

Interactions among Soil Biota in Coniferous Ecosystems

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ABSTRACT

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The dominance of ectomycorrhizae in most coniferous forest ecosystems profoundly alters the classical concept of the role of exudation and rhizodeposition of cell fragments in the formation of the rhizosphere. In the unaltered, non-ectomycorrhizal rhizosphere the soluble exudates and sloughed cells supporting higher populations of bacteria and other soil biota in the rhizosphere result from the root. The loss of root hairs and the presence of a sheath of fungal hyphae around roots in ectomycorrhizae, suggests that the exudates and sloughed cells will be mainly fungal in origin, creating a mycorrhizosphere. Unfortunately, very little quantitative data exist to test this hypothesis.

Recent work has shown that much of the rhizodeposition is in fact whole roots and mycorrhizae; soluble exudates and root cap plus mucigel account for only 3-15% of the organic matter produced in pot experiments. In forests, 3-5 times more organic matter in the form of roots and mycorrhizae is returned to the soil than is returned by decomposition of litter.

Data on biomass of bacteria, fungi and other mycorrhizosphere biota obtained by direct measurement or observation are very limited. Much of the research on interactions among biota has focused on host-pathogen interactions rather than quantification of the impact of biota on ecosystem processes.

INTRODUCTION

Interest in soil ecology has increased dramatically in recent years, as evidenced by numerous symposia, e.g. ecological interactions, tropical soil biology and tree root systems and their mycorrhizas. Many of the interactions among soil biota in coniferous ecosystems, occur in other ecosystems and the question really becomes what is unique about coniferous ecosystems that will modify or change the interactions common to all ecosystems. Beyond most conifers being evergreen, coniferous ecosystems are distinctive in that leaching losses from litter are slow and occur over a long period (Read et al., 1985). In addition,

many conifers are ectomycorrhizal. Some hardwoods are also ectomycorrhizal, but conifers differ in generally having lower nutrient requirements and use nutrients, particularly nitrogen, more efficiently than hardwoods (Edmonds, 1982). Given the importance of ectomycorrhizae, I have opted to focus the following discussion on interactions of soil organisms and trees with ectomycorrhizae in coniferous forests, starting with a review of their structure, followed by discussions of their importance in supplying carbon to soil organisms and their interactions with soil biota in the mycorrhizosphere.

Ectomycorrhizal structure

The classical concept of the root apex includes the presence of a root cap, meristematic zone, elongation zone and a zone of maturation. As growth occurs, the size of the root cap remains relatively constant, new cells being produced as the outer cells are sloughed. The root cap protects cells of the apical meristem and produces mucigel. Root hairs up to 1000 μm long and 10–15 μm in diameter are produced in the zone of maturation. They frequently persist for only a few days, although persistent, thick-walled root hairs have been observed (Russell, 1977). Functions proposed for root hairs include: (1) nutrient absorption, although there is no conclusive evidence of their importance; (2) anchorage for roots; (3) secretion of metabolic substrates for rhizosphere biota (Russell, 1977).

The classical concept of the root is modified slightly by vesicular–arbuscular mycorrhizae (VAM). The root is altered by the presence of a two-phase mycelial system; an internal mycelium within the cortex of the root and an external mycelium in the soil which varies considerably in extent and in some instances may even obscure the root (Harley and Smith, 1983). No matter how extensive the external mycelium, a hyphal sheath enclosing the roots is never formed. Estimates for the length of external hyphae vary from 1.3 to 1.4 m cm^{-1} of infected root length in clover and ryegrass, respectively (Tisdall and Oades, 1979) to 0.8 m cm^{-1} in onion (Sanders and Tinker, 1973). The external mycelium functionally extends the region of nutrient absorption for the plant far beyond the 1–2-mm zone generally ascribed to roots (Rhoads and Gerdemann, 1975), as well as providing connections for direct interplant transfer of carbon, phosphorus and perhaps other nutrients among neighboring plants (Chiariello et al., 1982; Whittingham and Read, 1982; Read et al., 1985).

