ECOSYSTEMATIC FUNCTIONS OF MYCORRHIZAE

James M. Trappe and Robert D. Fogel

USDA Forest Service
Pacific Northwest Forest and Range Experiment Station
Forestry Sciences Laboratory
Corvallis, Oregon 97331

Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331

ABSTRACT

The great majority of vascular plants have evolved to a dependence on mycorrhizae as the most metabolically active parts of their root systems. Most woody plants require mycorrhizae to survive, and most herbaceous plants need them to thrive. Despite their relatively small biomass, the mycorrhizal fungi (mycobionts) are vital for uptake and accumulation of ions from soil and translocation to hosts because of their high metabolic rate and strategically diffuse distribution in the upper soil layers. The mycobionts produce enzymes, auxins, vitamins, cytokinens, and other compounds that increase rootlet size and longevity. They commonly protect rootlets from pathogens. They absorb and translocate water to the host.

Most mycobionts, in turn, depend on their hosts for carbon products. Except for orchid mycobionts, few are capable of decomposing organic matter, although their respiration contributes significantly to evolution of CO_2 from soil. The fungal mycelium and sporocarps are sources of accumulated nutrients and energy for decomposers and consumers. Nutrients and carbon can be translocated from one vascular plant to another by a shared mycorrhizal mycelium.

The several thousand species of fungi believed to form mycorrhizae encompass great physiological diversity. They differ in numerous ways, including degree of host specificity, resistance to environmental extremes, selectivity in ion uptake, and production of biologically active products. Net effects of one mycobiont on a host can differ from those of another, although overall functions are shared by most.

As key links in belowground nutrient and energy cycling, mycorrhizae and their mycobionts can be ignored only at substantial peril of reaching unreal conclusions about ecosystem processes.

INTRODUCTION

In 1842 Vittadini proposed that tree rootlets are nourished by certain fungal mycelia which mantle them, as he had observed more than a decade earlier. This hypothesis was elaborated to a theory of mutualistic symbiosis by Frank (1885), who named the fungus-root organ "mycorrhiza." The concept of fungus-root symbiosis has since been the subject of extensive research, much controversy, hundreds of scientific and review papers, and numerous books (e.g., Kelley 1950, Lobanow 1960, Harley 1969, Hacskaylo 1971, Marks and Kozlowski 1973). Despite this massive documentation plant scientists commonly seem to little heed the phenomenon and its implications unless they are studying mycorrhizae *per se*.

The purpose of this review is to condense contemporary knowledge and hypotheses about mycorrhizae for ecosystematic researchers with emphasis on where and how mycorrhizae function in ecosystems and their processes. The relatively few papers to be cited have been selected as entry points into the larger body of literature.

THE SIGNIFICANCE OF MYCORRHIZAE

In broad terms, mycorrhizae function as a mutualistic, symbiotic biotrophy between a fungus (mycobiont) and a higher plant host (Lewis 1973). Each organism derives physiological and ecological benefits from the other, and each accrues a net gain. Most mycobionts and hosts have evolved to a strong interdependence on their mycorrhizal associates for survival in natural ecosystems (Harley 1969). The obligate nature of this biotrophic habit is strikingly illustrated by failures of attempts to introduce trees by seed to soils lacking appropriate mycobionts (Trappe and Strand 1969, Vozzo and Hacskaylo 1971, Mikola 1973) and by the refusal of many mycobionts to grow in culture in the absence of a suitable host (Gerdemann 1968, Palmer 1971). Even facultatively mycotrophic hosts (generally those with a high root/top ratio) grow markedly better with mycorrhizae than without (Clark 1969, Harley 1969, Khan 1972, Kleinschmidt and Gerdemann 1972).

KINDS OF MYCORRHIZAL ASSOCIATIONS

Species of more than 200 families and 1,000 genera of vascular plants from the tropics to the tundra have been examined for presence of mycorrhizae (Maeda 1954, Gerdemann 1968). Of these, only 14 families are regularly nonmycorrhizal. Occasional mycorrhizal members have been found in at least one of the 14, the Cyperaceae (e.g., Fontana 1963, Mejstřik 1965). Aquatic plants appear to lack mycorrhizae, but so also do roots of terrestrial mycorrhizal species when formed in near-saturated soil (Maeda 1954, Konoe 1962, Mejstřik 1965).

Two major groups of mycorrhizae traditionally have been separated in terms of infection anatomy. One, the endomycorrhizae, is highly artificial, being comprised of diverse categories of fungus-host associations related only in that the mycobiont routinely penetrates host cells to form organs that the host cells digest. Endomycorrhizae are more cogently understood as three major groups: vesicular-arbuscular (VA), by far the most widely distributed form of mycorrhizae; ericaceous; and orchidaceous. Other variants occur but are not well known (Harley 1969, Lewis 1973).

The second major group, the ectomycorrhizae, is reasonably coherent. Ectomycorrhizae are characterized by (1) a mantle of fungal tissue around the host rootlet and (2) penetration of the fungus between cells of the rootlet cortex (the "Hartig net") but not into the cells themselves. In well developed ectomycorrhizae, the Hartig net tissue completely encloses outer cortical cells, separating them one from the other. Morphological variants of seemingly similar function but with intracellular fungal growth have been termed ectendomycorrhizae.

VA mycorrhizae occur on the great majority of vascular plant species and apparently in virtually all terrestrial habitats that support those plants (Gerdemann 1968). The Pteridophyta, Cupressaceae, Taxodiaceae, and most taxa of monocotyledons and dicotyledons characteristically have VA infections. The Salicaceae often form VA mycorrhizae in youth, but older stages are typically ectomycorrhizal in many habitats (Dominik 1958, Fontana 1961). The mycobionts are chlamydosporic and azygosporic species of Endogonaceae (Phycomycetes); some 30 species are now recognized, but many more will undoubtedly be discovered (Gerdemann and Trappe 1974). They do not appear to be host specific, and several species are nearly worldwide in distribution.

Orchidaceous mycorrhizae, as the name implies, are confined to the Orchidales. The restricted occurrence of the orchids renders this mycorrhizal type inconsequential in most temperate and boreal ecosystems, although it is often important in the tropics. Research on these interesting complexes has been a prime source of knowledge about some of the basic aspects of mycotrophy. The mycobionts of orchidaceous mycorrhizae, so far as known, are Basidiomycetes in the Agaricales and Aphyllophorales (Campbell 1970, Furman and Trappe 1971, Warcup and Talbot 1971). Many are able to infect species in several orchid genera (Hadley 1970). In addition to their mycorrhizal role, they are regarded as accomplished saprophytes or pathogens on plants other than orchids (Furman and Trappe 1971).

