fig. 1. A hierarchical view of spheres of influence in soil as related to structure and function. (Beare et al. 1995)

ties that they mediate (Coleman et al. 1994; Beare et al. 1995).

B. Effects of Disturbance on Fungi

Soils are spatially heterogeneous because of their biologically mediated properties (Beare et al. 1995). A driving force for creating a spatially heterogeneous environment is the process of bioturbation (Hole 1982). These biologically mediated disturbances result in creation of a spatially heterogeneous environment, an outcome to system processes very different from the disturbances associated with land management practices, such as tillage or clearcut harvesting, that usually result in a loss of spatial heterogeneity.

For example, in the drilosphere, the grazing activities of microarthropods and millipedes change the size and distribution of litter on the soil surface, thereby increasing the surface area for fungal colonization and mixing the fragments with other debris (Beare et al. 1995). Macrofauna redistribute the litter in and upon the soil, creating a patchwork of both substrates and refugia for soil fungi, bacteria, and fauna (Lee and Pankhurst 1992). In the porosphere, the physical rearrangement of soil particles by growing roots and earthworm burrowing creates macropores that influence the preferential flow of water and nutrients. In the aggregatusphere and detritusphere, the relationship between soil organisms and bioturbation is considerable. A large amount of faunal feeding occurs on surface litter and associated fungal hyphae, resulting in the accumulation of particulate and fecal aggregates in surface soils. Earthworm casts also accumulate in the surface soils; however, the primary agent of aggregate stabilization is through the deposition of bacterial and fungal polysaccharides and by hyphal entanglement of particles. The continued inputs of microbial gums and glues, as well as fungal hyphae, are required for the long-term maintenance of the aggregate structure.

Conventional practices of land management usually result in a loss of the spatial heterogeneity of soil. With more sustainable practices, the goal of management is to create a more spatially heterogeneous habitat; e.g., tillage results in the physical disruption of the more transient fungal hyphal network. Furthermore, tillage mixes surface residues vertically within the soil profile while usually doing little direct damage to the aggregate structure (Angers et al. 1992); however, without the physical continuity of the hyphal network in place, the rewetting of dried aggregates will cause their disruption or slaking. Another phenomenon associated with plowing is a temporary flush in mineralization, which appears to be directly related to the exposure of organic residues to soil biota as a result of slaking (e.g., Elliott and Coleman 1988; Van Veen and Kuikman 1990). Some of the nutrient flush is attributed to disruption of the hyphal network (D.J. Lodge, unpubl. data). The amount of nutrient flush depends on (1) the overall amount of organic matter in the soil, (2) the quality of organic residues sequestered within the aggregated portion of the soil, and (3) the amount of microbial biomass and its activity.

C. Contributions of Fungi to Nutrient Cycling

In agricultural and forest ecosystems the primary role of saprophytic fungi is as contributors to nutrient cycling and soil organic matter (SOM) dynamics: SOM dynamics are influenced by saprophytic fungi through their regulation of the decomposition of plant residue (Swift et al. 1979; Beare et al. 1992), the production of polysaccharides (Chenu 1989), and the stabilization of soil aggregates (Van Veen and Kuikman 1990). Fungi are especially good decomposers of nutrient-poor plant polymers. Furthermore, saprophytic fungi possess several growth habits that enable them to grow in nitrogen-deficient environments (Paustian and Schnürer 1987). These habits include (1) lysis and reassimilation of nitrogen from degenerated hyphae (Levi et al. 1968). (2) directed growth to locally enriched nutrient sites (Levi and Cowling 1969; St. John et al. 1983; Boddy 1993), and (3) the translocation of cytoplasm to hyphal apices from mycelium in nitrogen-depleted regions (Cooke and Rayner 1984). Fungal hyphae may also translocate mineral nitrogen to nitrogen-poor substrates. Evidence for such translocation is indirect. The most convincing evidence comes from the observation that the absolute amount of nitrogen in a decomposing substrate increases during the early stages of decomposition (Berg and Söderström 1979 Aber and Melillo 1982; Holland and Coleman 1987). Also, the lateral and upward movement of ^{15}N-labeled inorganic nitrogen from

mineral soil to decomposing litter has been demonstrated (Schimel and Firestone 1989). Furthermore, the net immobilization of nitrogen in surface litter can be relieved by the application of fungicide (Beare et al. 1992).

Fungal biomass represents a significant pool of available nutrients in soils. The turnover of this component has important consequences for SOM and nutrient cycling. The availability of hyphal components and cell products in the form of cell walls, cytoplasm, and extracellular polysaccharides represents a relatively labile organic pool in soils. Anderson and Domsch (1980) have estimated from a survey of arable soils that the biomass of the microflora in agricultural soils has about 108 and 83 $kgha^{-1}$ of nitrogen and phosphorus, respectively. Hence, along with bacteria, fungal hyphae represent a major sink for plant nutrients.

The mycorrhizal fungus represents a considerable portion of the fungal biomass in most terrestrial ecosystems. The importance of mycorrhizal fungi in nutrient cycling is that, as symbionts, they provide a direct physical link between primary producers and decomposers. Processes influenced by mycorrhizal fungi include such host functions as phytosynthesis, nutrient uptake, and water usage. Mycorrhizal fungal influences on host functions can affect nutrient accumulation and alter nutrient ratios in plant tissues. In addition, mycorrhizae can affect plant nutrient uptake by affecting a host's growth rate and by influencing mineral ion uptake (Barea 1991; Marschner and Dell 1994).

It has been suggested that a fundamental role for arbuscular mycorrhizal (AM) fungal hyphae is to bridge the annular space within soil, producing a physical connection between the root surface and surrounding soil particles (Miller 1987). In creating such bridges, the hyphae increase the effective surface area of the root and decrease resistance to water flow to the root surface by allowing closer contact with the soil. This physical relationship between the root surface, hyphae, and soil matrix could be especially important to plants growing in soils of high conductive resistance or where drought is commonplace, and would also allow continued uptake of nutrients from the soil solution during a drought cycle.

