From Lamarckian fertilizers to fungal castles: recapturing the pre-1985 literature on endophytic and saprotrophic fungi associated with ectomycorrhizal root systems

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Abstract: The endophytic, mantle-inhabiting and rhizosphere-inhabiting microorganisms associated with ectomycorrhizal roots have been studied for over 100 years, but a surprising amount of the information obtained prior to the mid-1980's is difficult to access and understand. In large part, this is because research investigating local ecosystems and silvicultural practices was often considered regional in nature. It tended to be written up in many different languages and to be published in journals that were not widely distributed. After 1985, this scientific isolationism was broken up by the ubiquitous trend towards impact factor measurement and international publishing. The goal of the present review is to make still-relevant information from the pre-1985 ectomycorrhizosphere literature, especially its more strongly obscured elements, readily accessible to modern researchers. Also, some publications that fell into relative obscurity for historical reasons – in particular, studies seeming to reflect the brief association of Soviet mycorrhizal research of the early 1950's with the Lamarckian plant improvement ideas of T. D. Lysenko – are re-examined from current perspectives. The scattered data reveal considerable coherence despite the high ecological diversity they reflect. Endophytes such as members of the *Mycelium radicis atrovirens* complex – most prominently the species now known as *Phialocephala fortinii* – feature especially prominently in this area of study, and they received considerable attention beginning in the very early years of the 20th century. They were variously interpreted as potential symbionts or weak pathogens, an ambiguity that continues to the present day for many of these taxa despite the recent molecular clarification of species and population boundaries. The predominance of *P. fortinii* and other (normally) non-mycorrhizal "dark (or hyaline) sterile endophyte" fungi from stringently washed or surface-disinfected ectomycorrhizae in most ecosystems was shown repeatedly beginning with the studies of Elias Melin in the early 1920's. The adjacent rhizosphere soil typically contained sporulating fungi dominated by *Penicillium*, *Umbelopsis* and *Mortierella* species, sometimes accompanied by *Trichoderma* spp., *Cylindrocarpon destructans*, and various other microfungi. Microbiological investigations into whether ectomycorrhizae exerted a positive "rhizosphere effect" on numbers of fungal propagules in the surrounding soil showed that such effects were often less prominent in natural forests than in planted forests. Several studies showed a general reduction in microbial activity in the zone of ectomycorrhizal influence, and a particularly strong inhibition of soil organisms was shown in the symbiorhizosphere of *Tricholoma matsutake* and members of the genus *Tuber*. In relation to such cases, the adoption by mycologists of M. Ogawa's term "shiro", (castle, fortress) for the delimited, three-dimensional analogue of a fairy ring formed in soil by many ectomycorrhizal mycobionts is advocated. As relatively highly co-adapted communities, ectomycorrhizosphere organisms appeared to aid in root disease control, in part by harmlessly stimulating roots to produce defensive tannic materials. The production of these materials then appeared to favour the predominance of tannin-degrading *Penicillium* species in the rhizosphere. Rhizosphere inhabitants were shown to be involved in many types of nutrient and growth factor exchanges, but perhaps to be most important as solubilizers of refractory nutrients like inorganic phosphorus compounds and complex proteinaceous materials. Some potential pathogens like *Fusarium* spp. tended to be excluded from established forest soils, while *Cylindrocarpon destructans*, if present, tended to be confined to lower soil regions by microbial acidification of the upper soil zones. The complexity of microfungal communities and their known and potential interactions was high, and seemingly contradictory results often needed to be rationalized, e.g., *Trichoderma* spp. appeared to be favoured in the root zone in some ecosystems and partially excluded in others, and seemed to abet mycorrhiza formation and tree growth in some habitats but to cause damage to seedlings and mycorrhizal inoculum both *in vitro* and in the nursery. Modern techniques and bioinformatics methodologies will be needed to make progress towards understanding this complexity, but the multilingual and sometimes overlooked pre-1985 studies provide a very strong initial basis supporting further development.

Key words: ectomycorrhizae, mycorrhizosphere, DSE, ecology, soil fungi, forestry .