The wide distribution and diversity of the Ericales lends importance to the ericaceous mycorrhizae. Most members of the order form this characteristic type of mycorrhiza, although some genera (*Arbutus, Arctostaphylos*) form ecto- or ectendomycorrhizae instead (Christoph 1921, Trappe 1964, Zak 1974). Little is known about the mycobionts, although sporocarps of a *Clavaria* sp. (Basidiomycetes) have been serologically related to fungal tissue in the mycorrhiza of *Azalea* sp. (Seviour et al. 1973). The limited evidence available indicates that the mycobionts are not host specific within the Ericales (Nieuwdorp 1969).

Ectomycorrhizae are characteristic of root systems of many woody plant families, including the Betulaceae, Fagaceae, Pinaceae, Tiliaceae, and Salicaceae. Ecto- or ectendomycorrhizae are also formed in some genera of families whose other members form another type of mycorrhizae; for example, the Ericaceae, Leguminosae, Myrtaceae, and Rosaceae (Meyer 1973). The mycobiont species number in the thousands, with representatives in many genera in the higher Basidiomycetes, Ascomycetes, and zygosporic Endogonaceae. Entire genera and even families consist of obligate mycobionts. Many species associate with only a single genus or even subgenus of hosts, while others are nonspecific in this respect (Trappe 1962, 1971; Smith 1971; Chilvers 1973; Gerdemann and Trappe 1974).

DIFFERENCES IN ACTIVITY OF MYCOBIONTS

Differences between mycobiont activities and effects must be recognized in generalizations about ecosystematic functions of mycorrhizae. The great assemblage of fungi encompasses a broad spectrum of physiological and ecological traits. Differences are potentially magnified by interactions with similarly diverse hosts. Some of the conflicting views about functions of mycorrhizae undoubtedly stem from divergent experimental results attributable to use of different hosts and fungi in different experimental conditions. Indeed, little or no attention has been devoted to identity of the mycobiont in much of the work on mycorrhizal physiology. At the same time, emphasis of differences between mycobionts should not be permitted to obscure the general principles that obtain, especially since a given host plant in nature more often than not will have several different mycobionts forming mycorrhizae on its root system (Dominik 1961, Zak and Marx 1964). The following discussion is largely restricted to ectomycorrhizal fungi, because information on differences in other types is lacking or just emerging (Mosse 1972).

The host specificity of many mycobionts, their distinctive reactions to chemical reagents (Zak 1973), and phytochemical differences (Catalfomo and Trappe 1970) all suggest a potential for functional differences between species. Such differences are expressed in habitat preferences of different fungi, successional changes in mycobionts with aging of the host, seasonal fluctuations in prevalence of mycorrhiza-forming activity by different mycobionts, etc. (Dominik 1958, 1961; Mikola 1965; Anderson 1966). Specific differences between various mycobiont species and even strains within species have been demonstrated for temperature and moisture responses (Moser 1958, Hacskaylo et al. 1965, Mexal and Reid 1973), phosphorus solubilization and uptake (Bowen 1973, Mejstřik and Krause 1973), nitrogen utilization (Lundeberg 1970, Bowen 1973), production of enzymes, metabolites, and antibiotics (Lindeberg 1948, Slankis 1973, Marx 1973), and resistance of hyphae to decomposition by other organisms (Meyer 1970).

Differential growth response of vascular plant hosts to different mycobionts has been frequently recorded (Laiho 1970, Bowen 1973, Mikola 1973). Successional relationships of higher plants are intimately related to mycorrhizal associations as well. As Moser (1967) indicated, terrestrial plant communities tend to be dominated either by ectomycorrhizal or endomycorrhizal vascular plants. Upper timberlines around the world are characteristically ectomycorrhizal. Ectomycorrhizal hosts are the most successful woody dominants of various other nondesert extreme environments, for example, coal spoil banks in Pennsylvania (Schramm 1966). The evolution of capability in woody plants to withstand certain environmental extremes has included the ectomycorrhizal habit, although this generalization has its limitations. Select mycobionts adapted to these extremes have evolved concomitantly (Moser 1958, Marx and Bryan 1971).

Other adaptations in plants may also involve mycorrhizae as pivotal factors in succession. Attempts to establish ectomycorrhizal trees such as pines and birches in *Calluna* heathlands of the British Isles have regularly failed unless the *Calluna* is permanently removed. Living *Calluna* roots and mycorrhizae produce selective fungitoxins that inhibit ectomycorrhizal fungi of trees but not the ericaceous mycobionts of *Calluna* itself. Tree species that

compete well with other types of shrub layers suffer mycorrhizal deficiency and the accompanying severe nutrient deficiency when grown with *Calluna* (Handley 1963, Robinson 1972).

SPATIAL DISTRIBUTION AND BIOMASS OF MYCORRHIZAE

The study of mycorrhizal biomass and distribution in soil is fraught with difficulties, and data are accordingly scanty. Ectomycorrhizae are formed mostly on the fine root tips of the host. Generally they can be recognized with low-power magnification, but their separation from soil and critical examination is a tedious task. Moreover, removal from soil severs the fungal hyphae that grow from the rootlet into the soil. VA and other endomycorrhizae present further problems, because infections cannot be reliably evaluated without special staining procedures or chemical analyses. Despite these limitations, some generalizations and interesting facts are available from work done to date.

Mycorrhizae of terrestrial hosts are most abundant in the humus, fermentation, and immediately underlying layers of soil. Numbers of mycorrhizae below these layers decrease with increasing depth at rates depending on soil structure and fertility: "The better the site and biological conditions, the more evenly are the root tips distributed within the profile" (Meyer and Göttsche 1971). Reports of deepest ectomycorrhizae range from about 1 to 3 m for different soils and host plants (Meyer 1973); of VA mycorrhizae, 1.4 to 2.2 m (Konoe 1962).

Göbl (1965) sampled six subalpine spruce communities for total numbers of whole ectomycorrhizae. The A_F soil horizons ranged from 0 to 8,800/100 ml soil; A_H, 3,600 to 16,600; and B, 30 to 1,650. Meyer and Göttsche (1971) estimated the number of root tips in beech stands on five different soils. Since whole mycorrhizae are typically branched with two or more tips and since nonmycorrhizal tips were included, their count is not comparable to Göbl's. Number of tips in the A horizon ranged from 560/100 ml soil in a eutrophic brown earth to 45,600 in a podzol. They estimated the biomass of fine roots, including mycorrhizae, of one beech stand at 2,600 kg/ha for the entire soil profile. The upper six inches (15 cm) of soil of an Australian pine forest has been estimated to contain a mycorrhizal biomass of 1,400 kg/ha dry weight (Marks et al. 1968).

