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Introduction

In the early 1880s, Professor A. B. Frank, a distinguished forest pathologist of the Landwirtschaftlichen Hochschule in Berlin, was commissioned by the Minister Für Landwirtschaft, Domänen und Forsten, to undertake a systematic study to promote the production of truffles in Prussia. Although Frank did not succeed in growing truffles, he described the essential structure and functioning of a symbiotic relationship between trees and fungi that he termed a 'mykorrhiza,' from the Greek meaning 'fungus-root' (Frank, 1885). The association was mutualistic, he stated, because of the covering of the root by the host fungus and the lack of a detrimental response in the host tree. Moreover, the association was widespread, existing on all individuals observed of several tree species across Europe. Earlier morphological descriptions of these root-inhabiting fungi, Frank's observations, and the insights of Kamienski (1882) on the mutualism between *Monotropa* and its fungal associates, initiated interest in mycorrhizae and their importance in plant survival and production.

Despite the observational and experimental evidence demonstrating that intimate biological associations, such as mycorrhizae, are extremely important and widespread (Boucher, 1985), mutualistic symbioses are often considered as biological oddities, relatively unimportant in ecological and evolutionary processes. Williamson's (1972) paradigm, '[mutualism] is a fascinating biological topic, but its importance in populations in general is small' is widely quoted (e.g. May, 1974). Roughgarden, in his introductory population biology text, states that 'most examples [of mutualism] are tropical' (Roughgarden, 1979). May (1981) also states that there are few examples of mutualisms in temperate climates. May (1974, 1981) suggests that mutualism is mathematically unstable and thus there are few natural examples of importance.

Yet mutualism is an extremely ancient phenomenon in the history of

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life. Complex life forms began as symbioses of prokaryotic organisms (Margulis & Bermudes, 1985). The integration of mitochondria into another organism to create eukaryotic, single-celled organisms represents the most dramatic change in the biological world since the beginning of life, making possible the present incredible array of life forms. Other intimate organismal interactions resulted in the improved survival of both species and were responsible for initiating life in many habitats. Lichens, mutualistic associations between algae and fungi, are often the initial colonizers on unweathered geological materials. The ability of lichens to weather rock material chemically and physically provides a foundation of unconsolidated material in which plants can later gain a foothold.

Mycorrhiza, a mutualistic symbiosis between plants and fungi, may be one of the most important and least understood biological associations regulating community and ecosystem functioning (Harley, 1971). However, despite the extensive data base amassed since the late 1800s, few discussions of mycorrhizal dynamics have been incorporated into the general ecological literature at the population, community or ecosystem levels and, when it is mentioned, the association is often dismissed as unimportant. For example, most texts on population interactions omit mycorrhizal associations from discussions of coevolution (e.g. Roughgarden, 1979; Merrell, 1981). Barrett (1983) stated '...there is little evidence of the physiological basis of their association [plant–fungus mutualisms]'. Chapin *et al.* (1987) suggested that 'Mycorrhizal hyphae have small-diameter hyphae that increase the surface area of the root system but cost ten percent more to construct than the equivalent mass of roots,' and omitted any discussion of mycorrhizae in their review of plant nutrition. Vogt *et al.* (1986) described the Stark & Jordan (1978) paper on the importance of mycorrhizal mats in tropical forests as '*root mats*' in those [Amazonian] forests took up dissolved nutrients more efficiently than microbes...' (*italics mine*). Similar statements are commonplace despite the importance of mycorrhizae in such processes as short-circuiting the N-mineralization process in heathlands (e.g. Read, 1983) and the dominant role of mycorrhiza in P nutrition of plants (e.g. Harley, 1971).

deBary (1887) formalized the definitions and differentiated the types of symbioses over a hundred years ago. Symbiosis was simply defined as a state occurring when organisms live in intimate contact. He recognized several types of symbioses including parasitism, commensalism, amensalism, neutralism and mutualism. Symbiotic interactions can be described using +/0/– interactions (Figure 1.1). Although gradients can be seen

		SPECIES 1		
		+	0	—
S P E C I E S 2	+	MUTUALISM	COMMENSALISM	PARASITISM
	0	COMMENSALISM	NEUTRALISM	AMENSALISM
	—	PARASITISM	AMENSALISM	ANTAGONISM

Figure 1.1. Types of symbioses between organisms, derived from deBary (1887).

both evolutionarily (between generations) and in ecological time (within the life of an individual), deBary's definitions provide essential theoretical distinctions.

