

## THE ROOT MYCOBIOTA OF WOODY PLANTS

P.A. Volz<sup>1</sup> & V.P. Isikov<sup>2</sup>

<sup>1</sup>East Michigan Mycology Associates, 1805 Jackson Ave., Ann Arbor, Michigan  
48103-4039 U.S.A.

<sup>2</sup>Nikita Botanical Gardens, Krasnoarmejskaja Street N 10, Kv. 5, Yalta, Crimea  
334267 UKRAINE

### ABSTRACT

The fungal community of roots can be beneficial, detrimental, or a chance relationship of no significance to fungi and the roots of trees occupying the same soil territory. Interrelationships also are influenced by the physical quality and content of the soil, plant, and animal life present, and other additional members of the microbial population including bacteria, viruses, nematodes, and other micro-organisms. The environment in which the woody plant roots are found is selective due to the physical, chemical, and biological determinants present in the soil. This habitat is also influenced by the weather, the change of seasons, temperatures, light intensity, and diurnal periodicity in the form of rain, snow, fog, and dew, as well as degree, amount, and type of air pollutants that filter into the soil. The environment above the soil line also influences the environment in the soil, and all serve as factors governing the relationships and populations of fungi in association with roots of woody plants.

**KEY WORDS:** fungal ecology, root mycobiota, forest habitats

The soil - root - woody plant fungal community is a complexity that defies discussion even in a limited evaluation of fungal species present in the environment of the roots. The magnitude of a soil - root study is a topic that does not fit within the scope of a single chapter, therefore discussion is primarily directed to the fungi of roots of woody plants. Interspecific relations of fungi and roots create different degrees of association, residing together in some degree of association. An equilibrium or biotic balance of the fungi and roots could create a steady state of existence in which the root cell area and the fungal mycelium and reproductive cells are held in a fixed ratio of each other. The surrounding environment contains many variables, yet the capacity of fungal density, and root ratio remain somewhat steady, creating a homeostatic state. The relationships of tree roots and soil micro-fungi could range from loose association to close proximity of commensals, organisms that feed

together. One species profits by living together with the other. In commensal relations, one species converts an unavailable substance to an assimilated substance for the other. One species could exude a waste product that the other species associate could utilize or the product could inhibit the growth of potential competitive species. Also, one commensal species could directly provide nutrients, protection, moisture, or shelter for the other. The species could coexist under specific circumstances, both fungus and woody plant could easily, and frequently do, exist separately.

Tree roots and fungi could act as symbionts, each receiving mutually beneficial effects from the other. Both species are helpful to each other and receive an essential part of the microenvironment from the other. These associations could be species specific. A reliance exists, and frequently these associations are limited to individual symbionts which increases the growth rate of both the tree and the fungus. Enhanced metabolic activity of the root and the fungus could result in supplying organic nutrients, generate  $\text{CO}_2$  or  $\text{O}_2$ , removing  $\text{O}_2$ , assimilating  $\text{N}_2$ , or providing minute amounts of growth factors. Together the fungus and the tree root could provide physical support, supply inorganic nutrients, utilize metabolic wastes, protect against parasites, and shield against the environment.

Of course the root system of trees and the mycelium of fungi found in the same soil habitat remain in competition for certain nutrients, water, and the space that they occupy together. These organisms remain in rivalry for the same parameters. Parameters contributing to this competition include the rate of growth of both trees and fungi plus the growth of other organisms, both plants and animals inhabiting the soil. Tolerance to abiotic factors present in the same location influences survival and growth. The ability of the woody plants and the companion fungi to multiply, grow, and propagate new roots or hyphae at low concentrations of limiting nutrients influences the living team members. The capability and the efficiency of utilizing limiting nutrients could serve as the chief survival factor of one or both of the organisms present in the shared community. In this common territory, the ability to store and synthesize reserve substances in living cells is also vital to survival for the competing populations. Phosphorus uptake and below ground carbon utilization were measured using ectomycorrhizal *Thelephora terrestris* and non-mycorrhizal *Salix viminalis* L. Phosphorus inflow rates were three times as high for *T. terrestris* root systems as for *Salix* root systems (Jones *et al.* 1991). Nutrient requirements directly affect carbon economics of the woody plants.

At times, a species of a community creates interactions conflicting with other species. One species is suppressed because of toxins produced by the other species. The growth of one species utilizes the nutrients at that location and alters pH of the mutual habitat that interferes or enhances survival of other species present. The production of hydrogen peroxide, ammonia, and nitrite that accumulate during ammonium oxidation, and hydrogen sulfide accumulation occurs due to the presence of living organisms.

Few fungi, considering the total number and diversity of fungal species, function at all times as an obligate pathogen occupying an environment and serving as a disease causing agent on every opportunity for growth. Most fungal species do not cause disease. In a true parasitic association, the host becomes the food source of another organism. When the fungal organism in the soil invades tree root systems, a parasitic relationship becomes established. An opportunity is opened for the fungus existing in

close proximity to roots to establish disease. Frequently, micro-fungi grow in soil on organic matter that comprises the soil particles. Chance contact of the fungus with the root allows the fungal hyphae to associate with living cells of the root. Penetration of cell walls by the hyphae establishes a parasitic relationship, however, only a very limited number of micro-fungi are parasitic and never create an opportunity for living cell invasion.