All the data cited above were presumably taken from relatively young stands. The belowground biomass of a 450-yr-old stand of *Pseudotsuga menziesii* with an understory of 150-yr-old and younger *Tsuga heterophylla* in Oregon has been studied in detail by M. Ogawa and R. D. Fogel (unpublished data). They estimated that the top 10 cm of soil contains 5,150 to 5,420 kg/ha dry weight of ectomycorrhizae, about 11% of the total root biomass.

Biomass estimates of the mycobionts alone are much more difficult to obtain, since the hyphae grow individually or in fine strands or rhizomorphs in the soil. Even the production of fruiting bodies is a poor index, since it varies with weather and season from year to year. In one study, the fruiting bodies of a single species of ectomycorrhizal fungus during a single year totaled 180 kg/ha dry weight, including 5 kg of nitrogen. The carbohydrate required for this was equivalent to 1 m^3 of spruce timber, the likely upper limit of this fungal use of carbon (Harley 1971). In some soils the black ectomycorrhizal fungus, *Cenococcum graniforme* (Sow.) Ferd. and Winge, forms abundant sclerotia. A 2-ml soil sample from a spruce stand contained 82 sclerotia 0.5 mm or more in diameter (Göbl 1965); if representative, that would be a respectable 41 billion sclerotia per ha · cm. M. Ogawa and R. D. Fogel (unpublished data) estimated that the upper 10 cm of soil in the old growth *Pseudotsuga-Tsuga* forest mentioned above contained 148 to 209 kg/ha dry weight of *Cenococcum* sclerotia.

No biomass estimates of endomycorrhizal fungi have been published. However, the upper 10 cm of soil in an undisturbed *Acer*-dominated hardwood forest of northern Michigan was estimated to contain nearly 7 million sporocarps/ha of VA-mycorrhizal species of Endogonaceae (Kessler and Blank 1972).

STRUCTURE AND ACTIVITY OF MYCORRHIZAE

Although additional data on biomass of mycorrhizae and mycobionts would be useful, their form and physiological activity are more important considerations in cycling processes. Ectomycorrhizae typically have larger diameters than nonmycorrhizal rootlets and branch in various patterns dependent on physiological interactions of the fungi with host roots (Harley 1969, Slankis 1973). Mosse (1962) has shown that roots of *Trifolium* with VA mycorrhizal infection grow more vigorously and are longer and more branched than nonmycorrhizal roots of the same plant. Stimulation of root growth by mycorrhizal fungi has been recorded for other mycorrhizal types as well (Harley 1969).

All types of mycorrhizae share a feature even more effective than expanded surface area in terms of substrate exploitation: direct connection with the mycobiont hyphae that grow out individually or as fascicled strands or rhizomorphs to soil beyond the absorbing zone of the root itself. These hyphae function as extensions of the root system, absorbing and translocating materials from the soil to the host (Mosse 1959, Harley 1969, Bowen 1973). Genetically compatible hyphae can fuse, so that large networks of mycorrhizal mycelium can form in the soil. The networks vastly increase absorption capabilities of hosts and permit translocation of materials between hosts sharing a mycelial system (Reid and Woods 1969, Furman and Trappe 1971). Trappe (unpublished data) has traced a single hypha emerging from a *Pseudotsuga* + *Cenococcum* mycorrhiza in a rotten log. The hypha extended more than 2 m and had more than 120 lateral branches or fusions with other hyphae. At least 43 of these branches connected to other mycorrhizae: 34 to other mycorrhizae on the same tree and 9 to mycorrhizae of *Tsuga* roots growing in the same log. Sample counts on numerous mycorrhizae formed by *Cenococcum* with various host species showed that from 200 to over 2,000 individual hyphae emerge from single mycorrhizae.

The surface area represented by the mycelium may not be as important for absorption of ions or water as the way in which it is distributed. Burgess and Nicholas (1961) estimated that a single milliliter of soil can contain as much as 4 m of hyphae. These aspects of mycorrhizae are elaborated and excellently illustrated by Bowen (1973).

Mycorrhizae and their outgrowing mycelium are also physiologically well adapted for substrate exploitation. The fungi produce extracellular as well as intracellular auxins, vitamins, cytokinens,

enzymes, and other compounds which directly influence root tissue and ion uptake (Miller 1971, Bowen 1973, Miura and Hall 1973, Slankis 1973). The net effects of these fungal products can be judged by comparison with nonmycorrhizal roots: mycorrhizae characteristically are larger and more branched, live and function longer, and respire at greater rates (Harley 1969).

Increased rootlet longevity is a well-established result, particularly of ectomycorrhizal infection. Nonmycorrhizal short roots of ectomycorrhizal plants abort relatively soon after development, probably because their marginally sized apical meristems depend on external sources of growth regulators to continue activity (Wilcox 1967). Ectomycorrhizae, in contrast, persist and apparently function from several months to as long as 8 years (Orlov 1968, Harley 1969).

Ectomycorrhizal infection results in increased respiration of root systems (Harley 1969, Schweers and Meyer 1970). By dissection of *Fagus* ectomycorrhizae, Harley (1971) found that the fungal mantle averages about 40% of the dry weight of a mycorrhiza but accounts for about half of the respiration. He estimated that although the mycorrhizal mantle comprises only about 4% of the biomass of 55-year-old pine, it accounts for about 25% of the CO_2 evolved by the root system. His estimate does not include hyphae that grow away from the mycorrhiza into the soil, so it is conservative in the proportion of CO_2 respired by the total fungal components of the root system. Since the mycobionts are essentially extensions of root systems rather than decomposers, Harley points out that "...there may be reason for doubting whether measurement of soil respiration, even if this can be accurately performed, will be as valuable as we commonly suppose in estimating the rates of decomposition processes in soil."

THE MYCORRHIZOSPHERE

Stimulation or inhibition of microorganisms, including mycobionts, by exudates in the rhizosphere is a well-known phenomenon. Vančura and Hovadik (1965) compared root exudates of a typically nonmycorrhizal plant (*Brassica*) with five species that normally form VA mycorrhizae. The *Brassica* exudate differed strikingly from the other plants in being impoverished of sugars, both quantitatively and qualitatively.

Inclusion of a mycobiont in a rhizosphere alters the rhizospheric chemistry. The fungus utilizes some fractions of the root exudate and, in turn, contributes its own exudates to produce a mycorrhizosphere. Zak (1971) proposes that ectomycorrhizal fungi additionally deactivate or filter soil phytotoxins that are potentially damaging to roots.