The contributions of externally produced AM hyphae to nutrient cycling are considerable (Miller and Jastrow 1994). Although studies of below ground carbon allocation are few, they indicate that external AM hyphae represent approximately 26% of the labeled extraradical organic carbon pool (Jakobsen and Rosendahl 1990). Annual production of external hyphae in prairie soils is estimated to be 28 m cm^{-3} of soil, with a calculated annual hyphal turnover of 26% (Miller et al. 1995). Turnover rates appear to be faster for extraradical hyphae than for intraradical hyphae of roots (Hamel et al. 1990). This may be true for the relatively thin-walled, small-diameter hyphae; but a substantial portion of the AM hyphal network is composed of thick-walled runner or arterial hyphae (Friese and Allen 1991; Read 1992). These runner hyphae are likely to be longer lived and more recalcitrant than the thinner walled hyphae that are probably directly involved in nutrient acquisition. Also, a considerable proportion of the hyphae extracted from soil is either nonviable or highly vacuolated (Schubert et al. 1987; Sylvia 1988; Hamel et al. 1990), suggesting considerable persistence for these hyphae. Because hyphal cell walls also contain chitin, they may be a relatively passive source of nitrogen.

Although the amount of external mycorrhizal hyphae is probably an important factor in nutrient ion uptake, the positioning of the hyphae around the root and into the soil may be equally important; e.g., just as root architecture influences nutrient scavenging (Fitter 1985), the architecture of the external hyphae may also affect nutrient uptake (Read 1992). Furthermore, the reported differences in phosphorus uptake among isolates of AM fungi were independent of the amount of external hyphae produced, with the differences apparently related to the placement of hyphae in the surrounding soil (Abbott and Robson 1985; Jakobsen et al. 1992).

The external hyphae of AM fungi can also influence nutrient cycling within the rhizosphere by influencing soil pH and by producing organic acids. The usual explanation for the elevated phosphorus levels found in shoots of mycorrhizal plants is the increased surface area provided by the external hyphae associated with their root systems; however, it now appears that, like roots, hyphae apparently can form zones of phosphorus depletion and altered pH in the surrounding soil (Li et al. 1991). Acidification of the surrounding soil is believed to be a mechanism for enhancing the mobility of calcium-bound phosphates and possibly trace nutrients. In addition to proton extrusion, the production of low-molecular-weight organic acids by external hyphae may be a mecha-

nism behind soil acidification and increased phosphorus uptake (Li et al. 1991; Paris et al. 1995).

D. Contributions of Fungi to Soil Aggregation

An important component of a successful soil management strategy is the creation and maintenance of the soil aggregate structure (Miller and Jastrow 1992 b). The degree to which a soil has been degraded will determine the extent of formation versus maintenance of aggregates. The importance of aggregated soils in soil management comes not only from the role of aggregates in controlling soil erosion, but also because aggregates facilitate the maintenance of nutrient cycles. In arable systems, the nutrient reserve of a soil typically is maintained by inputs from crop residues and fertilizers. In grassland and forest systems, the nutrient reserve is typically maintained by inputs from litter. In temperate forest systems, litter accumulates mainly from leaf fall, while root turnover is more important in grasslands and the few tropical forests that have been studied. Unless organic inputs are protected within the soil aggregate structure, the accumulation of organic matter and the concomitant buildup of soil nutrients is usually minimal (Elliott and Coleman 1988). Without the physical protection afforded within stable aggregates. organic matter and associated nutrients may be rapidly lost via both mineralization and erosion (Elliott 1986; Beare et al. 1994a).

The binding substances that hold soil particles together have both mineral and organic origins. In soils where organic matter is the major binding agent, several types of substances contribute to creating stable soil aggregates. Inorganic and relatively persistent organic binding agents are important for the stabilization of microaggregates (<250µm diameter), but microaggregates subsequently are bound together into macroaggregates (>250µm diameter) by a variety of primary organic mechanisms (Tisdall and Oades 1982; Oades 1984). The hyphae of both mycorrhizal and saprophytic fungi, along with fibrous roots, bind soil particles and microaggregates into larger aggregated units (Gupta and Germida 1988; Miller and Jastrow 1990, 1992b; Tisdall 1991, 1994). Polysaccharides produced by bacteria, fungi, and roots can act as the gums and glues that bind and stabilize aggregates (Tisdall and Oades 1982; Oades 1984; Foster 1994). The breakdown products of plant residues resulting from the actions of bacteria and fungi are also important in contributing to the formation of soil aggregates (Elliott and Papendick 1986; Beare et al. 1994b; Cambardella and Elliott 1994).

The contribution of AM hyphae to the formation of soil aggregates is believed to be primarily due to a mechanism of physical entanglement. In this mechanism, hyphae enmesh microaggregates to create larger aggregated units. Furthermore, this mechanism can occur at higher levels of organization, whereby small macroaggregate units are packaged together to form larger macroaggregates (Miller and Jastrow 1992b). The relative importance of the various kinds of intermicroaggregate binding agents associated with the stabilization of macroaggregates may differ depending upon whether the soil region is rhizosphere, aggregatusphere, or detritusphere (Fig. 1). Several studies have demonstrated that polysaccharides and other organic compounds serve as the most important intermicroaggregate binding agents (e.g., Sparling and Cheshire 1985; Elliott 1986; Cambardella and Elliott 1994). Although other studies have suggested that polysaccharides and other organic materials function as persistent binding agents for microaggregates (Tisdall and Oades 1982; Oades 1984). the contribution of organic materials in stabilizing macroaggregates appears to be transient. The contribution of polysaccharides as binding agents may be more important in both detritusphere and aggregatusphere soils, where the saprophytic fungi are most active; while mycorrhizal hyphae may be more important in both the aggregatusphere and porosphere soils.

Visual evidence suggests that fungal hyphae are intimately involved in both the physical and chemical binding of soil particles into stable aggregates (Tisdall and Oades 1980; Gupta and Germida 1988; Perry et al. 1989; Oades and Waters 1991; Foster 1994). Additional evidence supports the role of AM hyphae in physical and chemical binding of soil aggregates (Tisdall and Oades 1980; Gupta and Germida 1988; Miller and Jastrow 1990). It appears that a simple hyphal entanglement mechanism apparently contributes to the formation of soil aggregates during an initial aggregative phase. Once they are formed, cementation of fungal hyphae to soil particles by organic or amorphous materials is a mechanism apparently involved in a later stabilization phase (e.g., Gupta and Germida 1988). This formation allows for intense biological activity to occur within these

macroaggregates, and substantial amounts of organic materials are deposited, further stabilizing both the macroaggregates and the microaggregates that comprise them.