Although the term mycorrhiza was coined in Frank's 1885 description, the structural and ecological characteristics had been recognized earlier. T. Hartig (1840) clearly illustrated an ectomycorrhiza, and orchid mycorrhizae were described as early as 1851 (see Kelly, 1950). Kamienski described the mutualistic nature of the monotropoid mycorrhiza in 1882 (see the recent translation by S. M. Berch, in Molina, 1985). Frank's (1885) description of a mycorrhiza contains several key elements. These include the mycelial network extending into the substrate as well as the root, and the essential role of the fungus in providing nutrients and water to the plant: '...er funktioniert im Bezug auf diese Ernaehrung als die Amme des Baumes' ('it [the mycorrhiza] functions in a nutrition relationship as a wet-nurse of the tree'). The early work was followed by an explosion of descriptions of mycorrhizal associations and arguments regarding the nature of this symbiosis. An increasing and extensive research effort continues today.

Several criteria can be used to distinguish mycorrhizae from other plant–fungus associations. The mutualistic nature of the interaction is a critical character that differentiates a mycorrhiza from other plant–fungus associations. Although the line between parasitism and mutualism is fine (e.g. Harley & Smith, 1983), and negative interactions between plant and fungus can occur both for given species and as environmental conditions change for any one species (e.g. Bethlenfalvay *et al.*, 1982; Buwulda & Goh, 1982; E. Allen & M. Allen, 1984, 1988), the relationship in a general sense is positive for both symbionts (Lewis, 1973). The structural nature of the relationship also distinguishes a mycorrhiza, despite the wide variety of types (discussed in detail in the next chapter); in this relationship, the fungus extends both into the host plant and into the

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surrounding substrate. Thus, materials move from substrate to host via the fungus. Finally, the relationship is primarily characterized by the flow of inorganic components from fungus to plant and organic components from plant to fungus. Although some experimental data indicate movements in the reverse directions, Lewis (1973) noted that the fungus is heterotrophic and cannot fix significant amounts of carbon, but is structurally and physiologically adapted to move inorganic nutrients (for a detailed discussion on these flows, see Chapter 5). Major exceptions appear to include the protocorm development in orchids (although not necessarily in the mature plant: Alexander *et al.*, 1984; Alexander & Hadley, 1984), and the monotropoid mycorrhizal association in which the fungus may not gain at all (Lewis, 1973). I will use the following definition for my discussion: a mycorrhiza is a mutualistic symbiosis between plant and fungus localized in a root or root-like structure in which energy moves primarily from plant to fungus and inorganic resources move from fungus to plant.

The importance of mycorrhizae is often ascribed simply to the abundance of the association coupled with the perception that if it were not adaptive, the symbiosis would have been selected against. While this argument should not be the sole criterion for importance, the fact of abundance should at least stimulate further interest. Mycorrhizal associations are found in a broad range of habitats. These include ecosystems ranging from aquatic (e.g. Sondergaard & Laegaard, 1977; Bagyaraj *et al.*, 1979) to deserts (e.g. Khudairi, 1969; Williams & Aldon, 1976; Singh & Varma, 1981) and from lowland tropical rain forests (e.g. St John, 1980a; Högborg, 1982; Janos, 1987) to high latitudes (e.g. Malloch & Malloch, 1981, 1982; Christie & Nicolson, 1983; Laursen, 1985), and high altitudes (e.g. Read & Haselwandter, 1981; E. Allen *et al.*, 1987), and in canopy epiphytes (Nadkarni, 1985). Not only are mycorrhizal associations geographically widespread, but within most communities surveyed, mycorrhizae are abundant both within individual root systems and among the array of plant species present. For example, in a semi-arid grassland, all of the dominant plant species had mycorrhizae, and up to 96% of the root length of the dominant species was mycorrhizal (Davidson & Christensen, 1977). In a lowland rain forest, St John (1980a) estimated that about 97% of the 'importance value' of plants represented was mycorrhizal.