Since fungal exudates commonly include antibiotics, the mycorrhizosphere exerts a selective force on its microbial populations (Rambelli 1973). Mycobionts with strong antibiotic activity can strikingly influence populations of organisms in soil well beyond the mycorrhizosphere (Ohara and Hamada 1967). Specific effects of mycobiont-produced antibiotics in the mycorrhizosphere can vary drastically, depending on the mycobiont involved, and few generalities can be induced from available data. However, the protective effect exerted by ectomycorrhizal fungi against root parasites is well documented. The fungal mantle physically [illegible]rs invading parasites. Penetration of mycobion[illegible]to root tissue elicits a resistance response by h[illegible] cells that deters pathogens (Krupa and Nylund 1972, Marx 1973). Antibiotics and deterrent metabolites produced by some mycobionts can be highly protective against specific root pathogens or consumers (Zak 1965, Marx 1973).

Mycobionts are not known to fix nitrogen. However, in some cases nitrogen-fixing organisms are components of and are possibly stimulated by the mycorrhizosphere (Rambelli 1973, Silvester and Bennett 1973). Association of nitrogen-fixers with mycobionts may be analogous to that with wood decay fungi in stems of living trees (Seidler et al. 1972). Trappe (unpublished data) has found chlamydospores and hyphae of a VA-mycorrhizal fungus encrusted with *Azotobacter* bacteria.

Strongly host-specific mycobionts, each producing its own peculiar array of metabolites, can be introduced into ecosystems by introduction of the host itself. Such introductions could profoundly influence the soil biota and impact of root diseases (Trappe 1972). A good example is the widely distributed, obligate mycorrhizal associate of *Alnus*, *Lactarius obscuratus* (Lasch) Fr. (Froidevaux 1974). Where grows the alder, there also grows the *Lactarius*, at least in the Pacific Northwest. If alder is absent, the fungus does not fruit and is presumably absent.

It should be noted that mycorrhizal fungi can also endanger rootlets by attracting rather than deterring deleterious organisms. Mycorrhizae can be physically disrupted and even killed by mycophagous nematodes which feed only on the fungi (Riffle 1971). Root-feeding nematodes can also penetrate ectomycorrhizal mantles to create infection courts for pathogens (Barham 1972). Some ectomycorrhizal mycobionts seem to produce an attractant to root aphids (Zak 1965).

WATER RELATIONS

Numerous experiments indicate that, for a given host species, mycorrhizal seedlings resist drought better than nonmycorrhizal ones (Shemakhanova 1962, Bowen 1973). Ectomycorrhizal fungi have been demonstrated to grow in solutions of much higher osmotic pressure than that which plasmolyzes root hairs of nonmycorrhizal roots, although tolerance of low water potentials varies markedly between mycobionts (Shemakhanova 1962, Mexal and Reid 1973). VA mycorrhizal infection has been shown to markedly increase water transport from soil through roots to host plant leaves (Safir et al. 1971).

Perhaps the most dramatic illustration of the water transporting role of mycorrhizal mycelium is the accidental discovery of a mycobiont supplying moisture to a severed spruce shoot (Simonsberger and Koberg 1967). Seedling shoots, cut off for other experimental purposes, were left lying on the soil surface. One of these was colonized by a mycobiont from the soil. The shoot retained green, apparently normal leaves for 8 months after decapitation; noncolonized shoots were desiccated and dead soon after decapitation.

Transport of water by mycobiont hyphae from soil to hosts may well be important to plants of limited root penetration. However, its significance to vegetation with deep roots that tap ground water is not obvious. Especially in regions of extended seasonal drought, the soil layers in which mycorrhizae are concentrated can be exhausted of available water. In such cases it seems more likely that the host would supply water from deep in the soil to the mycobionts

and mycorrhizosphere organisms. Since fungal tissues act as nutrient sinks (Harley 1969, Stark 1972), the chemical potential gradient could well be in the direction of root to fungus as well as from soil to fungus. When water is not available to the mycobiont from soil, the gradient from root to mycobiont might overcome some of the water demand from other parts of the plant. Indeed, provision of water from host to mycobiont might make possible the exploitation of nutrients from soil when upper soil layers are dry.

NUTRIENT CYCLING

Radiotracer studies with virtually all the macronutrients and several micronutrients have invariably confirmed uptake by mycobionts and translocation to the vascular plant hosts. Numerous experiments have confirmed with similar constancy that woody plants absolutely require the mycobiont for adequate nourishment from soil and that herbaceous mycorrhizal hosts at the very least grow better and have higher nutrient contents with the fungal symbiont than without. Uptake of phosphorus and certain micronutrients is particularly dependent on activity of the fungal symbionts (Gerdemann 1968, Clark 1969, Harley 1969, Trappe and Strand 1969, Gilmore 1971, Hayman and Mosse 1972, Daft and Nicolson 1972, Kleinschmidt and Gerdemann 1972, Bowen 1973, Jackson et al. 1973).

The implications of this dependence on mycobionts for active ion uptake are far-reaching. Perhaps no other aspect of ecosystem research calls for greater heed to Harley's (1971) admonition: "...the investigation of the physiology of ecosystems is so arduous that, whenever there is a reasonable doubt about the validity of a method or a question, it is important to try to resolve that doubt before embarking on a process of field sampling with all the labour that this entails. Too little time is usually spent on methodology because of an impatience to get results."

The physiology of ion uptake and translocation in mycorrhizal systems has been reviewed in detail by Harley (1969) and Bowen (1973) and is beyond the scope of this paper. However, it seems useful to exemplify the risks inherent in disregarding mycorrhizal fungi in nutrient uptake studies. Conflicting reports on availability of nitrate nitrogen to conifers have appeared in the literature. Douglas-fir roots do not reduce nitrate and therefore cannot be expected to use it. However, some (but not all) mycobionts of Douglas-fir have the nitrate reductase enzyme system. Experiments with nonmycorrhizal seedlings or seedlings with mycorrhizae formed with mycobionts lacking nitrate reductase would show that nitrate is unavailable to the tree. Experiments with seedlings having mycorrhizae formed with nitrate-reducing mycobionts would show the opposite (Li et al. 1972). I. Ho and C. Y. Li (unpublished data) have demonstrated that *Glomus mosseae* (Nicol. & Gerd.) Gerd. & Trappe, a widely distributed mycobiont of VA mycorrhizae, also reduces nitrate.