Electron microscopy studies further suggest that the decomposition process leads to the development of an aggregate hierarchy (Tiessen and Stewart 1988; Oades and Waters 1991). Particulate organic matter (POM) is often found at the core of microaggregates. where it is protected from rapid decomposition by encrustation with inorganic material. POM is now being recognized as an important pool of SOM and in some systems may represent up to 36% of the whole soil C regardless of tillage (Beare et al. 1994a). Originating as debris from roots, hyphae, and fecal matter, POM becomes incorporated into macroaggregates by physical and biological mechanisms (Coleman et al. 1994). This POM is eventually decomposed, leaving cavities surrounded by smaller microaggregates believed to be stabilized by the metabolic products and bodies of microbes that used the POM as a substrate (Oades and Waters 1991). Indirect evidence for the physical protection of SOM in both macro- and microaggregates comes from observations of increased mineralization when intact aggregates are disrupted (Elliott 1986; Gregorich et al. 1989; Beare et al. 1994a).

Very little information exists on the contributions of ectomycorrhizal fungi to soil aggregation. It has been suggested that ectomycorrhizal hyphae may create a very stable soil structure by producing stronger bonds with clays than do other hyphal types (Emerson et al. 1986). What is known is that ectomycorrhizal hyphae have the ability to extend considerable distances into the soil; exude polysaccharides and organic acids; and enmesh soil particles between them (Skinner and Bowen 1974; Foster 1981). Furthermore, the release of organic acids by hyphae may be a factor in the dissolution of clays (Leyval and Berthelin 1991).

IV. Fungi and Agriculture

Because of the various management practices used in agroecosystems, fungi experience vastly different disturbance regimes. The impacts of these disturbances are expressed directly and by their effects on food-web structure and function (Hendrix et al. 1986; Paustian et al. 1990; Beare et al. 1992). Under conventional management practices, the activities of the soil biota, including saprophytic and mycorrhizal fungi, have been largely marginalized by the use of agrochemicals, such as fungicides, herbicides, pesticides. and fertilizers, which suppress pests or bypass nutrient cycles; however, with increased societal pressures to reduce the use of agrochemicals and fertilizers, a greater reliance on processes influenced by soil biota, and especially fungi, will increase. Several areas of research with fungi offer promise for reducing the use of agrochemicals and intensive tillage regimes. These areas include the contributions of mycorrhizal fungi in plant production and soil aggregation, the use of fungi as biological agents for control of plant pathogens and insect and nematode pests (not discussed in this chapter), and the management of nutrient cycling through better use of saprophytic processes (Elliott and Coleman 1988; Bethlenfalvay and Linderman 1992; de Leij et al. 1995).

A. Tillage and Crop Rotation Effects on Fungi

Agricultural practices such as tillage, crop rotation, crop residue retention, and fertilizer use all affect the ecological niches available for occupancy by the soil biota. Simply put, an agricultural field is basically an experiment in natural selection where those organisms best adapted to those habitats and niches gradually replace those individuals not so well adapted (Rovira 1994). Of these practices, tillage most disrupts the soil fungal community (Table 1), resulting in a reduction of the soil's macroaggregate structure (e.g., Gupta and Germida 1988). The loss or reduction of this basic structural component of soil results in the destruction of many of the ecological niches suitable for soil fungi and bacteria. The practice of tillage serves many purposes, including preparation of seed bed, mechanical weed control, accelerated mineralization of nutrients from organic matter, and improved water capture and storage in the soil profile (Cook 1992). Unfortunately, tillage also sets the stage for soil erosion and loss of organic matter.

A major control point in conservation tillage is the management of crop residues. In conventional tillage practices, plowing results in the mixing of soil profiles and the burial of crop residues, whereas in no-tillage systems the soil is not plowed and residues are placed on the soil surface as

Table 1. Fungal and microbial properties of soil aggregate size classes from a native grassland soil and adjacent soil subjected to cultivation for 69 years. (Data from Gupta and Germida 1988)

Size class (mm)	Fungi ($10^4 \times$ cfu g^{-1})	Fungal biomass Length ($m\,g^{-1}$)	Fungal biomass Biovolume ($mm^3 g^{-1}$)	Microbial biomass C ($\mu g\,g^{-1}$)	Microbial biomass N ($\mu g\,g^{-1}$)
Native soil					
>1.00	11.7	874	3.74	1538	139
0.50–1.00	9.9	1276	12.89	1862	155
0.25–0.50	19.5	2163	10.85	1463	133
0.10–0.25	9.3	508	2.06	1161	124
<0.10	1.2	511	3.59	1106	124
Cultivated soil					
>1.00	2.8	180	0.98	886	86
0.50–1.00	2.5	166	11.12	946	92
0.25–0.50	6.5	543	3.63	859	90
0.10–0.25	0.5	144	1.70	655	82
<0.10	0.4	66	0.75	645	80

mulch. These differences in soil disturbance and residue placement can influence the composition and activity of the fungal community (Beare et al. 1993). Hendrix et al. (1986) and others (e.g., Beare et al. 1992), using a detritus food-web approach, demonstrated that no-tillage systems favored the fungal component of the soil microflora, resulting in the buildup of fungivorous microarthropods, nematodes, and earthworms. Alternatively, conventional tillage practices favored the bacterial component, resulting in the buildup of a completely different group of organisms by favoring protozoa, bacterivorous nematodes, and enchytraeids. The direct effects of the various tillage practices on fungi are related to physical disruption of the hyphal network and to the mixing of surface residues within the soil profile. Crop residues placed upon the soil surface are colonized predominately by saprophytic and facultatively pathogenic fungi, whereas residues mixed within the soil also have a significant bacterial component.