Ectomycorrhizae (ECM) produce an even more drastic alteration of the classical concept of the root than does the VAM symbiosis. In ECM, the root is modified by the presence of a 3-phase mycelial system; an internal mycelium (Hartig net) growing intracellularly in the primary cortex, a sheath of hyphae covering the root, and an external mycelium extending into the soil. An individual external hyphae may extend 2 m or more from the mantle and form more than 120 lateral branches; 200 to over 2000 individual hyphae have been

counted emerging from the mantle of a single ECM (Trappe and Fogel, 1977). Under the appropriate conditions, the external hyphae produce reproductive structures: mushrooms, truffles or sclerotia. The primary function of the external mycelium is extension of the zone of absorption and providing inter-plant connections for direct transfer of carbon (Reid and Woods, 1969; Read et al., 1985). The major function of the mantle appears to be storage, particularly for phosphorus and glycogen (Harley and Smith, 1983; Foster et al., 1983), while the Hartig net mycelium functions in exchange of resources between host and fungus. Not all root tips in ectomycorrhiza-dominated forests are mycorrhizal, but non-mycorrhizal root tips are very infrequent in soil cores (Neal et al., 1964; R. Fogel, personal observation). Ectomycorrhizae greatly extend the life of absorptive roots beyond the few days root hairs are active; ECM persist for 6–9 months with one report of a 13-year-old ECM (Fogel, 1983).

Other alterations of the classical root resulting from the formation of ECM as found in pine, besides the addition of the 3-phase mycelial system for absorption, include the lack or reduction in the size of the root cap, a very small apical meristem, and the lack of root hairs (Harley and Smith, 1983). Some of these modifications in the root apex may precede mycorrhizal infection and uninfected short roots of pine abort if not infected (Harley and Smith, 1983). Ectomycorrhizal fungi are also capable of forming Hartig nets in slow-growing long roots of red pine (Wilcox, 1971). Similar modifications occur in ectendomycorrhizae, but the mantle is much thinner and the cortical cells are penetrated by hyphae of the internal mycelium.

ROOT EXUDATES AND THE MYCORRHIZOSPHERE

Until recently, leaf litter was considered the main source of carbon entering the soil ecosystem. Studies of soil cores have changed this picture to one in which fine roots and mycorrhizae dominate the supply of organic matter with some indication, mostly theoretical and extrapolated from laboratory studies, that root exudates and rhizodeposition of sloughed cells, root caps, etc. might also constitute a significant source of energy for soil processes (Fogel, 1985; Newman, 1985).

The relative importance of roots and mycorrhizae vs. leaf litterfall as energy sources can be illustrated by our work in a Douglas-fir ecosystem (Fogel and Hunt, 1979, 1983; Hunt and Fogel, 1983). Other examples could be used, e.g. Vogt et al. (1983) and Persson (1980), but these latter studies are focused on roots and do not include data on leaf litter or secondary production in the form of fungal hyphae. In the second growth Douglas-fir stand studied by Fogel and Hunt (1979, 1983), amorphous soil organic matter comprises 40.3–41.9% of the total soil organic matter, non-mycorrhizal large and fine roots 32.3–35%, mycorrhizae 12%, forest litter 9.1%, and fungal hyphae, fruiting bodies and sclerotia 3.6–4.7%. In terms of throughput, or the organic matter input to the

soil ecosystem, the order of importance changes significantly. Mycorrhizae account for 53.5–54.9% of the input, followed by fungal structures 23–34.6%, fine roots 0–13.9%, and forest litter 10–10.4%. Soil hyphae and sclerotia of *Cenococcum geophilum* dominate fungal input, accounting for 94.5–96.1% of the total. If one assumes 40% of the dry weight of an ectomycorrhiza is mantle hyphae (Harley, 1971), the total fungal input is nearly doubled to 44.4–54.6% of the total input to the soil. Return of organic matter to the soil by ectomycorrhizae is 3–5 times larger than the return resulting from decomposition of above-ground litter. Other studies have also shown that the return of organic matter by fine roots and mycorrhizae is 3–5 times larger than that from litter (Edwards and Harris, 1977; Persson, 1978). The return of organic matter to the soil by ectomycorrhiza is accompanied by major releases of N, P and K (Fogel and Hunt, 1983).