INTRODUCTION

Of all the bodies of literature ever written about fungi and plants, one of the most difficult to survey must be that concerning fungi co-occurring with ectomycorrhizal symbionts on the roots of forest trees and other woody plants. Since 1985, this topic has more-or-less fused with the mainstream of science, but prior to that time, even though much very credible work was done, a good deal of the relevant literature was remarkably difficult to access and understand. There were two reasons for this. One was that this topic was conceived worldwide as one that would yield varying results from ecosystem to ecosystem, and this led to a strong tendency to conduct studies specifically focused on local plant communities, with results written up in national or regional journals and published in the national language. No body of biological literature more polyglot than this one can be found. The second was that at on at least two historical occasions, the underlying assumptions attributed to the research became discredited and appeared, falsely, to discredit the research itself. This led to white-outs in citation, where much worthwhile material dropped out of sight and seldom if ever reappeared. Indeed, a third epistemic white-out of this kind is in progress today, about which more will be said momentarily.

This area of research, which I will refer to in brief as ectomycorrhizosphere literature, waxes and wanes in activity levels over time as do most fields of ecological research. Currently, it is a dynamic area, propelled by the revolutionizing effect of simple molecular and array-based identification mechanisms for organisms, as well as by interest in global climate change, invasive organisms, biological control, and biological fertilization. The objective of the present review is to liberate some of the historical literature from mostly undeserved obscurity and to make the most salient information available to modern investigators. This is assuming they dare to be interested in information of this vintage: the third white-out mentioned above is a strong trend in current ecological writing to seem modern and dynamic by only citing literature from very recent studies. To someone who has read the older literature, this often has jarring effects, with discoveries from the 1920's, for example, being attributed with great excitement to studies from the 2000's. One is forced to wonder at times if ecology is in the process of dropping scientific progressiveness and becoming a steady-state system, an intellectual merry-go-round with regularly repeated cycles of rediscovery and amnesia. But in the case of ectomycorrhizosphere literature, some of the amnesia can be attributed to linguistic difficulties and to the first two epistemic white-outs, which are detailed below.

The field begins largely in German at the turn of the 20th century, with various researchers such as O. Hagem and E. Jahn following up on Albert B. Frank's (1885) discovery of the ectomycorrhizal association. The first white-out in this field occurred because some of the early researchers mistook the penicillia and *Zygomycota* they were isolating for mycorrhizal fungi, while Jahn in particular, though he know that these fungi were not symbionts invested in plant tissue, incurred skepticism by insisting on their close affinity to the plants, as seen in the dense growth around root surfaces that he referred to as "peritrophic mycorrhizae". The impression that early ectomycorrhizosphere researchers were simply confused about what was and was not important as a mycorrhizal symbiont tended to discredit the work done, even though later studies have largely confirmed the data and rendered occasional early interpretive errors trivial. Wars and depressions, in any case, coincided with the white-out in working to extinguish this German-language research front. Before it snuffed out, however, it managed to engender two satellite blazes that were instrumental to the development of 20th century forest mycology. In Sweden, Elias Melin, still writing mainly in German, became the recognized pioneer in the study of what later became known as dark sterile endophytes (DSE), and did authoritative work on the biology of the *Mycelium radicis atrovirens* complex, with his concept of the quasi-species *M. r. atrovirens* α (as opposed to some broader later concepts of *M. r. atrovirens*) now known mostly or entirely to correspond to the widespread and abundant *Phialocephala fortinii* C.J.K. Wang & H.E. Wilcox. He later moved on to study wood-staining fungi and wood-invading *Ophiostoma* species, a very pertinent topic in the century of Dutch Elm Disease, but also maintained a life-long research interest in ectomycorrhizal fungi. In the U.K., the great 20th century presiding genius of ectomycorrhizal research, John Laker Harley, began his rhizosphere-related studies by following up on a now obscure German-language publication (Bedr Chan 1923) on a dark sterile endophyte of beech, *Mycelium radicis fagi*, and then continued with a classic study on ectomycorrhizosphere fungi in the mid-1950's before switching permanently to studying mycorrhizal physiology, to the great benefit of the whole field of endeavour.