Tillage and crop rotation practices affect the growth of facultatively pathogenic fungi, e.g., the adoption of conservation tillage practice increases the incidence of foliar disease. This increase would be expected because the survival of foliar pathogens is often dependent on their association with host residues, and the rate of residue decomposition is slower if left on the soil surface (Rothrock 1992). Conservation tillage and cropping practices also influence disease incidence by indirect means; e.g., many grass species can be the primary host of the take-all fungus *Gaeumannomyces graminis* var. *tritici*, a major pathogen of wheat. Hence, when soils are placed into pasture to improve nutrient storage and soil structure, an unanticipated effect caused by the density of the pasture's grass content occurs with resumption of cropping, where a relationship exists between prior grass content and the amount of the take-all pathogen *G. graminis* var. *tritici* in the subsequent wheat crop (Fig. 2).

An association has also been demonstrated between the fungal pathogen *Rhizoctonia solani* and conservation tillage. In this case, tillage practices that conserve crop residues on or near the soil's surface create conditions ideal for the growth of *R. solani.* The relationship is caused by the strong competitive growth capability of *Rhizoctonia* on particulate organic matter (Rovira 1986, 1990). The practice of direct drilling allows for optimal conditions for the proliferation of the fungus. A primary mechanism for control of *Rhizocronia* in conventionally tilled soils is that the plowing breaks up the hyphal network in the soil and either kills portions of the hyphae or breaks the hyphae into less infective units (Neate 1994).

Tillage and crop rotation practices can also influence the AM fungus (Sieverding 1991; Johnson and Pfleger 1992; Abbott and Robson 1994; Kurle and Pfleger 1994). Many studies have demonstrated that past cropping and tillage practices influence the mycorrhizal fungi (e.g., Kruckelmann 1975; McGraw and Hendrix 1984;

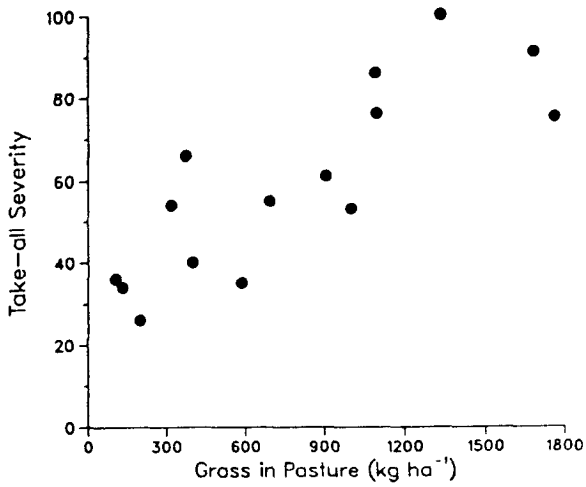

Fig. 2. A significant positive association exists between grass content of pastures and the density of the take-all fungus *Gaeumannomyces graminis* var. *tritici* (r^2= 0.71, P < 0.001). (After MacNish and Nicholas 1987)

Dodd et al. 1990; Johnson et al. 1991; Thompson 1991). Tillage results in maximum disturbance to the fungal propagules and hyphal network, reducing the effectiveness of the symbiosis (Read and Birch 1988). Studies in Ontario demonstrate that a reduction in phosphorus uptake by maize following the plowing of no-tillage soils is caused by the disruption of the AM hyphal network (O'Halloran et al. 1986). This disruption caused both a delay and a reduction in mycorrhizal colonization and subsequently in phosphorus uptake (Evans and Miller 1988). Furthermore, the effect of disturbance was not dependent on the length of time the soil had been under a no-till system (Fairchild and Miller 1990). The use of fallow rotations can also result in the expression of phosphorus deficiency, even though there may be no decrease in available phosphorus (Thompson 1987). The mechanism for the response appears to be caused by a reduction in AM propagules associated with the fallow practice.

Although most crops are dependent upon mycorrhizal fungi, roots of crops belonging to the chenopod and crucifer families usually do not possess mycorrhizal fungi. These two families include such crops as spinach, sugar beet, canola, rapeseed, and mustards. When such crops are used in rotations, they tend to lead to a reduction in mycorrhizal propagules, and appear to act in rotations like a fallow year (Thompson 1991). Hence, the yield of mycorrhiza-dependent crops after a nondependent crop may decline, if the needs of that crop for symbiont-supplied nutrients cannot be fulfilled (Fig. 3).

Cropping and tillage practices can also select for less efficient or even pathogenic mycorrhizal fungi. Rotations with sod crops are necessary to eliminate decline symptoms associated with the proliferation of a certain glomalean fungus when grown with tobacco as the host crop (Modjo and Hendrix 1986; Hendrix et al. 1995). Furthermore, those AM fungi that proliferate under tillage conditions may be less beneficial or even detrimental to those crops in which they proliferate (Johnson et al. 1992).

B. Role of Fungi in Soil Restorations

Depending on the degree of degradation of a soil. an important component of a successful restoration is the reestablishment of a nutrient reserve (Bradshaw et al. 1982). This reserve is initiated by the combination of atmospheric deposition, weathering, and detrital inputs from vegetation or by additions of organic amendments and fertilizers. Unless these organic inputs are stabilized, accrual of organic matter and microbial biomass and the concomitant buildup of nutrient reserves in soils are usually minimal. As described previously, organic residues are generally protected or stabilized within soils through the formation of soil aggregates. Hence, a major goal of any soil restoration should be to establish conditions that favor formation of stable soil macroaggregates, thereby facilitating an important step in the creation of a nutrient reserve (Miller and Jastrow 1992a,b).