The classical concept of interactions between soil organisms being more intensive adjacent to the root, the rhizosphere, is based on research indicating populations of bacteria and other soil biota are higher in the soil immediately adjacent to the root than in bulk soil. The higher populations are attributed to the production of root exudates. Carbohydrates, amino acids, organic acids, enzymes, auxins, vitamins and other compounds, some of which stimulate or inhibit fungi, bacteria and nematodes, have all been reported in exudates (Russell, 1977). Trees have been reported to exude more amino acids/amides than crop plants and comparable amounts of carbohydrates (Smith, 1977). Unfortunately, the quantity of material available to soil biota from rhizodeposition and exudation is difficult to estimate since the amount is influenced by nitrogen levels, phosphorus supply, age of roots, rate of shoot extension, temperature, water stress, and the presence of microorganisms (Russell, 1977). Reported estimates of soluble exudate production by living roots are usually within the range of 1–10 g per 100 g root dry weight increase; root-cap fragments plus mucigel may provide a further 2–5 g per 100 g (Newman, 1985).

Collection of exudates has been done mostly in solution culture under sterile conditions since microbes metabolize compounds on release. Smith (1976) employed this approach to collect exudates from unsubsized root tips of birch, beech and maple. The roots were first severed and allowed to produce new tips. The tips were then inserted into tubes filled with sterile distilled water, allowed to grow for 14 days, and the resulting microbe-free solutions analyzed for exudates. Exudates equaled 0.5–1.4% of the root weight in the tubes. After adjusting for the estimated number of root tips, length of growing season and species composition of the stand, Smith calculated that the annual production of exudates totaled 66.5 kg ha⁻¹ in a northern hardwood forest. These results cannot be reliably extrapolated to coniferous forests for several reasons: (1) growth in a non-aerated solution is undoubtedly different from growth in soil; (2) root growth was stimulated by the wounding; (3) the roots used are not typical of ectomycorrhizae.

An alternative approach for estimating exudate production involves supplying the tops of plants with ^{14}C , and measuring the proportion of labelled carbon collected in exudates. This approach produces a minimum estimate since the amount is determined by the balance between exudation and reabsorption of the label. Newman (1985) concludes after a review of radiolabelling experiments that "much of the insoluble "rhizodeposition" measured by ^{14}C labelling is in fact whole roots which are not in the rhizosphere." His analysis shows that soluble exudates and root cap plus mucigel together contribute only 3–15% of the organic matter contributed by the root itself, confirming results from soil-coring studies on the greater relative importance of fine roots and mycorrhizae as sources of carbon.

The dominance of ectomycorrhizae in most coniferous forests alters profoundly the classical concept of the role of exudation and rhizodeposition in the formation of the rhizosphere. The mantle of hyphae covering host tissues and the lack of root hairs represent major alterations in the morphology of the root. The hyphal mantle in beech ectomycorrhizae, for instance, comprises a large share of the mycorrhizal weight, 34–45% of the total dry weight (Harley and McCready, 1952); this figure does not include the biomass of hyphae forming the Hartig net. In comparison, the fungal proportion in VAM ranges from 4 to 17% of the total (root plus fungus) dry weight (Hepper, 1977). More important than the proportion represented by fungal hyphae is the presence of the sheath, a potential barrier disrupting the "normal" flow of materials in the classical rhizosphere. The mantle may act as a barrier and replace and/or supplement root exudates with fungal exudates. The highly-modified rhizosphere that may result from ECM formation has been termed a mycorrhizosphere owing to the sphere of influence being determined both by root exudates and metabolites produced by the mycorrhizal fungus (Foster and Marks, 1967; Davey, 1971; Rambelli, 1973).