In deeper layers of soil, fungal activity is generally associated with plant roots. Fungi growing in the vicinity of plant roots are frequently stimulated in growth compared to fungal species in soil away from the influence of roots (Barton 1957). The rhizosphere effect of roots of higher plants was discovered by Hiltner (1904). The rhizosphere root soil complex contains organic substances released from roots that stimulate micro-fungi spore germination as well as hyphal growth (Jackson 1957). Sterile mycelial forms are commonly found associated with roots of woody plants, presenting no obvious beneficial or detrimental association with the plants (Harley *et al.* 1955). Organic matter which accumulates in soil from roots is composed of insoluble cell wall debris, polysaccharide mucilages secreted by root cells, mucilages formed from polysaccharide hydrolysates of cell walls, and water soluble exudates given off by root tissue (Foster & Rovira 1973). Vitamins, enzymes, growth hormones, and other organic substances are found in plant exudates. Volatile organic acids, aldehydes, and unsaturated fatty acids are also produced by roots that inhibit and at times stimulate fungal growth (Fries 1973). Ethylene can be produced by roots which also regulates growth of micro-fungi (Burg 1962). Mucigel polysaccharides found on root caps are a rich source of substrates for micro-fungal as well as bacterial growth (Greaves & Darbyshire 1972).

Fungistatic properties of soil keep most fungal propagules under control through microbial competition and soil nutritional limiting factors retarding the growth of the organism. The stimulation of micro-organisms in the rhizosphere is caused by the presence of an increased supply of nutrients in the form of soluble inorganic and organic root excretions (Jackson 1960). The breakdown products of sloughed-off dead root cells, lowering of the concentration of certain mineral elements in the soil due to their absorption, soil desiccation from water absorption, and increase in soil carbonates following carbon dioxide production by the roots all directly relates to the rhizosphere community (Starkey 1929). However, a very high percentage of fungi in soils are present as inactive propagules (Warcup 1955). Sugars induce the germination of inhibited fungal spores, and these carbon sources are produced by root excretions by seedlings in quantities sufficient to have stimulating effects on the soil populations of fungi. Excretion of sugars occurs primarily in the young meristematic regions of roots (Jackson 1960). The rhizosphere effect itself may be studied along two broad lines, one concerning the plant influence on soil micropopulations, the other dealing with the influence of the rhizosphere microflora on the plant (Katznelson 1960).

Microflora populations in the rhizosphere increase as plants age. Greater quantities of organic matter become available through aging and death of plant roots for the growth of micro-fungi in the soil (Peterson 1958). Older roots are more vulnerable to damage by soil particles and invasion by micro-fungi into epidermal and cortical cells adjacent to the mucigel sheath (Old & Nicholson 1975). In woody plant roots, primary cortex is sloughed off during secondary growth which adds to the organic concentration in the rhizosphere of older trees. It was concluded that half of the root

system of apple trees (*Malus* spp.) is lost as cortical tissue each year (Rogers 1968). Also, the natural death of young root system of mature plants and of major branch roots also adds to the carbon, nitrogen, and mineral content of the rhizosphere, enhancing the growth of micro-fungi. Several hundred kilograms of biomass per hectare of soil accumulates from decomposing root systems (Head 1973).

Changes in tree physiology induced by environmental changes is also influential on rhizosphere micro-fungi populations. Beach (*Fagus sylvatica* L.) root surface fungi undergo significant changes (Harley & Waid 1955b). Low light intensities increase root colonization of *Cylindrocarpon* and *Rhizoctonia* species, while high light intensities increase populations of *Trichoderma* and *Gliomastix* species. Light intensity and temperature also influence the amount and availability of amino acid and organic acid content of exudate production (Rovira 1959; Smith 1972). Desiccation increases amino acid exudate release through roots to the soil adding to nutrients available for soil micro-fungi. Phosphorus (Katznelson *et al.* 1954), potassium (Rovira & Ridge 1973), and nitrogen (Bowen 1969) added to the soil as fertilizer also change exudate production in the root system and the amount of nutrients for the growth of fungi, depending on plant species, plant age, and various soil qualities. Soil micro-fungi interactions and associations with other micro-organisms in the rhizosphere are discussed in detail by Brown (1975), Curl & Truelove (1986), Mosse (1975), and Hale *et al.* (1978).

Root infection by fungi consists of an infinite series of gradations between primitive facultative parasite and obligate parasite associations (Garrett 1960). Most root associations by fungi are saprophytic, with few species causing disease in woody plants. The classic example of tree root disease in forest trees is *Armillaria mellea* root rot, first described in 1873 (Hartig 1873). Another classic parasite is gummosis disease of citrus, caused by *Phytophthora citrophthora*, first investigated in 1878 and continued through 1949 (Fraser 1949). The fungal attack is gradual and starts in young rootlets, slowly migrating upwards, finally exhausting the tree. The persistent *Armillaria* can remain six years or more in infected citrus roots of less than 30 mm in diameter (Bliss 1951). Carbon disulphide soil fumigation was first used to control *A. mellea* in infected roots, a method used for over 40 years. However, as *A. mellea* decreased in dominance, *Trichoderma viride* gradually increased to become the dominant soil borne fungus (Warcup 1952). Formalin treatment of soil also promoted dominance of *T. viride* which proved to be a much more tolerant fungal species with tree root association. When *Fomes lignosus*, *F. noxius*, and *Ganoderma pseudoferreum* infecting roots of rubber trees were controlled by dichloropropano-dichloropropylene treatment, this action also brought a similar dominance of *T. viride* in the soil (Altson 1950). Further study indicated chemical control of the fungal pathogens was less significant, but the antibiotic activity of *T. viride* was more effective in the soil habitat (Weindling 1941; Weindling 1934; Weindling 1932).