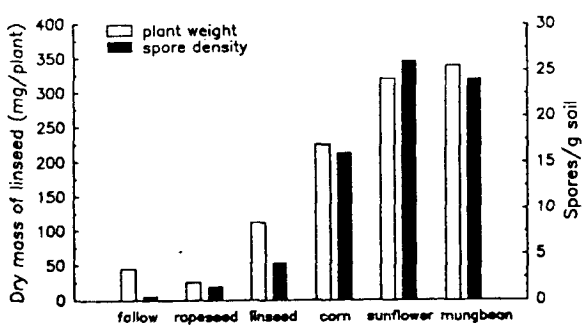

Fig. 3. The effects of a preceding crop on linseed production are related to mycorrhizal spore density. (Data from Thompson 1991)

Mycorrhizal fungal dynamics appear to be a good indicator for determining the consequences of different crop rotations on soil stability. Studies in Australia indicated that 50 years of crop rotation decreased the amount of stable macroagereregates and simultaneously decreased the lengths of roots and AM hyphae in the soil, as compared with soils from long-term pasture and natural sites (Tisdall and Oades 1980). The study found that the positive association between the amount of macroaggregates and the length of external mycorrhizal hyphae was related to the type of crop rotation and the frequency of fallow rotations (Fig. 4). A similar relationship also was found between macroaggregates and root length. This study indicated that frequent use of fallow in crop rotations can significantly decrease the amount of soil held as macroaggregates. Conversely, the longer a soil has a cover crop, the greater the amount of soil held as macroaggregates. The study also suggested that the loss of stable soil macroaggregates associated with fallow rotations may be caused, at least in part, by a reduction in the mycorrhizal fungus population that is brought on by both tillage and fallow disturbances.

Using a series of prairie reconstructions in the central Unitied States as a means of investigating the aggradative phase of a soil indicates that a stable soil aggregate structure can develop rapidly under prairie and pasture vegetation (Jastrow 1987; Miller and Jastrow 1990, 1992 b). The soil studied had been under cultivation for over 100 years; however, within 8 years after being planted to prairie species, the proportions of stable macroaggregates had approached that of a nearby prairie remnant (Jastrow 1987). The rapid recovery of soil aggregates was most likely due to a well-developed microaggregate structure that remained relatively intact during cropping in combination with a rapid reestablishment of a relatively dense root and hyphal network after the cessation of tillage (Miller and Jastrow 1992b). Both total root length and the length of roots colonized by AM fungi increased with time from disturbance (Cook et al. 1988). Furthermore, root and soil hyphal lengths were associated with increases in the proportion of soil held as water-stable macroaggregates (Miller and Jastrow 1990, 1992b).

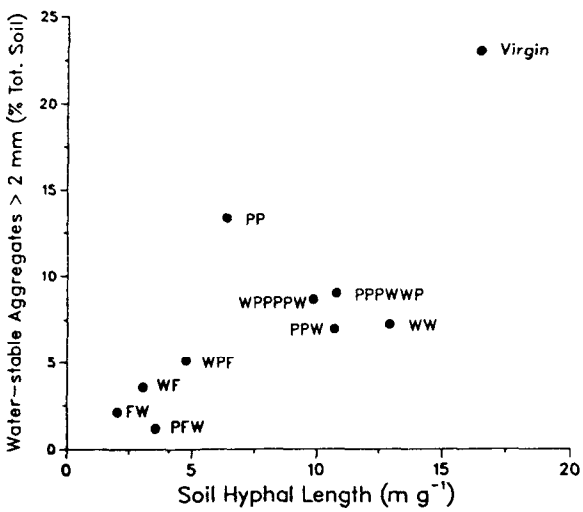

Fig. 4. The relationship between extraradical hyphae and percentage of water-stable aggregates for a soil under different crop rotations *PP* old pasture; *PPW* pasture-pasture-wheat; W wheat every year; *WPF* wheat-pasture-fallow, *PFW* pasture-fallow-wheat; *WF* wheat-fallow, FW fallow-wheat; *PPPWWP* and *WPPPPW 2* years wheat and 4 years pasture. (After Tisdall and Oades 1980)

The observed associations between plant species composition and aggregate formation appear to be related to the diameter size class of roots produced by the various species. The study found that a large portion of the effects of root size class on soil aggregation was due to indirect effects of root associations with mycorrhizal fungi (Miller and Jastrow 1990). Because of the effects of plant life-form on root morphology, some life-forms appear to be more effective than others in promoting aggregate formation. Hence, one of the mechanisms behind plant community composition acting as a control point for organic matter accumulation, and hence nutrient cycling, is based on the relationship between the morphology of the root and mycorrhizal fungi (Miller and Jastrow 1994).

In addition to the changes in hyphal lengths. Miller and Jastrow (1992b) found that the composition of the AM fungal community changed with the cessation of tillage and reconstruction of the prairie. Using spore biovolume as a measure of AM species contributions revealed that soils under conventional tillage practices were dominated by *Glomus constrictum* and *Glomus etuicatum.* However, with the cessation of cultivation, *Gigaspora gigantea* replaced *Glomus* as the dominant fungal group by the fifth growing season (Fig. 5). The spore biovolume of *Glomus* species was negatively associated with recovery time since disturbance, external hyphal length, and percent of soil held as macroaggregates; in contrast, *Gigaspora* was positively associated with extra-

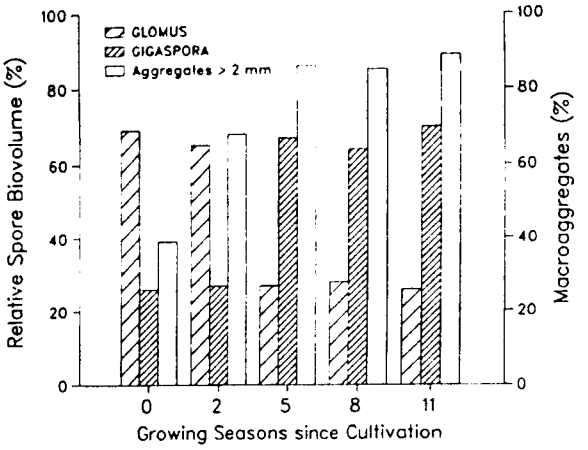

Fig. 5. Relative spore biovolumes of AM fungi and water-stable aggregates (macroaggregates) >2 mm (% of total soil) for row crop and reconstructed prairie soils (n = 10). (After Miller and Jastrow 1992b)

radical hyphal length and macroaggregation. Other investigators have also found *Gigaspora* to be more effective than *Glomus* in producing aggregates (Schreiner and Bethlenfalvay 1995). These trends suggest that AM fungi may differ in their sensitivities to disturbance and in their abilities to produce extraradical hyphae, both of which can influence the development of soil aggregates.