Mycorrhizal associations are widespread among plant families and appear to have evolved and spread with the earliest land plants. Stahl (1900) suggested that there are only a few nonmycotrophic families and

his designations are generally accepted today (e.g. Gerdemann, 1968; Trappe, 1981). Recent evidence suggests that these 'nonmycotrophic' groups may have mycorrhizal fungal invasions although the physiological relationships are not always defined (Newman & Reddell, 1987). For example, mycorrhizal activity has been reported in the Chenopodiaceae (Williams & Aldon, 1976; M. Allen, 1983), Brassicaceae (Tommerup, 1984; Glenn *et al.*, 1985), *Juncus* and *Carex* (Davidson & Christensen, 1977; Haselwandter & Read, 1980; Christie & Nicolson, 1983; Mejstrik, 1984; E. Allen *et al.*, 1987), *Equisetum* (Lohman, 1927; Koske *et al.*, 1985), *Isoetes* (Farmer, 1988) and hemiparasites (Alexander & Weber, 1985; Lesica & Antibus, 1986), all purported nonmycorrhizal plants. Evidence from the fossil record demonstrates an early appearance of mycorrhizal fungi in roots (Kidstone & Lang, 1921; Wagner & Taylor, 1981; Berch & Warner, 1985; Stubblefield *et al.*, 1987a). These observations, coupled with hypotheses about early terrestrial environments, led to the proposal that invasion of the land by plants depended in part on the evolution of mycorrhizae (Pirozynski & Malloch, 1975; Pirozynski, 1981), which provided essential acids in the acquisition of phosphorus (Fitter, 1985a). Biogeographical evidence also suggests that many of these associations developed early and moved with the plants (e.g. Horak, 1983; Christie & Nicolson, 1983; Halling & Ovrebo, 1987).

To be mutualistic, a relationship must be beneficial to both participants. Growth improvement by host plants in a mycorrhizal association has been demonstrated in studies dating back to Frank (1894). Because many mycorrhizal fungi cannot be grown in pure culture, the fungal symbiont often is presumed to be dependent upon the host plant. The criterion by which mutualism is determined is not a simple matter in all cases. In an agronomic or forestry sense, improved production is generally used as the criterion by which the benefits of mycorrhizae are judged. However, in an ecological context, improved fitness by both symbionts must be the ultimate criterion for judging mutualism, especially in native plants (see the excellent discussion in Lewis, 1973).

Determining the enhanced fitness or survival value of the association over a long time period is difficult or impossible. For example, the giant redwood, *Sequoiadendron giganteum*, is presumed to approach obligate dependence upon mycorrhizal fungi, but no study has maintained a nonmycorrhizal status to maturity and reproduction in the plant. The significance of mycorrhizae to plants is generally based on improved survival of individuals following transplantation into an exotic environment, biomass increases in experimental systems, or altered

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physiology that can be perceived as an improvement (e.g. increased nutrient uptake or increased drought tolerance). While these approaches are useful, they do not measure fitness. More efforts in this direction are needed.

Numerous studies of the responses of plants transplanted into new habitats have demonstrated the importance of mycorrhizae. Early attempts to establish an exotic forestry industry in Australia, the Caribbean islands, and Rhodesia found that mycorrhizal fungi had to be imported with the plants for those trees to survive (e.g. Kessell, 1927; Anon., 1931; Hatch, 1936; Briscoe, 1959; HacsKaylo, 1967). Work since the 1930s demonstrated that appropriate mycorrhizal fungi were essential to establishing shelterbelts in grasslands. These include studies from the North American grasslands (e.g. Hatch, 1936; White, 1941; Mikola, 1953; Goss, 1960), and the Ukrainian steppes (see Shemakhanova, 1962; Mishustin, 1967). More recently, experimental transplants and artificial inoculation studies on sterile mine spoil indicate that mycorrhizae improve survival and growth of host plants (e.g. Marx, 1975; Aldon, 1975); Carpenter & Allen, 1988). Survival of conifer seedlings beyond one growing season on the sterile pumice material of the Mount St Helens volcano appeared to require mycorrhizae (M. Allen, 1987a). Improved seed numbers and mass, parameters often related to fitness, have been shown with mycorrhizal establishment several times with different plants (e.g. Carling & Brown, 1980; Yocum, 1983; Carpenter & Allen, 1988). The essential roles of mycorrhizae in orchid culture and *Monotropa* survival have been known since the turn of the century (Kamienski, 1882; Bernard, 1909; Bjorkman, 1960).