A succession of fungi is noted in soil substrates (Garrett 1960). Substrates in all habitats, including soil, are in constant change, replacement, and depletion. Root surface micro-fungi exist topically and survive as epiphytes (Hiltner 1904). Initial invasion of the root surface is made by a sequence of saprophytic sugar fungi. Next in sequence are the cellulose decomposers, and finally the lignin-decomposing fungi invade root tissue. An ordered succession under continual change occurs. Maximum destruction of host tissue occurs when fungal parasites overwhelm the resistance of mature host plant roots in full growth vigor. The most vigorously growing trees

quickly succumb to fungal attack at the soil level by these destructive parasites (Waterston 1941). Species of *Rosellinia* found in the tropics as a saprophyte in surface litter under heavy shade can easily revert to becoming a destructive tree root invasive parasite.

Many of the tree root-inhabiting fungi exhibit an ectotrophic growth habit in that the invasion is continuous and indefinite over the host root system (Garrett 1960). *Fomes lignosus* and *Poria hypolateritia* behave in this way also (Petch 1928). In rubber plantations of Malaysia, *F. lignosus* was found to grow through the soil on continuous surfaces such as boulders and dead roots, however, nourishment was through infecting living roots (Napper 1932). It was also observed that sporophores of *F. annosus* may be attached to rootlets so fine that the attachment escapes notice, giving rise to misconceptions that *F. annosus* could live as a saprophyte on forest litter (Risbeth 1951). In reality it is a specialized root-inhabiting parasite of conifers and other trees.

The efficiency of rhizomorphs of *Armillaria mellea* from wood origins is quite remarkable. The strands can grow freely through the soil, extending 22 yards from an infected pit-prop in a mine-working (Ellis 1929), and 30 feet in a water tunnel leading out of a reservoir, in hard rock 200 feet below ground level (Findlay 1951). Rhizomorphs extend in all directions through the soil from a food base of infected wood. Nutrients are supplied by the wood but the soil gives support and possible water and mineral uptake as well. It was learned that ethanol and other short chain alcohols stimulate rhizomorph production (Weinhold 1963). The bulk of *A. mellea* rhizomorph growth requirements are obtained from root tissues, the quality of which may greatly influence rhizomorph production (Redfern 1970). When conifers are wounded or infected, the neighboring tissue frequently becomes impregnated with resin. Artificial infection of two blue-stain fungi (*Ceratocystis ips* and *C. minor*) was successful in pine trees with low resin exudation pressure but not in those with medium or high pressure (Mathre 1964). Volatile components of *Pinus ponderosa* Douglas ex Lawson & C. Lawson resin are toxic to *Fomes annosus* (Cobb et al. 1968). Also, the pinosylvins in infected sapwood of pine have mild fungitoxic properties to *F. annosus* infection (Shain 1967).

Fungi of soil and rhizosphere habitats, fungal distribution in soil, fungal activity in soil, root colonization and root diseases are topics of increased attention in later years. The volume of literature is astronomical (Dix & Webster 1995). Likewise, mycorrhizae are receiving increased attention in soil structure and biogeochemistry, soil reclamation, and biocontrol measures (Pfleger & Linderman 1994). More attention is also directed to the tropical forests of the earth as they relate to the whole earth ecology. Mature tropical forests of rubber [*Hevea brasiliensis* (Willd.) ex A. Juss.] Müll. Arg.], teak (*Tectona grandis* L.f.), and palms (*Elaeis guineensis* Jacq., *Cocos nucifera* L.) have a few pathogenic root lignicolous fungi such as *Rigidoporus lignosus*, *Ganoderma* spp., *Armillaria* sp., *Phellinus noxius*, *Sphaerostilbe repens*, and *Ustulina deusta*. Many other fungi are saprophytic or weak parasites such as *Favolaschia thwaitesii*, *Pycnoporus sanguineus*, *Hexagona apiaria*, *Dacryopinax spathularia*, *Auricularia polytricha*, *Cookeina sulcipes*, and *Phellinus gilvus* (Intini 1991).

It has been recently shown that ectomycorrhizal fungi of tree roots and shoot biotrophs are more host specific than root necrotrophs. Woody hosts are associated

with a greater number of mutualistic fungi than antagonistic fungi. Some hosts are resistant to fungal invasion and others are quite susceptible (Borowicz & Juliano 1991). Ectomycorrhizal fungi colonize roots and are not affected by the presence of saprophytic fungi. The ectomycorrhizal species tend to be more dominant than the saprobes (Shaw *et al.* 1995). Soil borne mycorrhizae fungi also are associated with and closely monitored for the crop production of Chile's citrus industry (Jiménez & Gallo 1993).

Ectotrophic growth patterns of the fungi in roots evolved into mycelial sheets or strands, or into rhizomorphs, or into individual hyphal threads. The growth variations are in response to overcome host resistance to infection by the tree roots (Garrett 1970). Rhizomorphs of *Armellaria mellea* grow from an apical meristem (Motta 1967). Density of the branching increases with the increase in nutrients to an optimum value, forming a fibrous growth pattern. Growth rate of rhizomorphs is much greater than unorganized individual hyphae of the same species. Mycorrhizae are widely distributed among the phanerogams. Only about 3% of phanerogams exhibit ectomycorrhizae, most belong to the endomycorrhizae (Meyer 1973). Various chemical compounds are involved in the formation of mycorrhizae such as orchinol (Gaumann *et al.* 1960).