Harley & Waid's well known and scientifically pivotal (1955a) paper on root washing techniques for study of the ectomycorrhizosphere seems to stand alone in the literature of its time – unless one reads Russian. In fact, the greatest surge of activity ever seen in this area occurred in the 1950's in the Soviet Union. The ectomycorrhizosphere boom in the Soviet Union lasted from approximately 1948 to approximately 1963. Its genesis lay in two historical movements, one scientific and the other political, or

more accurately, pseudoscientific. The scientific thrust came from the excitement about soil microbiology generated by a towering figure in Russian bacteriology, N. A. Krasil'nikov. (Note that the apostrophe in his surname simply indicates that the 'l' preceding it is pronounced like an English 'l' and not like the Russian "hard l," so it can be ignored completely unless one is transliterating back to Cyrillic). But the other source of impetus was more troublesome, namely, the Lamarckian pseudo-geneticist and Stalin favourite Trofim D. Lysenko. Socialist science had already acted in biology to supplant western notions of community ecology, based on a vision of John Wayne-like organisms competing ruggedly for resources, with Karl Möbius's (1877) concept of the biocoenosis, based on the idea that nutrient flows and other integrating factors made ecosystems function largely cooperatively (Later, the soil was integrated into this nutrient flow concept, generating the modern term biogeocoenosis). Lysenko's project was to extend this cooperative bio-ethos by supplanting the western notion of Mendelian genetics, with its inalienable individual characteristics, with a Lamarckian reality where a beneficial environment could favourably alter the genotype. In the years of Stalin's Terror, especially the late 1940's and early 50's, it was quite daring to write a biological paper without quoting Lysenko and perhaps Stalin as well in the Introduction. Thus, for example, in the introduction to Sideri & Zolotun's (1952) *Improvement of conditions for the growth of oak on the eroded soils of Zaporozh'ye*:

"Academic T. D. Lysenko teaches that as a result of changes in nutrition, changes occur not just to the body of the organism but also to its breed or genotype. Furthermore, the breed does not merely adjust temporarily. The result, as a rule, is the transmission of form through heredity. From this viewpoint, we examine fertilizer, which changes the conditions of the nutritional environment, as a factor reducing the activity of pathogenic organisms in the rhizosphere of young oaks and stimulating the development of the symbiotic properties of mycorrhizae."

In fact, though Lysenko was officially in governmental favour for several years after this paragraph was written, he is seldom if ever mentioned in rhizosphere literature after 1952. As Medvedev (1971) has pointed out, botanists were among the first to denounce Lysenko's ideas publicly, and it is doubtful that his ideas ever attracted more than the most fearfully obliged lip service in soil biology. The opening phrase of Sideri & Zolotun's paragraph, the then-ubiquitous "*Akademik T. D. Lysenko uchit, chto…*" can be read as reverential, but also, to those familiar with Soviet nuance, as a rather blunt distancing mechanism: "it's his idea – not mine." In general, however, scientific funding proposals divide into two types, panics and panacaeas, and the fact is that the panacaea vision of improving forestry at low cost through manipulating rhizosphere conditions, whether or not via the revolutionizing of genotypes, funded ten years of intense soil biological industry. Very little of it, in retrospect, is scientifically unsound except in one unrelated factor, namely, the general disregard of statistical testing that was a curious hallmark of the Soviet science of that era (and something that was exported in Soviet educational programs to much of the developing world, where it persists to this day in some areas). Often the data tables presented contain enough information that anyone wanting to do statistics *a posteriori* can do so, and some later authors did this.

The present article gives only a partial view of the 1950's Soviet ectomycorrhizosphere studies, in that many of them were focused on bacterial rather than fungal influences on mycorrhizae. In regard to bacteria, in the present context it suffices to say that Garbaye's concept of mycorrhizal helper bacteria, dating to the late 1980's (de Oliveira & Garbaye 1989, Garbaye 1994), was by no means an unprecedented development, though whether the pseudomonads and other rhizobacteria considered helpful by Soviet researchers would pass modern tests of efficacy is difficult to estimate. Some early rhizobacterial inoculation results are discussed below in the context of parallel microfungal inoculation trials.