V. Fungi and Forestry

Forests that are managed for recreation, timber, pulpwood, or other forest products differ widely in tree diversity, their dominant mycorrhizal fungal associates, the seral stage that is being managed, climate, seasonality, and decomposability of litterfall. For example, tree plantations and many native temperate and boreal forests are dominated by one or a few tree species, whereas many tropical forests are speciose; a single hectare of lowland Amazonian forest in Ecuador was reported to have over 470 tree species greater than 10cm in diameter at breast height (Valencia et al. 1994). Such underlying differences among forest ecosystems will greatly influence how fungi respend to disturbances related to forestry practices.

A. Nutient Additions in Forest Systems

Fertilization and atmospheric inputs of nitrogen can influence the rate at which fungal decomposers recycle nutrients from organic matter, but such effects may differ among forest types. Rates of leaf decomposition differ among tree species and forest ecosystems, primarily because of limitations on the growth and activity of fungal decomposers imposed by differences in concentrations of mineral nutrients in the fallen leaves, climate, and abundance of lignin and other recalcitrant or toxic secondary plant compounds (e.g., Meentemeyer 1978; Swift et al. 1979; Aber and Melillo 1982; Vogt et al. 1986). Low nitrogen concentrations in fallen litter are often more limiting to nutrient cycling in temperate forests, whereas the availability of phosphorus is often more important in lowland tropical forests (Vitousek and Sanford 1986). although phosphorus concentrations can also be important in temperate coniferous systems (Dyer et al. 1990). Many successional forest trees produce highly decomposable leaf litterfall containing higher concentrations of nutrients and labile carbon and lower concentrations of secondary chemicals than species from later successional stages (Bazzaz 1979; Grime 1979; Marks 1974). Therefore, the effects of episodic fertilization or chronic additions of nitrogen via air pollutants on litter decomposer fungi and the rate of decomposition may depend on the forest species composition and may be correlated with climate.

In a late successional subtropical wet forest in Puerto Rico, complete fertilization accelerated decomposition of fine roots that had very low nutrient concentrations, thus lowering the dead root standing stocks after 9 months (Parrotta and Lodge 1991). Fertilization apparently also accelerated decomposition of leaf litter in the same experiment, as indicated by a higher turnover rate. Production of leaf litter was significantly increased by fertilization, while standing stocks of litter did not differ among treatments at low elevation; litterfall was greater and litter standing stocks lower in fertilized than in control plots at high elevation (Zimmerman et al. 1995).

Despite higher rates of leaf decomposition, certain decomposer fungi were apparently negatively affected by fertilization in the previous study. Superficial and interstitial mycelia of decompose basidiomycetes completely disappeared from the litter layer in fertilized plots, and the diversity and abundance of their fruitifications were also reduced compared with control plots (DJ Lodge, S Cantrell, and O Oscar, unpublished data), suggesting that the fungal decomposer community may have changed in response to repeated

fertilization. Similarly, Heinrich and Wojewoda (1976) found that fertilization of forest plots in Poland significantly decreased the number of fruiting bodies of basidiomycetes that decompose SOM and wood. Shifts in the composition of the fungal decomposer community in response to fertilization may reflect differential sensitivity among species to salt stress (Castillo Cabello et al. 1994) or reduced competitive advantage of fungi that use hyphal cords and rhizomorphs to translocate nutrients into nutrient-depauperate food bases (Boddy 1993; Lodge 1993), The disappearance of cord-forming basidiomycetes may have a negative impact on the ecosystem in terms of loss of SOM and nutrients. Absence of cords formed by basidiomycetes in the litter layer had previously been found to significantly increase the rate of litter export from steep slopes during storms and subsequent soil erosion from the exposed surfaces (Lodge and Asbury 1988). Thus, there may be contrasting responses to fertilization in different ecosystem-level processes that are mediated or influenced by fungi. In standard forestry practices, fertilization generally occurs only at planting or post-thinning at 10 to 15 years (Barrett 1962; Oliver 1986), so negative long-term impacts on litter fungi are probably less than in the experiments cited previously.

Addition of mineral nutrients that are limiting to the growth of fungal decomposers might reasonably be expected to consistently increase the rate of decomposition, but this is not always the case. Although higher nitrogen and phosphorus concentrations were correlated with higher initial rates of decomposition of coniferous litter in Sweden, later decomposition and N-mineralization were inhibited (Berg et al. 1982, 1987). As noted in a review by Berg (1986), later decomposition may be slowed by ammonium and amino acid repression of fungal ligninolytic enzymes and by the completing of nitrogen with phenolic compounds to form particularly recalcitrant products (Nommik and Vahtras 1982; Stevenson 1982). Palm and Sanchez (1990) found that leguminous leaves that naturally contained high concentrations of both nitrogen and polyphenolic compounds decayed more slowly in tropical agroecosystems than predicted from their nitrogen concentrations alone, indicating that the negative interaction between nitrogen and polyphenolics is a widespread phenomenon. Berg and Ekbohm (1991) hypothesized that nitrogen and phosphorus initially stimulate microbial decomposition and nitrogen mineralization, thereby increasing the rate of release of nitrogen compounds that react with aromatic compounds to form resistant residues. Söderström et al. (1983) found that annual fertilization of Scots pine plantations caused slowing of the long-term decomposition rate and a 50% reduction in microbial respiration and abundance in humus. The addition of nitrogen through fertilization or air pollutants may therefore be expected to increase the rate of total decomposition in forests where litter contains low concentrations of both nitrogen and polyphenolic compounds, but may slow complete decomposition in forests where litter contains high concentrations of polyphenolics and low concentrations of nitrogen (Berg and Ekbohm 1991).