Many trees would not be capable of developing massive sizes without the symbiotic relationship of the root-inhabiting fungi. Without mycorrhizae, pine trees would be more aptly considered pine bushes. Obligate ectomycorrhizal trees include the genera *Abies*, *Larix*, *Picea*, *Pinus*, *Carpinus*, *Fagus*, and *Quercus* (Meyer 1968). More typical facultative ectomycorrhizal genera are *Cupressus*, *Juniperus*, *Salix*, *Betula*, *Corylus*, *Alnus*, *Ulmus*, *Pyrus*, *Acer*, and *Eucalyptus* (Meyer 1973). These trees survive well in the absence of ectomycorrhizal fungi. Endomycorrhizal trees are abundant in tropical forests of the lowlands, ectomycorrhizal trees are frequently pioneers on wastelands. Endophytic infection development by *Glomus* in sugar maple roots revealed changes in cortical cells similar to other woody plant hosts. Large intracellular hyphae enter the cortical tissue while arbuscules formed from initiation points at various places on the intracellular hyphae (Yawney & Schultz 1990). The arbuscules in the roots are the sites of transfer between the host and endophyte.

Mycorrhizal root association by fungi was first observed by Frank (1885). The benefits of this symbiotic association are numerous and the extent of these associations in the literature of early investigators is well reviewed by Rayner (1927) and Kelley (1950). Mycorrhiza are classified into two groups. Ectomycorrhiza fungi form a mantle around roots and intercellular hyphae grow within the root cortex. Forest tree associations are ectotrophic and most of the fungi are Basidiomycetes. Endotrophic mycorrhizae are inter- and intra-cellular in the host cortical cells.

Due to the growth patterns, ectotrophic mycorrhizal fungi are considered to have evolved from specialized root pathogens (Garrett 1970). Of equal possibility, these specialized symbionts may have evolved from saprophytic root surface fungi (Harley 1948). The growth relations of these fungi have developed an efficient mechanism in quite a delicate balance of host-parasite association and host-resistance tolerance. Further characterizing this fungal growth, infection of short roots is truly ectotrophic with a fungal mycelial sheath covering the root surface. Long roots are penetrated internally as an extension of the Hartig net of fungal tissue internally in the host root cortex (Robertson 1954). Two modes of ectotrophic infection of *Fomes annosus* on

*Pinus sylvestris* L. (Scots pine) are possible (Risbeth 1951). In alkaline soils, the fungus grows freely on the root surface, forming pronounced sheet-like mycelial aggregates. Acid soils delay or totally suppress epiphytic mycelium, and slows infection with the root cylinder infections at times ahead of the epiphytic growth. Ectotrophic advance on the outside of roots in alkaline soils is much ahead of the fungal growth in acid soils (Wallis 1961).

Douglas fir [*Pseudotsuga taxifolia* (Lamb.) Britton], larch (*Larix decidua* Mill.), and spruce [*Picea abies* (L.) H. Karst] resistance to inner wood tissue infection is lower than that in species of pine, so infection is more severe (Risbeth 1951). Fungal growth from saprophyte to parasite is definite per tree genus, following defined patterns from initial infection to advanced tree disease. The degree of resistance to infection from *Fomes annosus* in pines is correlated with the complexity and activity of resin canal systems (Gibbs 1968; Gibbs 1967). The toxicity factor of resin to *F. annosus* and four timber bluestain fungi was studied (Cobb *et al.* 1968). Crude oleorecin and components of the volatile turpentine fraction, purified by fractional distillation reduced hyphal growth of *F. annosus* and the bluestain fungi by various degrees when the fungi were exposed to a vapor saturated atmosphere. The nine terpentine components were identified as two monocyclic, four bicyclic, and one open-chain terpene, and two alkanes. The alkane n-heptane was the most fungistatic, completely inhibiting hyphal growth of *F. annosus* and the wood bluestain fungus *Ceratosystis pilulifera*.

Tree mycorrhizal formation and structure is directly associated with many factors affecting root development (Marks & Foster 1973). These factors include fertilizers (Zottl 1964), light (Kinugawa 1965), girdling, decapitation, and defoliation of shoots (Richardson 1953), temperature (Barney 1951), soil moisture and aeration (Mikola 1967), auxins (Slankis 1958), minerals (Davis 1949), bacterial physiology (Wichner & Libbert 1968), root disease (Zak 1964), and carbon, vitamin, and nitrogen source (Gibson 1961). An ecto- endomycorrhizal condition is common in aging mycorrhizae with the intracellular penetration of cortical cells (Marks & Foster 1967). One mycorrhizal type can be replaced by another when root growth resumes after a dormant period.

Mycorrhizal partnership can form between a single tree species and a number of different fungi (Zak & Marx 1964). Like roots, shoots, and individual hyphae, rhizomorphs grow from the apex of the structure, as long as minerals are present, provided by the host root and the soil through which it is passing. Rhizomorphs will continue to grow only for as long as the apices are covered by an unbroken film of water (Griffin 1969). The presence and importance of mycorrhizae in forest soils is the mutual support the trees and fungi have for each other, the subject of symbiosis between autotroph and heterotroph (Harley 1975).