Very little evidence exists to show a quantitative difference between classical rhizospheres and mycorrhizospheres. Most of the research on metabolites of ectomycorrhizal fungi has concentrated on compounds affecting the host, e.g. growth hormones, or inhibiting microbes, e.g. antibiotics, rather than simple sugars, amino acids or organic acids. Most of the ectomycorrhizal fungi tested produce auxins in culture, and some but not all have been shown to produce substances capable of promoting the growth of cytokinin-dependent soybean callus (Harley and Smith, 1983). Graham and Linderman (1979) report the production of ethylene by ectomycorrhizal fungi in liquid culture. *Suillus variegatus* produces ethanol, isobutanol, isoamyl alcohol, acetoin and isobutyric acid in culture (Krupa and Fries, 1971). Production of bacteriostatic and fungistatic substances is strain-specific in ectomycorrhizal fungi and consequently highly variable (Marx, 1973). Of 26 species examined by Krywolap (1971), six produce substances active against both Gram-positive and Gram-negative bacteria, 11 are active against Gram-negative bacteria only, no inhib-

itory activity is found in the culture media of 4 species. The active compounds *Leucopaxillus cerealis* var. *piceina* produces have been identified as diatretyne nitrile and diatretyne-3. The nitrile is very inhibitory against both bacteria and fungi whereas the diatretyne-3 has only a bacteriostatic action (Marx, 1969). Ectomycorrhizal fungi have also been shown to produce hydroxamate siderophores that enhance iron absorption at neutral and alkaline pH (Szaniszlo et al., 1981), acid phosphatases (Dighton, 1983), phytase (Harley and Smith, 1983), and polyphenol oxidases (Giltrap, 1982). Cellulases and pectinases may be produced by some ectomycorrhizal fungi (Harley and Smith, 1983). No references apparently exist describing sugars exuded by ectomycorrhizal fungi, even though it is known that these fungi convert host sugars, i.e. glucose and fructose, to fungal sugars and alcohols, i.e. trehalose and mannitol, that are unavailable to the host and are not found in non-mycorrhizal roots (Harley and Smith, 1983). The extrapolation of in vitro studies to field conditions is difficult because production of secondary compounds is often very sensitive to culture conditions.

One type of fungal exudation that has been studied in an ecosystems context is the production of calcium oxalate. Crystals of calcium oxalate are found covering older hyphae of some ectomycorrhizal fungi and may be present in the ECM mantle (Malajczuk and Cromack, 1982). Fungal mats of the ectomycorrhizal basidiomycete, *Hysterangium crassum*, accumulate 20 times more calcium oxalate in the soil A-horizon than in adjacent uncolonized soil. *H. crassum* mats are one of the few locations earthworms are found in the acid forest soils of western Oregon presumably because of their requirement for calcium (R. Fogel, unpublished data). Although calcium oxalate cannot be utilized as a sole carbon source by most organisms, it is interesting to note that calcium-oxalate decomposing bacteria have been isolated from the gut and casts of earthworms. Oxalate production by ectomycorrhizal fungi may explain increased rates of weathering and nutrient release by ECM as compared with non-mycorrhizal roots (Cromack et al., 1977). Oxalic acid is the only fungal exudate that has also been reported in tree-root exudates (Bowen and Theodorou, 1973; Smith, 1977).

INTERACTIONS AMONG BIOTA IN THE MYCORRHIZOSPHERE

One of the major problems in understanding interactions among soil biota is reconstructing the spatial and temporal distributions of populations of organisms. The traditional methods employed in studying soil biota involve separating them from soil to determine their abundance and biomass. The process of separating the organism of interest from soil destroys spatial relationships and often obscures relationships between the organism and its food source, etc. Another major problem in understanding relationships results from a narrow focus on one organism or perhaps two organisms often caused by the training

of the researcher in mycology, invertebrate zoology, ecosystems ecology etc. coupled with the problems of studying intact systems. The problems of narrow focus are readily apparent in trying to extrapolate some good studies of food preferences of nematodes to the ecosystem level. The necessary data for one or the other population are often not available because of the narrow focus of most studies. The discussion that follows is therefore limited to studies that either describe observed populations or suggest interactions that might occur in the mycorrhizosphere.