B. Effects of Air Pollution and Fertilization on Fungi

The decline in fruiting bodies of ectomycorrhizal fungi in Europe (Derbsch and Schmitt 1987; Termorshuizen and Schaffers 1987; Jakucs 1988; Arnolds 1989; Fellner 1989, 1993; Nauta and Vellinga 1993) has been attributed to direct and indirect effects of air pollution (Arnolds 1991). While ectomycorrhizal fungi have decreased. fruiting by wood decay fungi has increased in central Europe (Fellner 1993). Application of nitrogen fertilizer was found to cause similar declines in the diversity or abundance (or both) of ectomycorrhizal fungal species (Fiedler and Hunger 1963, Heinrich and Wojewoda 1976, Schlechte 1991). Ectomycorrhizal and ericoid mycorrhizal fungi are thought to confer special advantages to plants in the uptake of nitrogen from organic residues in environments in which the availability or uptake of nitrogen is limited (Read 1991). which may help explain why chronic additions of nitrogen from air pollutants are associated with declines in ectomycorrhizal fungi and their associated host trees.

Some fungal responses to air pollution maybe related to soil pH. Bååth et al. (1979) found that active hyphae of soil fungi were decreased by application of artificial acidified rain. Not all ectomycorrhizal fungi have been negatively affected by air pollution. For instance, Fellner (1993) found that certain *Cortinarius* species in the subgenus *Dermocybe* that are favored by acidic conditions were increasing in highly acidified forests. Schlechte (1991) found that moderate

amelioration of soil pH through application of dolomitic limestone had a stabilizing effect on ectotrophic fungal communities in chronically acidified acid forests. However, addition of some forms of lime have been found to adversely affect the abundance or diversity of ectomycorrhizal fungal fruiting bodies (Fiedler and Hunger 1963; Heinrich and Wojcwoda 1976; Hera 1959).

C. Forestry Practices for Pulpwood and Lumber Production

In sustainable pulpwood forestry, monospecific stands are often planted and harvested on short rotations, using tree species from an early seral stage such as pines or other conifers, certain eucalyptus, white birch, aspen and poplars. Such even-aged management practices have been predominant in the United States for pulpwood and lumber since 1950 (Oliver 1986). In such cases, clearcut harvesting, sometimes followed by burning of slash, is often used to regenerate the species. Though such forestry practices are often viewed as severe by environmentalists, these management practices often mimic natural disturbances to which those early seral stage tree species and their associated fungi are adapted (Oliver 1986). For example, some forest types, especially certain pines, are dependent on fire for their establishment and the maintenance of their integrity (Oliver 1986).

D. Effect of Site Preparation on Fungi

The effects of different intensities of site preparation and silvicultural practices on microbial biomass and microbial nutrient stores before replanting of pine were studied in the southeastern United States by Vitousek and Matson (1984). They compared (1) whole-tree versus stem-only harvest; (2) chopping the harvest debris versus shearing and piling of all debris and forest floor into wind rows followed by disking of the mineral soil; and (3) application of herbicide. Vitousek and Matson (1984, 1985) found that microbial nutrient immobilization was effective in preventing leaching losses of nitrogen when the forest floor was left intact (chopping) but not when the forest floor was removed (shearing/piling/disking). Losses of nitrate to streamwater and groundwater via leaching (Berman and Likens 1979; Vitousek and Melillo 1979; Robertson and Tiedje 1984) and atmospheric losses through denitrification occur in forests that have been cleared, but microorganisms in the forest floor and soil immobilize and conserve most of the nitrogen that is mineralized in response to the disturbance (Marks and Berman 1972; Vitousek and Matson 1984, 1985). Large woody debris (slash) and whole-tree harvesting had little effect on microbial immobilization of nitrogen, at least during the short-term study (2 years), but herbicides may have been toxic to microorganisms, thus increasing leaching losses of nitrogen (Vitousek and Matson 1985).

Although burning of coarse woody debris (slash) is considered an appropriate management practice for regeneration of Douglas fir in the Pacific Northwest (Oliver 1986). broadcast burning following clearcuts (Harvey et al. 1980a) and partial cuts (Harvey et al. 1980b) has been found to greatly decrease the abundance of active ectomycorrhizae in the forest floor, and levels of ectomycorrhizal fungal inoculum became insufficient for regeneration if replanting was delayed until the next dry season (July). Broadcast burning has been misapplied to old-growth true fir forests, resulting in mortality of young trees, predisposition of the firs to fungi that decay stems (Oliver 1986), and destruction of the litter fungal community. Highly decayed coarse woody debris is important for maintenance of ectomycorrhizal fungi in the northern Rocky Mountains during the hot dry summers (Harvey et al. 1980a, b). In addition to affording a moist refugium to mycorrhizae during drought, ectomycorrhizal fungi apparently obtain part of their nitrogen from organic sources including rotting wood (Read et al. 1989). Thus removal of coarse woody debris from forests by whole-tree harvesting or burning of woody debris following harvest may have negative effects on ectomycorrhizal fungi and tree nutrition, especially in areas with seasonal drought (Harvey et al. 1980a,b).

Others have also reported that the severity of a particular management activity can affect the persistence of ectomycorrhizal fungi in the northwestern United States (e.g., Perry et al. 1982; Schoenberger and Perry 1982; Amaranthus and Perry 1987), Moreover, studies of younger clearcuts stands indicate that prompt regeneration may be important to secure adequate formation of indigenous fungi; suggesting that mycorrhizal nursery stock may be more useful on older and more severely burned sites (Pilz and Perry 1984).

Studies of site preparation effects on mycorrhizal fungi from tropical forest systems are practically nonexistent. The few studies that have been conducted demonstrate disturbances due to site preparation reduce AM fungal propagule levels and species composition compared to undisturbed forest levels (Alexander et al. 1992; Mason et al. 1992; Wilson et al. 1992). In a Cameroon study, mycorrhizal spore loss appeared to be related to the severity of disturbance, with decreases being greatest in stands with vegetation completely removed. Reduced spore numbers from manually cleared stands were not as severe as those cleared by mechanical methods, and planting of the stands with *Terminalia* seedlings allowed for their recovery, although mycorrhizal species composition remained altered (Mason et al. 1992). Similar findings were made in a *Terminalia* plantation in the Côte d'Ivoire, where, even though site preparation effects on spore numbers were less easily differentiated, manual clearing of vegetation resulted in less spore reduction than did mechanical means (Wilson et al. 1992). Also, spore numbers recovered more rapidly in the manually cleared stand; AM fungal richness increased greatly under both methods of clearcutting, although species balance under manual clearcutting was closer to the undisturbed forest. These studies suggest that selective harvest practices do minimal damage to the mycorrhizal community in that they support extensive mycelial networks, which for natural systems are the primary source of infection for tree seedlings (Alexander et al. 1992). The reduced levels for mycorrhizal roots, hyphae, and spores in heavily logged systems are due to the mortality of root fragments containing mycorrhizal hyphae. Hence, clearing practices that allow for the continued existence of a mycelial network may be preferable ecologically and silviculturally (Table 2).