Alkaline soils as compared with acid soils allowed for more rapid growth of *Fomes annosus* (Risbeth 1950), and moisture stress increased susceptibility of *Pinus taeda* L. (loblolly pine) to infection (Towers & Stambaugh 1968). Growth inhibition and antagonism caused by bacteria and other fungi against another fungus takes place in the root zone. The degree of *Trichoderma viride* antagonistic effects against *F. annosus* is related to particular strain isolates (Mughogho 1968). Forest root exudates contain a combination of amino acids, carbohydrates, and organic acids according to species and soil type (Smith 1969). The concentration of exudate in the rhizosphere

depends on rate of movement in soil and uptake by micro-fungi. The rhizosphere of young fir seedlings contains 0.3 (in millions) total number of fungi in 1 g soil, overcrowded prime firs contain 0.02, old firs (*Abies alba* Mill.) 0.08, and in the soil of a fir plantation 0.065 (Maliszewska & Moreau 1960). There is a more varied flora in the soil and rhizosphere of young firs. *Trichoderma viride* is present in soil around roots of young firs, also in soils carrying a good regeneration. This species is absent in soils offering a poor regeneration of fir seedlings, and in the rhizospheres of old trees. The presence, and often abundance of *T. viride* can serve as the index of soil fertility for a wide variety of plant species.

Tree seedling fungal studies have been contained in controlled environments in the laboratory and controlled plots in nature for a better understanding of study parameters. Seedlings of live oak (*Quercus virginiana* Mill.), Chinese tallow tree [*Sapium sebiferum* (L.) Roxb.], and Texas mountain laurel [*Sophora secundiflora* (Gomez-Ortega) Lagerh. ex DC.] were inoculated with either ectomycorrhizal fungi (*Pisolithus tinctorius*) or vesicular-arbuscular mycorrhizal (VAM) endomycorrhizal fungi (*Glomus fasciculatum*, *Gigaspora margarita*, and *Glomus mosseae*) and transplanted into nature (Davis & Call 1990). The inoculated trees showed greater growth and survival than non-inoculated controls. Under controlled conditions, in roots of lodgepole pine seedlings, some competition in root association is noted by ectomycorrhizal and saprotrophic fungi (Shaw *et al.* 1995). The saprotroph *Collybia maculata* significantly retarded rate of colonization of lodgepole pine seedling roots by *P. involutus*.

Hundreds if not thousands of species of both macro- and micro-fungi reside in soil habitats making part if not all their life cycles in the soil environment. Roots of woody plants, as well as grasses and herbaceous species, create microenvironments for the establishment and growth of fungal hyphae and spore structures depending on the family and order to which they belong. The root cap is a protective region of the meristematic end of the root which per surface volume sloughs off the greatest quantity of cells into the sod as the root extends farther from the tree trunk and deeper into the soil. These sloughed off cap cells provide a rich carbon and nitrogen source of nutrients immediately around the root tip for the establishment of fungal growth. One saprophytic species by chance in the vicinity of the root begins growth in the enriched soil. Spores or other fungal elements of other species of micro-fungi soon establish themselves in close proximity to the growing roots. One or more species becomes dominant in the root environment according to the quantity and quality of nutrients accumulated as waste material from the woody and herbaceous plants. Established micro-fungal species present also add to the soil nutrients as waste products are produced and dead fungal cells accumulate in the root environment. A distinct micro-environment begins to evolve around the roots which supports the growth of other fungi and other microbes as they become established in the community.

Epidermal cells and cortical cells, resins, suberins, high molecular weight carbon compounds, nitrogen, and vitamins become available to the root environment as the fungal populations evolve, as new species become dominant and established species fade away. This material from the trees is deposited in the soil immediately adjacent to the root surface and remains in high concentrations around the expanding root as growth in circumference continues during each growing season of the tree. Deuteromycetes remain the dominant species of the saprophytic community but some specialized Basidiomycetes, Ascomycetes, and Phycmycetes are found in a root



bound community of micro-organisms according to other physical factors in the soil such as moisture content, aeration, available minerals, and varying relationships of the fungal species with the tree roots. Needle leaf tree species generally are devoid of root hairs and fungal hyphae form a symbiotic attachment with the tree roots. The fungus benefits from the relationship by obtaining glucose and other carbon sources from the tree supplied by photosynthesis. The tree benefits from the presence of the fungal hyphae by greatly increasing the surface to volume ratio capacity of the roots for the absorption of water and minerals into the host plant.

Host specific fungi are brought into the soil micro-environment with the establishment of various trees. The more broad spectrum saprophytes that grow equally well on many carbon and nitrogen sources establish their growth without the presence of host trees (Volz *et al.* 1992). Some of these fungi readily grow on organic material originating from human or animal sources, yet pathogenicity is not established unless the fungus is introduced into a potential host (Volz *et al.* 1993). Mycorrhizal fungi are mostly symbiotic, benefitting both themselves and their hosts as they grow together. If a fungal species penetrates the host root cortical or vascular system, a pathogenic relationship is established that could extend through the roots into the above ground portion of the tree such as the wood rot fungi to ultimately cause death to the tree or part of the tree. The tree species may have the capacity to outgrow its invader for a period of time, but survival is made more difficult under harsh environmental and seasonal changes experienced by the host tree. Eventually over a period of years, the tree will lose the battle to survive growth of the invading fungus pathogen, and death to the tree will occur. However, most fungal species found in the soil are micro-fungi that utilize organic matter and cause no harm to the tree species or other plants and animals of the forest (Volz *et al.* 1994).