Bacteria

Bacteria are closely associated with the mantle in ECM. Direct light microscopy shows that only 5–10% of the root surface is covered by bacteria (Rovira, 1979). Transmission electron microscopy of radiata pine ECM by Foster and Marks (1967) revealed the absence of bacteria on the inner portion of the mantle within 0–4 μm of the cortex. In some ECM, bacteria are found deep within the mantle in the interhyphal spaces if mantles are loosely woven. The largest bacterial populations ($111\text{--}222 \times 10^9$ cells cm^{-3}) exist in the outermost portion of the mantle 4–16 μm from the cortex and in the adjacent rhizosphere soil. Smaller populations (14×10^9 cells cm^{-3}) are found in the bulk soil. Bacterial species colonizing the mycorrhizosphere may be determined, in part, by the ectomycorrhizal fungus, although the specific exudates responsible have not been identified. The bacteria of a black ECM of radiata pine differed from those of red and white ECM observed by Foster and Marks (1967). The bacteria associated with the latter two ECM were usually ovoid ($3 \times 0.6 \mu\text{m}$) and were found either singly or in small colonies. Similar ovoid bacteria were occasionally found associated with the black ECM, but the most frequent bacterium was an elongated ($5 \times 0.5 \mu\text{m}$) species. Unfortunately the bacteria were not further characterized. Early reports of nitrogen fixing by ECM arise from “bacterial contaminates” (Richards and Voigt, 1964). Neal et al. (1964) reported a lower percentage of *Streptomyces* from the mycorrhizosphere of Douglas-fir ECM and adjacent suberized root rhizospheres than in bulk soil. Plate counts of bacteria were significantly higher ($P \leq 0.05$) in the mycorrhizosphere than in non-rhizosphere soil. Different bacterial phenotypes dominated the colonies isolated from three morphologically-distinct Douglas-fir ECM. Dilution plating has shown that yellow birch ECM have 1.6 times more bacteria associated with them than “normal” roots (Katznelson et al., 1962). Bacteria requiring complex nutritional factors appeared to be relatively more numerous on birch ECM, as expected if fungal exudates are a major, or the only, component of exudates in the mycorrhizosphere. Seventeen percent of the bacterial isolates from mycorrhizae required complex or unknown factors for growth, whereas only 1% of the isolates from “normal” roots required complex media. Conifer roots studied by Oswald and Ferchau (1968) also showed some differ-

ences in specificity of bacterial associates. Of 51 species isolated, 7 were found only on non-mycorrhizal roots, 22 were found only on ECM, and 22 were common to both. No information has been published on mycorrhizal effects of nitrogen fixation of non-leguminous hosts including alder and other ectomycorrhizal hosts (Trappe, 1979).

Fungi

Our knowledge of the activity of non-mycorrhizal fungi in the rhizosphere is based on dilution plating; a method favoring species producing large numbers of easily-germinated spores, but providing little data on non-spore producing fungi. At best, data resulting from this method are an index of past growth conditions. The few published photos of ECM surfaces (Foster and Marks, 1967) do not show the presence of any non-mycorrhizal fungi. Fontana and Luppi (1966) isolated 66 fungal taxa from pine, larch, oak, chestnut and corylus ECM by dilution plating. Species diversity and abundance was generally higher on mycorrhizal roots than on non-mycorrhizal roots. Fewer molds were isolated from the mycorrhizospheres of three morphologically-distinct Douglas-fir ECM than in bulk soil (Neal et al., 1964). Fungi obtained from the mycorrhizosphere were predominantly *Penicillium* taxa together with *Aspergillus* and *Trichoderma* species. These non-mycorrhizal taxa producing massive quantities of spores were also abundant in non-rhizosphere soil. In a study of washed mycorrhizal and non-mycorrhizal roots of yellow birch, 14 genera of fungi were associated with ECM, including one pathogen; 8 genera, including 3 pathogens, were isolated from non-mycorrhizal roots (Katznelson et al., 1962). Washing removes spores from the root surface as the absence of *Trichoderma*, *Aspergillus* and *Penicillium* from the non-mycorrhizal roots studied indicates.

Animals

Visser (1985) in her review of the role of soil invertebrates in determining the composition of soil microbial communities identifies three main mechanisms for their influence: (1) comminution, channeling and mixing; (2) grazing; (3) dispersal of diaspores. Very little information exists on the importance of these invertebrate mechanisms in the mycorrhizosphere, except some hints that grazing might be significant.

Nematodes are very abundant in soils of coniferous ecosystems and a great many types of symbioses are exhibited by this group. Distribution of nematodes is often aggregated or clumped, probably reflecting the distribution of their food source, thereby making reliable population estimates difficult, especially from random soil cores (Goodell, 1982). Time-lapse films of root growth

of apple trees in the East Malling rhizotron show large numbers of nematodes appearing in the rhizosphere when the cortex and epidermis are being sloughed, and then moving out of view when all of the material is consumed.