Table 2. The most probable number (MPN propagules per 100 g fresh soil ± SE) of AM fungi in the top 15 cm of soil for Malaysian forest sites under different logging intensities (n = 5). (Data from Alexander et al. 1992)

	MPN
Undisturbed	307.5 ± 13.8a
Selectively logged	291.2 ± 7.8a
Heavily logged	75.3 ± 2.6b
Heavily logged (eroded)	6.0 ± 1.5c

Values followed by the same letter are not significantly different ($p < 0.05$, Duncan's Multiple Range Test).

Stumps of felled trees, roots in the soil, and other woody residues left from forestry operations often provide essential resources for pathogenic fungi and those that cause root or stem decay (Boyce 1961), e.g., stumps and woody debris have been found to increase mortality from root rots by certain *Armillaria* species in tropical and temperate plantations (Rishbeth 1985; Wargo and Barrington 1991), although raised water tables and shock following thinning and partial cuts may be predisposing factors (Wargo and Barrington 1991). Increased availability of nutrients, especially nitrogen, after logging and fire is known to improve the growth and survival of many root pathogens and to increase the disease incidence (Matson and Boone 1984). In contrast, increased nitrogen mineralization following logging apparently increases the resistance of *Tsuga mertensiana* to laminated root rot caused by *Phellinus weirii* (Matson and Boone 1984). Feeder root rots caused by *Fusarium* and *Phytophthora* species are favored by soil conditions following fire, as well as by increased soil moisture following harvesting.

E. Effects of Woody Debris on Ecosystem Processes

The removal of woody storm debris dramatically affected forest recovery and productivity in Puerto Rico following damage from hurricane Hugo by altering fungal competition for nutrients (Zimmerman et al. 1995). The results of this study are relevant to management of woody debris (slash) following a partial or selective harvest. Plots from which woody debris was removed and those that received complete fertilization recovered their canopies and productivity more rapidly than the control plots (Zimmerman et al. 1995). The massive deposition of organic matter carbon on the forest floor apparently stimulated microbial production and nutrient immobilization, reducing the availability of nutrients to trees in the control plots, whereas fertilization released the trees from nutrient competition with decomposers, predominantly fungi (Lodge et al. 1994; Zimmerman et al. 1995).. However, bole increment growth was greater only in the fertilization treatment, and removal of woody debris is expected to have a longer-term negative impact on forest productivity through its effects on reduced SOM inputs from decomposing wood and consequent lower

phosphorus availability (Sanford et al. 1991). The removal of woody debris following a forest disturbance may therefore have opposing short- and long-term consequence for forest recovery and productivity, so it is the balance of the short- and long-term goals that will determine the appropriate management strategy.

F. Effect of Opening the Canopy and Moisture Fluctuations on Fungi

Opening of a forest canopy by storms or from logging causes dramatic environmental changes on the forest floor. Canopy removal reduces transpiration and is often accompanied by higher soil moistture or raised water tables; however, the litter and humus layers may experience more rapid drying as a result of greater exposure to solar irradiation and wind. Moisture is often cited as a primary factor controlling fungal biomass (Parkinson et al. 1968; Soderstrom 1979; Lodge 1993; Lodge et al. 1994) but temperature can also be important (Flanagan and Van Cleve 1977). Fluctuations in fungal and microbial biomass in response to normal wetting and drying cycles are thought to be important in determining the fate of limiting nutrients and maintaining forest productivity (Lodge et al. 1994). Following a major disturbance, stress tolerance in some fungal species allows them to replace other species that are less tolerant, such as the replacement of *Collybia johnstonii* by marasmioid species of basidiomycete litter decomposers following hurricane Hugo in Puerto Rico (Lodge and Cantrell 1995). Thus, the overall response of fungal biomass to factors such as moisture fluctuations may be more obscure than the responses of individual species and may depend on the severity and scale of the disturbance.

VI. Conclusions

Unfortunately, few examples exist for fungi and their response to management practices used in agriculture and foresty. Nevertheless, this chapter represents the gleaning from a wide variety of sources ranging from decomposition studies, to detrital food-web investigations, to research on soil aggregation, all of which suggest an important role for fungi in managed systems. Moreover, obstacles to identifying the contribution of fungi in managed systems have been just as much methodological as conceptual.

Although our ability to quantify the various fungal components (especially their activities) is still limited, major conceptual breakthroughs have occurred on how we view soils. Two important conceptual advances are the hierarchical theory of soil structure (Tisdall and Oades 1982) and the "spheres of influence" view of soil systems (Coleman et al. 1994; Beare et al. 1995). In both of these conceptual views of soils, the contributions of fungi are considerable. Furthermore, the perturbations imposed by management practices have played an important role in the development of these views. Fungal responses to disturbance offer an opportunity to test these two compelling theories of soil structure and function.

A necessary step in developing sustainable management practices in agriculture and forestry will require identifying practices that allow for controlled manipulations of the fungal community. Nevertheless, our ability to manipulate fungi is rather limited, but such manipulations are not impossible. Research is needed to better understand the response of both the saprophytic hyphae and the mycorrhizal hyphal network to disturbances associated with different management practices. Of crucial importance is the development of management practices that maximize nutrient uptake but are not detrimental to the litter layer and the soil aggregation process. Specifically, research is needed on how disruption of the mycorrhizal hyphal network takes place via tillage and rotation effects in agriculture (e.g., fallow or nonmycorrhizal host crops); and harvesting and site preparation effects in forestry (e.g.. clearcut or slash removal) to the soil aggregate structure. Research also needs to be directed at developing management practices that take advantage of the nutrient pools associated with the fungal hyphae. These kinds of studies would represent important steps in controlling the soil's labile nutrient pools.

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