## REFERENCES

- Alston, R.A. 1950. Diseases of the root system. Reports of the Rubber Institute of Malaya. 1945-1948. pp. 96-100.
- Barney, C.W. 1951. Effects of soil temperature and light intensity on root growth of loblolly pine seedlings. *Plant Physiology* 26:146-153.
- Barton, R. 1957. Germination of oospores of *Pythium mamillatum* in response to exudates from living seedlings. *Nature* 180:613-614.
- Bliss, D.E. 1951. The destruction of *Armillaria mellea* in citrus soils. *Phytopathology* 41:665-683.
- Borowicz, V.A. & S.A. Juliano. 1991. Specificity in host - fungus associations. *Evolutionary Ecology* 5:385-392.
- Bowen, G.D. 1969. Nutrient status effects on loss of amides and amino acids from pine roots. *Plant and Soil* 30:139-142.
- Brown, M.E. 1975. Rhizosphere microorganisms, opportunists, bandits or benefactors. In: N. Walker (ed.), *Soil Microbiology*, John Wiley and Sons, Inc., New York, New York. Pp. 21-38.
- Burg, S.P. 1962. The physiology of ethylene formation. *Annual Review of Plant Physiology*. 13:265-302.

- Cobb, F.W., M. Krstic, M. Zavarin, & H.W. Barber. 1968. Inhibitory effects of volatile oleoresin, components on *Fomes annosus* and four *Ceratocystis* species. *Phytologia* 58:1327-1335.
- Curl, E.A. & B. Truelove. *The Rhizosphere*. Springer-Verlag, New York, New York. 183 pp.
- Davis, D.E. 1949. Some effects of calcium deficiency on the anatomy of *Pinus taeda*. *Amer. J. Bot.* 36:276-283.
- Davis, F.T., Jr. & C.A. Call. 1990. Mycorrhizae and growth of selected woody plant species in lignite overburden in Texas USA. *Agriculture, Ecosystems, and Environment* 31:243-252.
- Dix, N.J. & J. Webster. 1995. *Fungal Ecology*. Chapman and Hall, Inc., New York, New York. 549 pp.
- Ellis, E.H. 1929. *Armillaria mellea* in a mine-working. *Trans. Brit. Mycol. Soc.* 14:305-307.
- Findlay, W.P.K. 1951. The development of *Armillaria mellea* rhizomorphs in a water tunnel. *Trans. Brit. Mycol. Soc.* 34:145-147.
- Foster, R.C. & A.D. Rovira. 1973. The rhizosphere of wheat roots studied by electron microscopy of ultra-thin sections. *Bulletins from the Ecological Research Committee, Stockholm, Sweden* 17:93-102.
- Frank, A.B. 1885. Über die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. *Berliner Deutsche Botanische Gesellschaft* 3:128-145.
- Fraser, L. 1949. A gummosis disease of citrus in relation to its environment. *Proc. Linn. Soc. New South Wales* 74:5-18.
- Fries, N. 1973. Effects of volatile organic compounds on the growth and development of fungi. *Trans. Brit. Mycol. Soc.* 60:1-21.
- Garrett, S.D. 1970. *Pathogenic Root Infecting Fungi*. Cambridge University Press, Cambridge, Great Britain. 294 pp.
- Garrett, S.D. 1960. *Biology of Root Infecting Fungi*. Cambridge University Press, Cambridge, Great Britain. 293 pp.
- Gaumann, E.J., E.J. Nuesch, & R.H. Rimpau. 1960. Weitere Untersuchungen über die Chemischen Abwehrreaktionen der Orchideen. *Phytopathologisch Zeitschrift* 38:274-283.
- Gibbs, J.N. 1968. Resin and the resistance of conifers to *Fomes annosus*. *Ann. Bot.* 46:649-665.
- Gibbs, J.N. 1967. a study of the epiphytic growth habit of *Fomes annosus*. *Ann. Bot.* 31:755-774.
- Gibson, I.A.S. 1961. A note on variation between isolates of *Armillaria mellea* (Vahl. ex Fr.) Kummer. *Trans. Brit. Mycol. Soc.* 44:123-128.
- Greaves, M.P. & J.F. Darbyshire. 1972. The ultrastructure of the mucilaginous layer on plant roots. *Soil Biology and Biochemistry* 4:443-449.
- Griffin, D.M. 1969. Effect of soil moisture and aeration on fungal activity, an introduction. In: T.A. Toussoun, R.V. Bega, & P.E. Nelson (eds.). *Root Diseases and Soil-Borne Pathogens*, University of California Press, Berkeley, California. Pp. 24-87.
- Hale, M.G., L.D. Moore, & G.J. Griffin. 1978. Interactions between non-pathogenic soil microorganisms and plants. In: Y.R. Dommergues & S.V. Krupa (eds.). *Ecology of Root Pathogens*, Elsevier Book Publishers, Inc., New York, New York. Pp. 163-197.