The ecological importance of the association to the fungi has been more difficult to prove. In general, the fungus has been presumed to be obligately dependent on the plant because many of the fungi are difficult to culture (see Schenck, 1982). A few field studies suggest that the mycorrhizal fungi have improved activity with a host plant present (e.g. Rommell, 1939; Bjorkman, 1944; E. Allen & M. Allen, 1986).

A major limit to our understanding of mycorrhizal ecology resides in our inability to perceive the scale at which the two symbionts interact with each other and their environment. Often the concepts of population, community, ecosystem and landscape are perceived as linearly increasing size units. This perception has led to difficulties in understanding the ecology of the fungus in particular. An individual fungus may 'perceive' only a few cubic centimeters. Thus, the community of organisms with which it directly interacts may focus along a few centimeters of root length

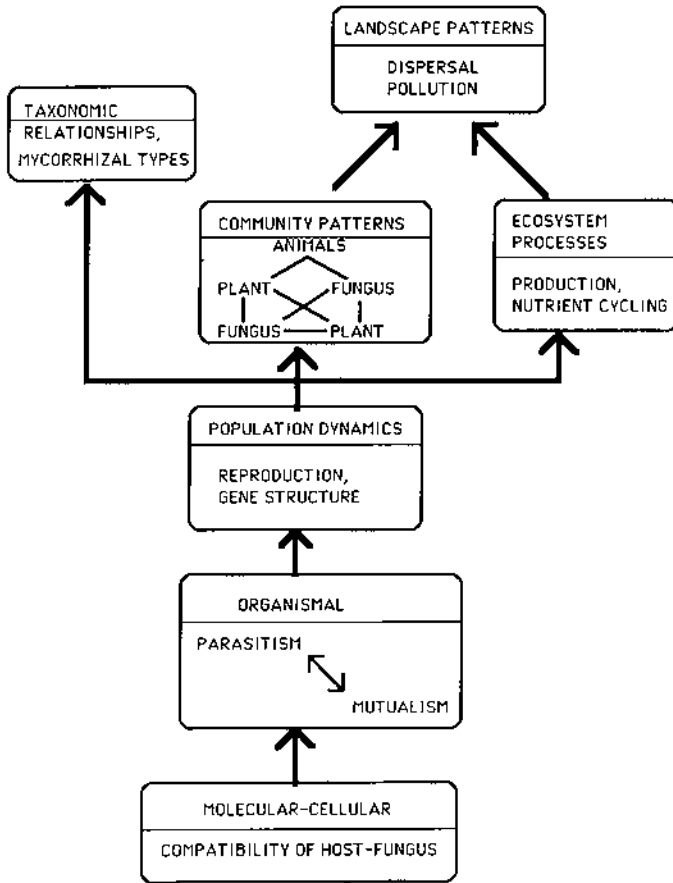


Figure 1.2. Hierarchical approach used to describe the ecology of mycorrhizae. Based on the 'individualist' concept (e.g. MacMahon *et al.*, 1978).

and extend outward only a short distance. In this treatment, I use the hierarchical approach proposed by MacMahon and colleagues (1978) wherein populations, communities and ecosystems are not simply increasing size units but rather are systems that elicit differing types of interactions (see Figure 1.2). With this approach, the relationships of fungus and plant can be distinguished in an ecological, rather than a production agricultural, perspective.

Although the number of mycorrhizasts has increased dramatically in the last few years, the number of research scientists with a basic understanding of mycorrhizae in natural vegetation remains small.

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Ecologists, in particular, have ignored mycorrhizal relationships, and this has often led to major difficulties in interpreting ecological data. For example, concentrating only on vertical rooting structure while ignoring the lateral development of mycorrhizal hyphae can lead to gross errors in measuring the spatial distribution of plant nutrient uptake activity (e.g. Parrish & Bazzaz, 1976). Thus a main goal of this book is to initiate an appreciation of the importance of mycorrhizae within the field of ecology in the hope that future ecologists will incorporate an understanding of this symbiosis in their own research.