The high respiration and diverse enzyme systems of mycobionts indicate strongly active ion uptake (Theodorou 1968, Harley 1971, Bartlett and Lewis 1973). Stark (1972) found that sporocarps of ectomycorrhizal fungi commonly contain substantially greater concentrations than pine needles of Cu, K, N, Na, P, and Zn on a dry weight basis. Sporocarps usually decay or are eaten by insects or larger animals within a few weeks after they appear. Thus they are ephemeral but relatively concentrated sources of macro- and micronutrients to decomposers and consumers. The longer lived fungal rhizomorphs in soil, however, contained even higher concentrations (expressed as significantly higher multiples of the concentration in pine needles): Ca (6.3 to 8.1), Cu (4.1 to 6.7), Fe (18.8 to 26.3), N (1.9 to 2.7), and Zn (2.0 to 11.0). Some rhizomorph samples also significantly exceeded pine needles in concentrations of Mg (up to 2.4), Mn (up to 2.3), Na (up to 1.4), and P (up to 2.2). Only K was consistently found at lower concentrations in rhizomorphs than in pine needles.

The rhizomorphs studied by Stark were not necessarily formed by mycobionts. However, Harley (1969) and his colleagues have demonstrated that mycorrhizal mantles accumulate phosphate which passes steadily to the host. Stark's data on rhizomorphs suggest a likelihood that mycobionts function similarly with cations. Moreover, mycelial networks of mycobionts shared by two or more plants probably permit interchange of ions from one host to another (Woods and Brock 1964). In effect, the sharing of mycorrhizal fungi lends credence to the concept of ecosystems operating as polymerous organisms.

In addition to absorbing and translocating elements, the fungal tissues serve as sinks for nutrients that might otherwise be leached from soil. Stark (1972) exposed living rhizomorphs and rhizomorphs killed both by autoclaving and oven drying to leaching equivalent to a year of precipitation at the collection sites. In all cases, rhizomorphs retained more than 99% of the elemental content under study. Presumably, these elements would be available to rhizomorph decomposers or consumers, as is the case with nutrients in sporocarps.

CARBON CYCLING

^{14}C-labeled photosynthate moves readily from chlorophyllous hosts to their mycobionts (Melin and Nilsson 1957, Reid and Woods 1969, Ho and Trappe 1973). In view of the high respiration rates and considerable biomass production of the mycobionts, neglecting mycobiont use of photosynthetically fixed C in calculations of gross primary productivity of hosts can substantially increase margins of error. The photosynthate is available to the fungi in many and varied products (Vančura and Hovadik 1965, Slankis et al. 1964). Which of these are important to the fungi is unknown, except for simple carbohydrates and thiamin (Hacskaylo 1973). In any event, the fungi generally fruit only when linked to a host; many do not grow at all, even in the most sophisticated culture media, without their host (Gerdemann 1968, Laiho 1970, Hacskaylo 1973).

^{14}C research on achlorophyllous epiparasitic Ericales such as *Monotropa* and *Hypopitys* spp. has demonstrated that photosynthates as well as cations are transferred from one mycorrhizal host to another through a shared mycobiont. In these cases the achlorophyllous members are the most dependent components of an anatomically linked system. They rely on the mycobiont for nutrient absorption and on a photosynthesizing plant for energy translocated via the mycobiont (Björkman 1960, Furman and Trappe 1971). The dependence of epiparasitic Ericales on the coincidence of two other compatible organisms probably accounts for their localized occurrence, which older hypotheses on saprophytism by these plants could not explain.

Transfer of ^{14}C from one green plant to another via mycobionts has been demonstrated in laboratory experiments (Reid and Woods 1969). This phenomenon probably also occurs in ecosystems. If so, concepts

of shade tolerance may need revision, since understory plants could epiparasitize overstory plants when mutually compatible mycobionts were present.

The orchidaceous mycorrhizae deserve special mention, because their mycobionts appear to be effective saprophytes or even parasites on other plants. *Armillariella mellea* (Vahl ex Fr.) Karst. is a widespread orchid symbiont (Campbell 1962, 1970) as well as an effective saprophyte and pathogen on diverse other plants. Campbell (1962) has found that its rhizomorphs connect achlorophyllous orchid mycorrhizae with tree roots that the fungus is actively parasitizing. Even in green orchids, ^{14}C moves from the mycorrhizal fungus to the orchid when the fungus has an exogenous supply of carbohydrate (Smith 1967).

Except for the orchidaceous fungi, the great majority of mycobionts exhibit little or no saprophytic ability (Gerdemann 1968, Harley 1969). Some ectomycorrhizal fungi violate this generalization and conceivably can be locally significant in decomposition processes (Lindeberg 1948, Laiho 1970). Results of field experiments by Gadgil and Gadgil (1971), however, suggest that some mycobionts can even inhibit litter decomposition by antagonizing the saprophytic fungi.

Mycorrhizal fungi contribute energy directly to animal mycophagists, including nematodes, arthropods, molluscs, and mammals (Ingold 1971, Riffle 1971). The mycophagists play an important role in dispersal of fungal propagules, especially of truffles and other mycobionts of subterranean fruiting habit. Some animals are highly specialized in this food habit. For example, the red-backed mouse, *Clethrionomys occidentalis californicus* (Merriam), appears to subsist almost entirely on hypogeous mycobionts throughout the year (C. Maser, R. Nussbaum, and J. M. Trappe, unpublished data).

A conceptual model of carbon cycling in ecosystems, diagrammed by Harley (1971), sums up the relationships discussed here.

CONCLUSIONS

Mycobionts join other soil organisms in additional effects on ecosystems, for example, soil aggregation (Bowen 1973). They constitute, in fact, vital components of many ecosystematic processes. The ecosystem investigator cannot ignore them if his goal is to understand the real world. To paraphrase Harley (1971) in a somewhat broader context, the difficulties in estimating the ecological roles of fungi will not disappear by ignoring them as so many have done in the past. The 16th century poet, Robert Southwell, presaged these remarks in a book of verse sympathetically entitled "Sainte Peter's Complaynte." In one, "Scorne not the least," he wrote: "He that high growth on Cedars did bestow: Gave also lowly mushrumpes leave to grow."

ACKNOWLEDGMENTS

The preparation of this paper, contribution no. 85 of the Coniferous Forest Biome, was supported in part by National Science Foundation Grant GB-36810X to the Coniferous Forest Biome, Ecosystem Analysis Studies, US/IBP.

REFERENCES

Anderson, J. 1966. Indagini sulla micorrizia in alcune specie di eucalitto nell Italia centrale. Pubbl. Cent. Agric. For. (Roma) 8:259-274.

Barham, R. O. 1972. Effect of nematodes and *Phytophthora cinnamomi* on mycorrhizae of shortleaf pine seedlings. Phytopathology 62:801.

Bartlett, E. M., and Lewis, D. H. 1973. Surface phosphatase activity of mycorrhizal roots of beech. Soil Biol. Biochem. 5:249-257.