- Harley, J.L. 1975. Problems of mycotrophy. In: F.E. Sanders, B. Mosse, & P.B. Tinker (eds.). *Endomycorrhizas*, Academic Press, Inc., New York, New York. Pp. 1-25.
- Harley, J.L. 1948. Mycorrhiza and soil ecology. *Biological Reviews* 23:137-158.
- Harley, J.L. & J.S. Waid. 1955a. A method of studying active mycelia on living roots and other surfaces in the soil. *Trans. Brit. Mycol. Soc.* 38:104-118.
- Harley, J.L. & J.S. Waid. 1955b. The effect of light upon the roots of beech and its surface population. *Plant and Soil* 7:96-112.
- Hartig, R. 1873. Vorläufige Mitteilung über den Parasitismus von *Agaricus melleus* und dessen Rhizomorphen. *Botanische Zeitschrift*. 31:295-297.
- Head, G.C. 1973. Shedding of roots. In: T. Kozlowski (ed.). *Physiological Ecology*, Academic Press, Inc., New York, New York. Pp. 237-286.
- Hiltner, L. 1904. Über neue Erfahrungen und Problems auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Grundungung und Brache. *Arb. Dtsch. Landw.-Bes.* 98:59-78.
- Intini, M.G. 1991. Some common species of tropical lignicolous fungi. *International Journal of Tropical Plant Diseases* 9:1-14.
- Jackson, R.M. 1960. Soil fungistasis and the rhizosphere. In: D. Parkinson & J.S. Waid (eds.). *The Ecology of Soil Fungi*, Academic Press, Inc., New York, New York. Pp. 168-181.
- Jackson, R.M. 1957. Fungistasis as a factor in the rhizosphere phenomenon. *Nature* 180:96-97.
- Jiménez, R.M. & D.P. Gallo. 1993. Vesicular arbuscular mycorrhizal fungi (VAM) associated with citrus trees in the Azapa Valley I region of Chile. *Idesia* 12:63-69.
- Jones, M.D., D.M. Durall, & P.B. Tinker. 1991. Fluxes of carbon and phosphorus between symbionts in willow ectomycorrhizas and their changes with time. *New Phytologist* 119:99-106.
- Katznelson, H. 1960. Observations on the rhizosphere effect. In: D. Parkinson & J.S. Waid (eds.). *The Ecology of Soil Fungi*, Academic Press, Inc., New York, New York. Pp. 192-201.
- Katznelson, H., J.W. Rouatt, & J.M.B. Payne. 1954. Liberation of amino acids by plant roots in relation to desiccation. *Nature* 174:1110-1111.
- Kelley, A.P. 1950. *Mycotrophy in Plants*. Chronica Botanica, Co., Waltham, Massachusetts. Pp. 1-98.
- Kinugawa, K. 1965. Effect of day length and temperature on growth and formation of mycorrhizal short root of the seedling of *Tinus densiflora*. *Bot. Mag. (Tokyo)* 78:366-374.
- Maliszewska, W. & R. Moreau. 1960. A study of the fungal microflora in the rhizosphere of fir (*Abies alba* Mill.). In: D. Parkinson & J.S. Waid (eds.). *The Ecology of Soil Fungi*, Academic Press, Inc., New York, New York. Pp. 209-220.
- Marks, G.C. & R.C. Foster. 1973. Structure, morphogenesis and ultrastructure of ectomycorrhizae. In: G.C. Marks & T.T. Kozlowski (eds.). *Ectomycorrhizae, Their Ecology and Physiology*, Academic Press, Inc., New York, New York. Pp. 2-35.
- Marks, G.C. & R.C. Foster. 1967. Succession of mycorrhizal associations on individual roots of radiata pine. *Australian Forestry* 29:238-246.
- Mathre, D.E. 1964. Pathogenicity of *Ceratocystis ips* and *Ceratocystis minor* to *Pinus ponderosa*. *Boyce Thompson Inst. Plant Res.* 22:363-388.

- Meyer, F.H. 1973. Distribution of ectomycorrhizae in nature and man-made forests. In: G.C. Marks & T.T. Kozłowski (eds.). *Ectomycorrhizae, Their Ecology and Physiology*, Academic Press, Inc., New York, New York. Pp. 79-106.
- Meyer, F.H. 1968. Mykorrhiza. In: K. Mellinshoff (ed.). *Haldenbegrenung Ruhrgebiet*, Schriftenr. Siedlungsverb. Ruhrkohlenbezirk., Berlin, Germany. Pp. 118-123.
- Mikola, P. 1967. The effect of mycorrhizal inoculation on the growth and root respiration of scotch pine seedlings. Proc. International Union of Forestry Res. Organizations, Sect. 24. Pp. 100-101.
- Mosse, B. 1975. A microbiologist's view of root anatomy. In: N. Walker (ed.). *Soil Microbiology*, Butterworth's, Ltd., London, Great Britain. Pp. 39-66.
- Motta, J. 1967. A note on the mitotic apparatus in the rhizomorph meristem of *Armillaria mellea*. *Mycologia* 59:370-375.
- Mughogho, L.K. 1968. The fungus flora of fumigated soils. Trans. Brit. Mycol. Soc. 51:441-459.
- Napper, R.P.N. 1932. Observations on the root disease of rubber trees caused by *Fomes lignosus*. Journal of the Rubber Research Inst. of Malaya 4:5-33.
- Old, K.M. & T.H. Nicholson. 1975. Electron microscopical studies of the microflora of roots of sand dune grasses. New Phytologist 74:51-58.
- Petch, T. 1928. The parasitism of tea root fungi. Tea Quarterly 1:10-15.
- Peterson, E.A. 1958. Observations on fungi associated with plant roots. Can. J. Microbiology 4:257-265.
- Pfleger, F.L. & R.G. Linderman. 1994. *Mycorrhizae and Plant Health*. APS Press, Inc., New York, New York. 360 pp.
- Rayner, M.C. 1927. *Mycorrhiza*. Cambridge University Press, Cambridge, Great Britain. Pp. 1-47.
- Redfern, D.B. 1970. The ecology of *Armillaria mellea* rhizomorph growth through soil. In: T.A. Toussoun, R.V. Bega, & P.E. Nelson. *Root Diseases and Soil-Borne Pathogens*, University of California Press, Berkeley, California. Pp. 147-150.
- Richardson, S.C. 1953. Studies on the root growth of *Acer saccharinum*. II. Factors affecting root growth where photosynthesis is curtailed. Proc. Kon. Ned. Akad. Wetensch., Ser. C 56:366-372.
- Risbeth, J. 1950. Observations on the biology of *Fomes annosus* with particular reference to East Anglian pine plantations. I. The outbreaks of disease and ecological states of the fungus. Ann. Bot. 14:365-383.
- Risbeth, J. 1951. Observations on the biology of *Fomes annosus* with particular reference to East Anglian pine plantations. II. Spore production, stump infection, and saprophyte activity in stumps. American Botanist, London 15:1-21.
- Risbeth, J. 1951. Observations on the biology of *Fomes annosus* with particular reference to East Anglian pine plantations. III. Natural and experimental infection of pines and some factors affecting severity of the disease. Ann. Bot. 15:221-246.
- Risbeth, J. 1951. Butt rot by *Fomes annosus* Fr. in East Anglian conifer plantations and its relation to tree killing. Forestry 24:113-120.
- Robertson, N.F. 1954. Studies on the mycorrhiza of *Pinus sylvestris*. New Phytologist 53:253-283.
- Rogers, W.S. 1968. Amount of cortical and epidermal tissue shed from roots of apple. Journ. of Hort. Sci. 43:527-528.