Mycophagous nematodes have been shown to reduce growth of cultures of ectomycorrhizal fungi (Riffle, 1967). Feeding by *Aphelenchus avenae* caused the hyphal walls to collapse or hyphal tips to shrivel for some distance around the puncture. *Aphelenchoides cibolensis* fed and reproduced on 53 of 58 ectomycorrhizal and root-rot fungi tested under laboratory conditions (Riffle, 1971). The fungi tested showed varying degrees of reduction in growth, or even died, indicating the potential for nematodes to reduce or inhibit ECM formation under natural conditions. Shortleaf pine ECM parasitized by *Cricone-moides rusticum* lacked a mantle and Hartig net (Jackson, 1948). Similarly, *Aphelenchus avenae*, consumed the ECM mantle of red pine in vitro (Sutherland and Fortin, 1968). The best host for this species was *Amanita rubescens* followed by *Suillus punctipes*, *S. granulatus*, *S. luteus*, *Russula emetica*, *Cenococcum graniforme* (= *geophilum*), and *Rhizopogon roseolus*. The latter apparently produced a substance which was toxic to the nematodes. Nematodes preferred hyphal tips for feeding and did not enter healthy, intact roots.

ECM may also be damaged by nematodes penetrating the fungal mantle to feed on the root tissues or to produce eggs. Swollen females have been found in a number of different ECM. *Hoplolaimus tylenchiformis* and *Meloidodera floridensis* penetrated ECM and lateral roots of slash pine and loblolly pine to feed on the cortex (Ruehle, 1962). Pot experiments on parasitism of these two pines by *H. galeatus* showed that both male and female nematodes penetrated the ECM mantle to feed on the cortex (Ruehle and Marx, 1971). Although the fungus was only slightly damaged, wounding by nematodes may permit entry of root pathogens, but probably does not lessen resistance shown by some ECM to fungal attack because the cortical cells are still protected by the Hartig net hyphae (Riffle, 1971). A more direct effect of wounding is a reduction in the benefits of ECM through leakage and consumption of photosynthate.

Some small mites, *Acarina* spp., were found to be regularly associated with ECM of loblolly pine (Danielson, in Davey, 1971).

Large numbers of collembola are found in coniferous forests. Hagvar (1982), for instance, calculated Collembola numbers range from 31 500 to 201 400 m⁻² in the top 12 cm of soil. Despite their abundance, almost no information is available on their interactions with ECM. Collembola studies concentrate on their role in litter decomposition, with sampling usually confined to the upper 10–12 cm of the soil. The one reference I was able to locate compares the preference of 4 ectomycorrhizal and 4 saprotrophic fungi as food for *Onychiurus armatus* (Shaw, 1985). In vitro, the hyphae of the ectomycorrhizal fungus *Lactarius rufus* are the most highly preferred of the 8 fungi tested. The other ectomycorrhizal fungi, *Paxillus involutus*, *Heboloma crustuliniforme*, and *Rhizopogon luteolus* are the least preferred, perhaps owing to toxins.

Aphids, probably *Pemphigus piceae*, have been observed feeding on Douglas-

fir ECM (Zak, 1965). A similar aphid was also observed on western hemlock and Sitka spruce ECM. Infestations were highest on ECM formed in rotten logs. A second aphid, *Prociphilus americanus*, was observed feeding on suberized roots of noble fir, but not ECM. Infestation varied by type of ECM, with the black ECM formed by *Cenococcum geophilum* more resistant than two different brown types of ECM. The thick-walled hyphae of *Cenococcum* presumably deterred attack. Aphids may have pierced the mantle to feed on root tissue, but this is not clear from the descriptions. The presence of an unidentified blue-green mold on recently-attacked ECM surfaces suggests non-mycorrhizal fungi and pathogens may invade damaged ECM.