Björkman, E. 1960. *Monotropa hypopitys* L.- an epiparasite on tree roots. Physiol. Plant. 13:308-327.

Bowen, G. D. 1973. Mineral nutrition of ectomycorrhizae, p. 151-205. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae- Their ecology and physiology. Academic Press, Inc., New York and London.

Burgess, A., and Nicholas, D. F. 1961. The use of soil sections in studying the amount of fungal hyphae in soil. Soil Sci. 92:25-29.

Campbell, E. O. 1962. The mycorrhiza of *Gastrodia cunninghamii* Hook. Trans. R. Soc. N.Z. 1:289-296.

Campbell, E. O. 1970. Morphology of the fungal association in three species of *Corallorhiza* in Michigan. Mich. Bot. 9:108-113.

Catalfomo, P., and Trappe, J. M. 1970. Ectomycorrhizal fungi: a phytochemical survey. Northwest Sci. 44:19-24.

Chilvers, G. A. 1973. Host range of some eucalypt mycorrhizal fungi. Aust. J. Bot. 21:103-111.

Christoph, H. 1921. Untersuchungen uber die mykotrophen Verhältnisse der "Ericales" und die Keimung von Pirolaceen. Bot. Centralbl. Beih. 38:115-157.

Clark, F. B. 1969. Endotrophic mycorrhizal infection of tree seedlings with *Endogone* spores. For. Sci. 15:134-137.

Daft, M. J., and Nicolson, T. H. 1972. Effect of *Endogone* mycorrhiza on plant growth. IV. Quantitative relationships between the growth of the host and the development of the endophyte in tomato and maize. New Phytol. 71:287-295.

Dominik, T. 1958. Studium nad mikotrofizmem rodzaju *Populus*. Inst. Badaw. Lesn. Pr. 181:117-172.

Dominik, T. 1961. Studies on mycorrhizae. U.S. Dep. Commer. Transl. TT 65-50333 (1966) from Folia For. Pol. Ser. A. Lesn. 5:3-160.

Fontana, A. 1961. Primo contributo allo studio delle micorrize dei pioppi in Piemonte. Allionia 7:87-129.

Fontana, A. 1963. Micorrize ectotrofiche in una ciperacea: *Kobresia bellardi* Degl. G. Bot. Ital. 70:639-641.

Frank, B. 1885. Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. Ber. Dtsch. Bot. Ges. 3:128-145.

Froidevaux, L. 1973. The ectomycorrhizal association, *Alnus rubra + Lactarius obscuratus*. Can. J. For. Res. 3(4):601-603.

Furman, T. E., and Trappe, J. M. 1971. Phylogeny and ecology of mycotrophic achlorophyllous angiosperms. Q. Rev. Biol. 46:219-225.

Gadgil, R. L., and Gadgil, P. D. 1971. Mycorrhiza and litter decomposition. Nature 233:133.

Gerdemann, J. W. 1968. Vesicular-arbuscular mycorrhiza and plant growth. Annu. Rev. Phytopathol. 6:397-418.

Gerdemann, J. W., and J. M. Trappe. 1974. The Endogonaceae in the Pacific Northwest. Mycologia Mem. No. 5, New York Botanical Gardens, Bronx, N.Y. 76 p.

Gilmore, A. E. 1971. The influence of endotrophic mycorrhizae on the growth of peach seedlings. J. Am. Soc. Hort. Sci. 96:35-38.

Göbl, F. 1965. Mykorrhizauntersuchungen in einem subalpinen Fichtenwald. Mitt. Forstl. Bundesversuchsanst. Mariabrunn 66:173-195.

Hacskaylo, E. (ed.) 1971. Mycorrhizae. USDA For. Serv. Misc. Publ. 1189, Washington, D.C. 255 p.

Hacskaylo, E. 1973. Carbohydrate physiology of ectomycorrhizae, p. 207-230. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York and London.

Hacskaylo, E., Palmer, J., and Vozzo, J. 1965. Effect of temperature on growth and respiration of ectotrophic mycorrhizal fungi. Mycologia 57:748-756.

Hadley, G. 1970. Non-specificity of symbiotic infection in orchid mycorrhiza. New Phytol. 69:1015-1023.

Handley, W. R. C. 1963. Mycorrhizal associations and *Calluna* heathland afforestation. For. Comm. Bull. 36:1-70.

Harley, J. L. 1969. The biology of mycorrhiza. Leonard Hill, London. 334 p.

Harley, J. L. 1971. Fungi in ecosystems. J. Appl. Ecol. 8:627-642.

Hayman, D. S., and Mosse, B. 1972. Plant growth responses to vesicular-arbuscular mycorrhiza. III. Increased uptake of labile P from soil. New Phytol. 71:41-47.

Ho, I., and Trappe, J. 1973. Translocation of ^{14}C from *Festuca* plants to their endomycorrhizal fungi. Nature New Biol. 244:30-31.

Ingold, C. T. 1971. Fungal Spores--Their Liberation and Dispersal. Clarendon Press, Oxford. 302 p.

Jackson, N. E., Miller, R. H., and Franklin, R. E. 1973. The influence of vesicular-arbuscular mycorrhizae on uptake of ^{90}Sr from soil by soybeans. Soil Biol. Biochem. 5:205-212.

Kelley, A. P. 1950. Mycotrophy in plants. Chronica Botanica Co., Waltham, Mass. 223 p.

Kessler, K. J., and Blank, R. W. 1972. *Endogone* sporocarps associated with sugar maple. Mycologia 64:634-638.

Khan, A. G. 1972. The effect of vesicular-arbuscular mycorrhizal associations on growth of cereals. I. Effects on maize growth. New Phytol. 71:613-619.

Kleinschmidt, G. D., and Gerdemann, J. W. 1972. Stunting of citrus seedlings in fumigated nursery soils related to the absence of endomycorrhizae. Phytopathology 62:1447-1453.

Konoe, R. 1962. On the vertical distribution of the endotrophic mycorrhiza in *Metasequoia*. Osaka City Univ. J. Biol. 13:105-110.

Krupa, S., and Nylund, J. E. 1972. Studies on ectomycorrhizae of pine. III. Growth inhibition of two root pathogenic fungi by volatile organic constituents of ectomycorrhizal root systems of *Pinus sylvestris* L. Eur. J. For. Pathol. 2:88-94.

Laiho, O. 1970. *Paxillus involutus* as a mycorrhizal symbiont of forest trees. Acta For. Fenn. 106:1-72.

Lewis, D. H. 1973. Concepts in fungal nutrition and the origin of biotrophy. Biol. Rev. 48:261-278.