- Rovira, A.D. 1959. Plant root excretions in relation to the rhizosphere effect. IV. Influence of plant species, age of plant, light, temperature and calcium nutrition on exudation. *Plant and Soil* 11:53-64.
- Rovira, A.D. & E.H. Ridge. 1973. Exudation of C<sup>14</sup> labelled compounds from wheat roots: influence of nutrients, microorganisms and added organic compounds. *New Phytologist* 72:1081-1087.
- Shain, L. 1967. Resistance of sapwood in stems of loblolly pine to infection by *Fomes annosus*. *Phytopathology* 57:1034-1045.
- Shaw, T.M., J. Dighton, & F.E. Sanders. 1995. Interactions between ectomycorrhizal and saprotrophic fungi on agar and in association with seedlings of lodgepole pine (*Pinus contorta*). *Mycological Research* 99:159-165.
- Slankis, V. 1958. The role of auxin and other exudates in mycorrhizal symbiosis of forest trees. In: K.V. Thimann (ed.). *Physiology of Forest Trees*, Roland Press, New York, New York. Pp. 427-443.
- Smith, W.H. 1972. The influence of artificial defoliation on exudates of sugar maple. *Soil Biology and Biochemistry* 4:111-113.
- Smith, W.H. 1969. Release of organic materials from the roots of tree seedlings. *Forest Science* 15:138-142.
- Starkey, R.I. 1929. Some influences of the development of higher plants upon the microorganisms in the soil. *Soil Sciences* 27:319-334.
- Towers, B. & W.J. Stambaugh. 1968. The influence of induced soil moisture stress upon *Fomes annosus* root rot of loblolly pine. *Phytopathology* 58:269-272.
- Volz, P.A., J.D. Boos, & S.P. Wasser. 1992. Soil micro-fungi of Israel. *Ukraine Jour. Bot.* 49:87-92.
- Volz, P.A., A.M. Hamblin, R.W. Han, C.C. Snabes, G.T. Tziahanas, & S.P. Wasser. 1993. The keratinophilic fungi from historic sites of St. Petersburg (Russia). *Ukraine Jour. Bot.* 50:45-55.
- Volz, P.A. D.J. Najarian, & S.P. Wasser. 1994. Soil-borne micro-fungi of the Crimea. *Ukraine Jour. Bot.* 51:63-72.
- Wallis, G.W. 1961. Infection of scots pine roots by *Fomes annosus*. *Can. J. Bot.* 39:109-121.
- Warcup, J.H. 1955. On the origin of colonies of fungi developing on soil-dilution plates. *Trans. Brit. Mycol. Soc.* 38:298-301.
- Warcup, J.H. 1952. Effect of partial sterilization by steam or formalin on damping off of sitka spruce. *Trans. Brit. Mycol. Soc.* 35:248-262.
- Waterston, J.M. 1941. Observations on the parasitism of *Rosellinia pepo*. *Pathology and Tropical Agriculture, Trin.* 18:174-184.
- Weindling, R. 1941. Experimental consideration of the mold toxins of *Gliocladium* and *Trichoderma*. *Phytopathology* 31:991-1003.
- Weindling, R. 1934. Studies on a lethal principal effective in the parasitic action of *Trichoderma lignorum* on *Rhizoctonia solani* and other soil fungi. *Phytopathology* 24:1153-1179.
- Weindling, R. 1932. *Trichoderma lignorum* as a parasite of other soil fungi. *Phytopathology* 22:837-845.
- Weinhold, A.R. 1963. Rhizomorph production by *Armillaria mellea* induced by ethanol and related compounds. *Science* 142:1065-1066.
- Wichner, S. & E. Libbert. 1968. Interactions between plants and epiphytic bacteria regarding the auxin metabolism. *Plant Physiology* 21:500-511.
- Yawney, W.J. & R.C. Schultz. 1990. Anatomy of a vesicular arbuscular endomycorrhizal symbiosis between sugar maple *Acer saccharum* March and *Glomus etunicatum* Becker and Gerdemann. *New Phytologist* 114:47-58.

- Zak, B. 1964. Role of mycorrhizae in root disease. *Ann. Rev. Phytopathology* 2:377-382.
- Zak, H. & D.H. Marx. 1964. Isolation of mycorrhizal fungi from roots of individual slash pine. *Forest Science* 10:214-223.
- Zottl, A. 1964. The effect of fertilization on the distribution of fine roots in spruce stands. *Mitt. Staats. Forstverw. Bayerns.*, No. 34. 333 pp.