2

Structure–functioning relationships

The early descriptions of mycorrhizae were based on the morphology of the fungus–host contact zones, the extramatrical hyphae, and the altered root morphologies associated with the symbiosis. The most important feature of the association appears to be the ability of the extramatrical hyphae to take up and transport resources to the plant from the soil outside depletion zones created by the root itself. Overall, knowledge of the structure of mycorrhizal symbioses can dictate an understanding sufficient both for differentiating among the types and for describing the functioning of the association in general. In this chapter, I describe the types of mycorrhizae and their distribution, the structure of the fungal symbiont and the structure of the plant symbiont, and discuss the relationship of the structures to the functioning of mycorrhizae in their environment.

Types of mycorrhizae and their distribution

An early research focus attempted to describe the types of mycorrhizal associations according to symbiont morphology and host–taxon relationships. This focus continues today and is continually being refined with the use of more advanced techniques, especially electron microscopy. As more observations are made, a greater complexity in structure and an increasing diversity of types is encountered. This suggests that a greater emphasis needs to be placed on structure–functioning relationships with an eye toward integrating processes of interest among types as well as toward documenting definitive characteristics among the types of mycorrhizal associations.

Frank (1887, 1891) distinguished two morphological types of mycorrhizae based on whether the fungus penetrated the root cortical cell walls. (N.B. In no reported case does the fungus penetrate the plasmalemma of the host, a common misconception.) He described the two types as

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endomycorrhizae (penetrating the cell wall) and ectomycorrhizae (no penetration of the cell wall). Other types have been described subsequently, but common practice delineates ecto- (those with the fungus outside the plant cells), ectendo- (those wherein the fungus penetrates the cortical cells but also forms a mantle surrounding the root), and endomycorrhizae (those with hyphae penetrating the cell walls but lacking a mantle). These categories now may be inadequate representations for describing the complex suite of interactions among mycorrhizae.

Wilde *et al.* (1979) and Iyer *et al.* (1980) differentiated endocellular, ectocellular, ectendocellular, and epirhizal mycorrhizal types and suggested that all other descriptions are inadequate. However, these are not really different from the classical groupings except for the addition of the epirhizal form. Harley (1969) discussed in detail the characteristics of a mycorrhiza and noted that there are numerous examples of rhizoplane fungi which might temporarily improve growth. But, as no lasting, coevolutionary relationship could be demonstrated, the rhizoplane fungi (epirhizal) should not be considered as members in mycorrhizal symbioses. The definition of symbiosis (deBary, 1887) clearly implies an intimate, evolutionary relationship, and only when this is shown for rhizoplane fungi, can they properly be referred to as mycorrhizal.

Read (1983) revised the classification system of Lewis (1973) and suggested that mycorrhizal groupings could best be understood in an ecosystem context (Figure 2.1). This system incorporates the types of mycorrhizal associations described to date. In Read's system, the biomes also provide a functioning basis upon which to understand the basic ecology of each relationship. The basic characteristics of the groupings depend upon elevation or latitude gradients, and upon nitrogen and phosphorus availability. As latitude or elevation increases, soils change from mull humus or mineral soil toward a mor soil with a shift from mycorrhizal supply of inorganic nutrients via vesicular-arbuscular (VA) mycorrhizae to the supply of organic nutrients to the host by ericoid mycorrhizae. The ectomycorrhizae are intermediate.

The major limits of Read's distinctions on a biome basis are two-fold. The first takes into consideration the recent work on orchid mycorrhizae by Hadley and colleagues. They demonstrated that in the *Goodyera repens*-*Ceratobasidium cornigerum* system, carbon was transported from fungus to plant only during the protocorm and plantlet stage (Alexander & Hadley, 1985). In the mature plant, the mycorrhiza acts like most other mycorrhizae, transporting phosphorus to the plant with carbon moving from plant to fungus (Alexander *et al.*, 1984). Orchid and 'saprophytic'