Li, C. Y., Lu, K. C., Trappe, J. M., and Bollen, W. B. 1972. Nitrate-reducing capacity of roots and nodules of *Alnus rubra* and roots of *Pseudotsuga menziesii*. Plant Soil 37:409-414.

Lindeberg, G. 1948. On the occurrence of polyphenol oxidases in soil-inhabiting Basidiomycetes. Physiol. Plant 1:196-205.

Lobanow, N. W. 1960. Mykotrophie der Holzpflanzen. Deutscher Verlag der Wissenschaften, Berlin. 352 p.

Lundeberg, G. 1970. Utilization of various nitrogen sources, in particular bound soil nitrogen, by mycorrhizal fungi. Stud. For. Suec. 79:1-95.

Maeda, M. 1954. The meaning of mycorrhiza in regard to systematic botany. Kumamoto J. Sci. B 3:57-84.

Marks, G. C., Ditchburne, N., and Foster, R. C. 1968. Quantitative estimates of mycorrhiza populations in radiata pine forests. Aust. For. 32:26-38.

Marks, G. C., and Kozlowski, T. T. (eds.) 1973. Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York and London. 444 p.

Marx, D. H. 1973. Mycorrhizae and feeder root diseases, p. 351-382. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York and London.

Marx, D. H., and Bryan, W. C. 1971. Influence of ectomycorrhizae on survival and growth of aseptic seedlings of loblolly pine at high temperatures. For. Sci. 17:37-41.

Mejstřik, V. 1965. Study of the development of endotrophic mycorrhiza in the association of *Cladietum marisci*, p. 283-290. *In* J. Macura and V. Vančura (eds.) Plant microbes relationships. Czech. Acad. Sci., Prague.

Mejstřik, V. K., and Krause, H. H. 1973. Uptake of ^{32}P by *Pinus radiata* roots inoculated with *Suillus luteus* and *Cenococcum graniforme* from different sources of available phosphate. New Phytol. 72:137-140.

Melin, E., and Nilsson, H. 1957. Transport of ^{14}C-labelled photosynthate to the fungal associate of pine mycorrhiza. Sven. Bot. Tidskr. 51(1):166-186.

Mexal, J., and Reid, C. P. P. 1973. The growth of selected mycorrhizal fungi in response to induced water stress. Can. J. Bot. 51:1579-1588.

Meyer, F. H. 1970. Abbau von Pilzmycel im Boden. Z. Pflanzenernaehr. Bodenkd. 127:193-199.

Meyer, F. H. 1973. Distribution of ectomycorrhizae in native and man-made forests, p. 79-105. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York.

Meyer, F. H., and Göttsche, D. 1971. Distribution of root tips and tender roots of beech, p. 48-52. *In* H. Ellenberg (ed.) Ecological studies, analysis and synthesis, Vol. 2. Springer-Verlag, Berlin.

Mikola, P. 1965. Studies on the ectendotrophic mycorrhiza of pine. Acta For. Fenn. 79:1-56.

Mikola, P. 1973. Application of mycorrhizal symbiosis in forestry practice, p. 383-411. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York.

Miller, C. O. 1971. Cytokinen production by mycorrhizal fungi, p. 168-174. *In* E. Hacskaylo (ed.) Mycorrhizae. USDA For. Serv. Misc. Publ. 1189, Washington, D.C.

Miura, G., and Hall, R. H. 1973. Trans-ribosylzeatin. Its biosynthesis in *Zea mays* endosperm and the mycorrhizal fungus, *Rhizopogon roseolus*. Plant Physiol. 51:563-569.

Moser, M. 1958. Der einfluss tiefer temperaturen auf das wachstum und die lebenstätigheit höherer pilze mit spezieller berücksichtigung von mykorrhizapilzen. Sydowia 12:386-399.

Moser, M. 1967. Die ektotrophe ernährungswiese an der waldgrenze. Mitt. Forstl. Bundes-versuchsanst. Wien 75:357-380.

Mosse, B. 1959. Observations on the extra-matrical mycelium of a vesicular-arbuscular endophyte. Trans. Br. Mycol. Soc. 42:439-448.

Mosse, B. 1962. The establishment of vesicular-arbuscular mycorrhiza under aseptic conditions. J. Gen. Microbiol. 27:509-520.

Mosse, B. 1972. Effects of different *Endogone* strains on the growth of *Paspalum notatum*. Nature 239:221-223.

Nieuwdorp, P. J. 1969. Some investigations on the mycorrhiza of *Calluna, Erica,* and *Vaccinium*. Acta Bot. Neerl. 18:180-196.

Ohara, H., and Hamada, M. 1967. Disappearance of bacteria from the zone of active mycorrhizas in *Tricholoma matsutake* (S. Ito and Imai) Singer. Nature 213:528-529.

Orlov, A. J. 1968. Development and live duration of the pine feeding roots, p. 139-145. *In* M. S. Ghilarov, V. A. Kovda, L. N. Novichkova-Ivanova, L. E. Rodin, and V. M. Sveshnikova (eds.) Methods of productivity studies in root systems and rhizosphere organisms. Nauka, Leningrad, USSR.

Palmer, J. G. 1971. Techniques and procedures for culturing ectomycorrhizal fungi, p. 132-144. *In* E. Hacskaylo (ed.) Mycorrhizae. USDA For. Serv. Misc. Publ. 1189, Washington, D.C.

Rambelli, A. 1973. The rhizosphere of mycorrhizae, p. 299-349. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York.

Reid, C. P. P., and Woods, F. W. 1969. Translocation of C^{14}-labeled compounds in mycorrhizae and its implications in interplant nutrient cycling. Ecology 50:179-187.

Riffle, J. 1971. Effect of nematodes on root inhabiting fungi, p. 97-113. *In* E. Hacskaylo (ed.) Mycorrhizae. USDA For. Serv. Misc. Publ. 1189, Washington, D.C.

Robinson, R. K. 1972. The production by roots of *Calluna vulgaris* of a factor inhibitory to growth of some mycorrhizal fungi. J. Ecol. 60:219-224.

Safir, G. R., Boyer, J. S., and Gerdemann, J. W. 1971. Mycorrhizal enhancement of water transport in soybean. Science 172:581-583.

Schramm, J. R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Trans. Am. Philos. Soc. N.S. 56:1-194.

Schweers, W., and Meyer, F. H. 1970. Einfluss der Mykorrhiza auf den transport von Assimilaten in die Wurzel. Ber. Dtsch. Bot. Ges. 83:109-119.

Seidler, R. J., Aho, P. E., Raju, P. N., and Evans, H. J. 1972. Nitrogen fixation by bacterial isolates from decay in living white fir trees [*Abies concolor* (Gord. and Glend.) Lindl.]. J. Gen. Microbiol. 73:413-416.