In addition to the ECM, the extramatrical mycelium and reproductive structures are potential sources of food. The conceptual problem of mycorrhizal hyphae being present in the lower organic layers of the soil have not been addressed in carbon models or in the voluminous literature on the interactions between fungi and invertebrates in decomposition. Mycorrhizal fungi and saprotrophic fungi represent different trophic levels, if one views mycorrhizal fungi as functional, inseparable extensions of the plant root system much like the tight association between bionts in the lichen association. The problem in using this concept to refine models is that hyphae of mycorrhizal and saprotrophic fungi, with few exceptions, are indistinguishable.

Fruiting bodies and sclerotia of saprotrophic and mycorrhizal fungi can be distinguished and long lists of ectomycorrhizal fungi are available (Trappe, 1962; Harley and Harley, 1987). Very little is known about the interactions of *Cenococcum geophilum* sclerotia, very common in coniferous forests, and animals, but mushrooms and truffles, *sensu lato*, are an important food for many animals, including small mammals (Fogel and Trappe, 1978). A large proportion of the spores present in the digestive systems of small mammals from coniferous forests in western Oregon were produced by mycorrhizal fungi (Maser et al., 1978). Basidiomycetes were the most frequent group, 61% compared with Ascomycetes 23% and Endogonaceae (VAM symbionts) 13%. The relationship between truffles, false-truffles and small mammals is highly evolved with olfactory clues to location of sporocarps being produced by the fungus at maturity. Truffles are nearly completely dependent on small mammals for dispersal, since the production of sporocarps below ground and loss of active spore discharge mechanisms precludes aerial dispersal; some mammals in turn are almost completely dependent on truffles for food.

Mushrooms, truffles and false-truffles produced by ectomycorrhizal fungi are also utilized by invertebrates (Fogel, 1975; Fogel and Peck, 1975) and may even support a small food web consisting of fly larvae, bacteria, nematodes, mycophagous beetles and predatory beetles (R. Fogel, unpublished data). Mycophagous and bacteriophagous nematodes are common in mushrooms produced by ectomycorrhizal fungi in a radiata pine forest (Walker, 1984).

SYNTHESIS

Nearly all of the theory on the effect of interactions among soil biota on ecosystem processes has been developed in vesicular–arbuscular mycorrhiza dominated systems (e.g. Coleman et al., 1983; Anderson et al., 1985; Coleman, 1985; Visser, 1985). The absorbing roots of many coniferous trees are overwhelmingly ectomycorrhizal and differ significantly in morphology from non-mycorrhizal and VAM root systems. The ecosystematic implications of this morphological change, especially the presence of a mycelial sheath or mantle, are very poorly understood.

One implication of the ECM mantle is that “root” exudates are primarily fungal in origin and the differences in exudate chemistry will affect the species composition of the biota near the ECM, creating a mycorrhizosphere. Species differences in the mycorrhizosphere bacteria and/or fungi in turn will affect the species of soil animals present. A number of predictions on the factors determining species diversity in the mycorrhizosphere, nearly all untested, arise from this scenario. These predictions include: (1) mycorrhizosphere bacteria will utilize fungal-produced mannitol or trehalose rather than sucrose, glucose or fructose as simple carbon sources; (2) fungal exudates will be produced over a period of months compared with a few days in actively growing non-mycorrhizal roots; (3) senescent ectomycorrhizae are the main substrate available for microbes; (4) ectomycorrhizal fungi as *k*-selected species will produce a broad range of secondary compounds to inhibit mycovores; (5) nematodes parasitizing root hairs will be few in number; (6) species diversity of mycorrhizal fungi will be higher than in VAM systems; (7) the diversity of ectomycorrhizal fungi present will produce a great variety of mycorrhizospheres owing to strain and species differences in production of secondary compounds, strand or rhizomorph formation, wall thickness of hyphae, and cell-wall chemistry, e.g. fungal melanin; (8) the mycorrhizospheres produced by the same mycorrhizal fungus on quite different hosts, e.g. pines and oaks, will be more similar than mycorrhizospheres produced by different fungi on the same host.

The creation of a mycorrhizosphere distinct from the rhizosphere of most plants, hinges on postulated differences in exudate production. Unfortunately, the critical experiment comparing the exudates produced by infected and non-infected short roots of an ectomycorrhizal host has not been done. Data, especially quantitative data, are sorely needed on identity of simple carbohydrates, amino acids, antibiotics and organic acids produced in the mycorrhizosphere.

More data are available on the biota present in the mycorrhizosphere. The data are of limited value, however, in modeling ecosystem processes since they consist mostly of abundance data or at most qualitative data or descriptions of interactions between two species, e.g. aphid–mycorrhiza, nematode–mycorrhiza.

Direct studies, observation using mini-rhizotrons, manipulations using maxi-

rhizotrons or radiolabelling experiments, have great potential for improving our understanding of interactions in both time and space. Reconstruction of food webs from abundance data, derived from soil cores and classification of fauna by general feeding class or trophic group is inadequate. Very often the food items are indistinguishable, as exemplified by mycorrhizal and saprotrophic hyphae, or mouth parts may not accurately reflect feeding. Walter et al. (1986) found in vitro that even when "fungivorous" mites were offered yeast and algal cells 11–56% of the mites, *Tyrophagus* spp., fed on nematodes. A study of invertebrates feeding on living ^{32}P -labelled clover roots revealed that coleopteran larvae and earthworms were the most heavily labelled; a surprise since earthworms are generally classified as saprophages, not root feeders (Baylis et al., 1986). Magnusson and Sohlenius (1980) and Sohlenius (1980) in one of the few studies of losses to below-ground herbivory by nematodes were unable to separate root and fungal feeding nematodes in their study, obscuring interactions among 3 trophic levels.

Direct observations have not been exploited fully in studying the movement of biota and the timing of interactions. Nearly all of the papers reviewed on nematodes and collembola during the preparation of this paper restricted sampling to a depth of 10 cm, rarely deeper. Nematodes are known to occur at greater depths. Studies on the phytoparasitic nematode, *Meloidogyne incognita*, in a fumigated tomato field showed that this animal can migrate 120 cm vertically to infect tomato roots (Johnson and McKeen, 1973). It was not determined whether movement of this species is random or directed, or whether movement proceeds rapidly before or after tomato roots have penetrated below the zone of fumigation, where permanent populations are found. The timing question is also of interest. Time-lapse photography of apple roots in the East Malling rhizotron showed nematodes appearing in mass when the cortex of unuberized roots is being sloughed, feeding, and then moving away from the root. Soil cores and other bulk soil samples stand a very good chance of missing or otherwise underestimating the abundance of these nematodes since the population is highly patchy in both time and space owing to their feeding on roots at a particular developmental stage.

Nearly all of the collembola studies also restricted sampling to the top 10–12 cm, although the agroecosystem literature indicates that species with small bodies may be found at considerable depths in sandy soils (Curl and Truelove, 1985). Collembola are consistently more abundant in the rhizosphere of cotton than 20-cm distant (Wiggins et al., 1979). Vertical movement of Collembola and other mesofauna is determined in part by soil pore size. Root surfaces might also be important avenues for migration. Faiz and Weatherley (1982) have shown experimentally that sunflower root tissues may contract as much as 25% of their turgid volume when water potential of the leaves falls to -15 bars, producing a gap for movement at the root–soil interface. Loss of the pri-

mary cortex can cause a 50% reduction in diameter of apple roots (Atkinson and Wilson, 1979).

More interdisciplinary research, or at least communication, is needed. Almost no mention is made of the interaction of macrofauna other than earthworms with roots in the ecological literature, although beetles may be important in some systems. Pine root weevils, *Hylobius rhizophagous*, and white grubs, *Phyllophage* spp., are major causes of tree mortality in young jack and red-pine plantations in the Lake States. Despite their importance and names indicative of root feeding, very little is known about their interactions with other biota other than the larvae feed on "rootlets" or "fibrous roots" (Fowler and Wilson, 1971; Goyer and Benjamin, 1972). Similarly, there is very little integration of knowledge about fungal pathogens into the forest soil-biology literature. Root rots are chronic in most native forests, causing losses of 115 million cubic feet of timber in Oregon and Washington forests or 4% of the annual growth (Childs and Shea, 1967). These figures do not include losses due to fine root diseases and underestimate chronic losses from infections of large roots that survive indefinitely.

Clearly, numerous opportunities abound for making major, fundamental contributions to our understanding of the interactions among biota in coniferous ecosystems.

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