Seviour, R. J., Willing, R. R., and Chilvers, G. A. 1973. Basidiocarps associated with ericoid mycorrhizas. New Phytol. 72:381-385.

Shemakhanova, N. M. 1962. Mycotrophy of woody plants. Akad. Nauk SSSR, Moscow. U.S. Dep. Commer. Transl. TT 66-51073, Washington, D.C. 329 p.

Silvester, W. B., and Bennett, K. J. 1973. Acetylene reduction by roots and associated soil of New Zealand conifers. Soil Biol. Biochem. 5:171-179.

Simonsberger, P., and Koberg, H. 1967. Der pilz als lebensretter--Mykorrhizapilz *Thelephora terrestris* bewahrt abgeschnittenen fichtensämling vor dem vertrocknen. Mikrokosmos 5:147-149.

Slankis, V. 1973. Hormonal relationships in mycorrhizal development, p. 231-298. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York.

Slankis, V., Runeckles, V. C., and Krotkov, G. 1964. Metabolites liberated by roots of white pine (*Pinus strobus* L.) seedlings. Physiol. Plant. 17:301-313.

Smith, A. H. 1971. Taxonomy of ectomycorrhiza-forming fungi, p. 1-8. *In* E. Hacskaylo (ed.) Mycorrhizae. USDA For. Serv. Misc. Publ. 1189, Washington, D.C.

Smith, S. E. 1967. Carbohydrate translocation in orchid mycorrhizas. New Phytol. 66:371-378.

Stark, N. 1972. Nutrient cycling pathways and litter fungi. BioScience 22:355-360.

Theodorou, C. 1968. Inositol phosphates in needles of *Pinus radiata* D. Don and the phytase activity of mycorrhizal fungi. 9th Int. Congr. Soil Sci. Trans. 3:483-490.

Trappe, J. M. 1962. Fungus associates of ectotrophic mycorrhizae. Bot. Rev. 28:538-606.

Trappe, J. M. 1964. Mycorrhizal hosts and distribution of *Cenococcum graniforme*. Lloydia 27:100-106.

Trappe, J. M. 1971. Mycorrhiza-forming Ascomycetes, p. 19-37. *In* E. Hacskaylo (ed.) Mycorrhizae. USDA For. Serv. Misc. Publ. 1189, Washington, D.C.

Trappe, J. M. 1972. Regulation of soil organisms by red alder: a potential system for control of *Poria weirii*. Oreg. State Univ. Sch. For. Symp. 3:35-51.

Trappe, J. M., and Strand, R. F. 1969. Mycorrhizal deficiency in a Douglas-fir region nursery. For. Sci. 15:381-389.

Vančura, V., and Hovadik, A. 1965. Composition of root exudates in the course of plant development, p. 21-25. *In* J. Macura and V. Vančura (eds.) Plant microbes relationships. Czech. Acad. Sci., Prague.

Vittadini, C. 1842. Monographia Lycoperdineorum. Augustae Taurinorum, Torino. 93 p.

Vozzo, J. A., and Hacskaylo, E. 1971. Inoculation of *Pinus caribaea* with ectomycorrhizal fungi in Puerto Rico. For. Sci. 17:239-245.

Warcup, J. H., and Talbot, P. H. B. 1971. Perfect states of rhizoctonias associated with orchids. II. New Phytol. 70:35-40.

Wilcox, H. 1967. Seasonal patterns of root initiation and mycorrhizal development in *Pinus resinosa* Ait. XIV Int. Union For. Res. Organ. 5:29-39.

Woods, F. W., and Brock, K. 1964. Interspecific transfer of Ca^{45} and P^{32} by root systems. Ecology 45:886-889.

Zak, B. 1965. Aphids feeding on mycorrhizae of Douglas-fir. For. Sci. 11:410-411.

Zak, B. 1971. Detoxification of autoclaved soil by a mycorrhizal fungus. Pac. Northwest For. & Range Exp. Sta. USDA For. Serv. Note PNW-159. Portland, Ore. 4 p.

Zak, B. 1973. Classification of ectomycorrhizae, p. 43-78. *In* G. C. Marks and T. T. Kozlowski (eds.) Ectomycorrhizae--Their ecology and physiology. Academic Press, Inc., New York.

Zak, B. 1974. Ectendomycorrhiza of Pacific madrone (*Arbutus menziesii*). Trans. Br. Mycol. Soc. 62(1):202-204.

Zak, B., and Marx, D. 1964. Isolation of mycorrhizal fungi from roots of individual slash pines. For. Sci. 10:214-222.

DISCUSSION

Q1. Barber. On the relationship of mycorrhizae and phosphorus nutrition it is known that there is less phosphorus uptake in wheat grown in nonsterile soil compared with sterile soil. Would you comment on this?

A1. Trappe. Nonsterile soil does not necessarily mean mycorrhizal. Unless the roots were examined for mycorrhizal infection, there is no way to tell what was involved in such results.

Q2. Peterson. Does the lack of mineral nutrients control growth in a wet climate?

A2. Trappe. Not necessarily; mycorrhizal fungi are strongly aerobic and the low rate of diffusion of oxygen is likely to control their growth.

Q3. Mark. Is there any significance in the predominance of ectotrophic mycorrhizae near the treeline? I ask this since in New Zealand, where endotrophic mycorrhizae appear to be almost universally important, we nevertheless find the ectotrophic type in our main treeline genus *Nothofagus*.

A3. Trappe. Moser was referring to woody species in which case we would expect such a relationship.

Q4. Billings. Are differences in the mycorrhizal association of gymnosperms and of nongymnosperms expected?

A4. Trappe. Yes; host specificity is common in ectomycorrhizal fungi, although some species such as *Cenococcum graniforme* form mycorrhizae with both gymnosperms and nongymnosperms.

Q5. Romney. What are the upper temperature limits for mycorrhizal growth?

A5. Trappe. Ectomycorrhizae generally grow well up to 20 or 25°C in experiments; 30°C or higher seems to be limiting. Of course, species and ecotypes of both fungi and hosts differ in response to temperature, so exceptions can be expected. I am not aware of good temperature data on endomycorrhizae.

Comment: Romney. In the Mojave Desert, the temperature at the 10-cm soil depth can exceed 30°C for 6 months of the year. Under these conditions, abundant mycorrhizae are found in the litter but not elsewhere.

Reproduced from "The belowground ecosystem: A synthesis of plant-associated processes, p. 205-214, Range Sci. Dep. Sci. Ser. No. 26, Colorado State Univ., Fort Collins, by the Forest Service, U.S. Department of Agriculture, for official use. 1977

GPO 990-991