Soviet ectomycorrhizosphere research reached its culmination in 1962 in the massive ecological monograph *Mycotrophy of woody plants*, written by N. M. Shemakhanova. Then, abruptly, it disappeared completely, and its literature, apart from the 1967 English translation of Shemakhanova, was all but effaced in the second great ectomycorrhizosphere white-out. Whether this was because, for example, the research thrust failed as a panacaea, or because it was tainted by its lysenkoist background, is unknown to me, though there have been suggestions that the increased availability of cheap, artificially produced nitrogen fertilizers in the Soviet Union placed a damper on the biofertilizer research front, inclusive of the mycorrhizal front. In any case, the field was clearly invalidated in some way and science moved on to the next Five-Year Plan. The Soviet work on rhizospheres of forest trees done later in the 1960's generally made no mention of mycorrhizae.

Again, however, activity in the field was maintained by a satellite blaze, which was the emerging Polish school led by mycorrhizal biologist Tadeusz Dominik, and mycorrhizosphere/DSE biologist Karol Mańka. The latter and his students and associates began to produce a series of very ambitious studies on the rhizospheres and the soil environment of forest trees; this project continued into the 1980's in the work of Stefan Kowalski. Some of the very detailed studies

are nearly impossible to obtain; I was able to see one (Mańka & Gierczak 1961) only because Richard Korf from Cornell Univ. sent me the only copy known to exist in North America – his own personal reprint. During the time that the Mańka laboratory was active, the rest of the world became alive to the topic of the mycorrhizosphere – a word that was coined in 1967 by Foster & Marks (1967). Researchers in Canada, the U.S., Italy, Australia, Japan, the U.K. and India mobilized, a modern era began, and the field came full circle at the turn of the 1980's when tree decline forced Germany back into the forest rhizosphere business. By that time, the Reagan-neoconservative economic thrust in science, with its manufacture of the measured impact factor as the scientific equivalent of stock market value, had begun to alter the form of scientific communication, and the use of English and international journals was well on the way to being obligatory in all fields. When, in a crack heard around the world, the *Annales de l'Institut Pasteur* in 1989 announced a decision to begin to publish English-language literature and to rename itself *Research in Microbiology*, the scientific milieu that had formed the publications reviewed below was finished. The work, however, still emerges as the gold from the multilingual and often obscurely published ore.

This review begins with papers investigating the identities and quantities of fungi active in the ectomycorrhizosphere, and then goes on to discuss some recurring ecological topics in the research of this era, most of which are of undiminished interest today. It is anticipated that most readers will have access to the free online or pdf version and be able to seek out particular species and other subjects of interest through word-search. The organization of the historical synopsis making up the first part of this review therefore remains predominantly chronological and geographic.

ELUCIDATING THE MICROFUNGAL SPECIES AND ASSEMBLAGES ASSOCIATED WITH ECTOMYCORRHIZAL ROOTS

Early studies

Confusion is sometimes a boon to scientific research, and the study of mycorrhizosphere fungi provides an interesting case in point. The first researchers to identify and describe mycorrhizosphere fungi, and to observe their effects on plant roots *in vitro*, were workers who anticipated that these fungi would be mycorrhiza-formers. Möller (1903) isolated various *Zygomycetes*, including *Mucor ramannianus* A. Möller [currently *Umbelopsis ramanniana* (A. Möller) W. Gams], *M. spinosus* Tiegh. (now *M. plumbeus* Bonord.) and *M. heterogamus* Vuill. [now *Zygorhynchus heterogamus* (Vuill.) Vuill.] from washed mycorrhizal roots of pine in Germany. He quickly established in resynthesis experimens with pot plants that they were non-mycorrhizal fungi, though they tended strongly to be associated with the tree roots. He also determined that they did not seem to be responsible for some intracellular invasions he found in root cortical cells that he thought might be an intracellular mycorrhizal type. His description of the hyphae in these cells as dark suggests that Möller may have been examining DSE structures. Peklo (1909) was not so fortunate with his resynthesis trials: he published results that he thought indicated the mycorrhizal nature of Penicillia isolated from roots of *Carpinus* and *Fagus*. In retrospect, he appears to have been the victim of techniques that failed to exclude airborne basidiospores from pot experiments. Nonetheless, he must be given credit for his observations on mycorrhizosphere Penicillia. He found strains similar to *Penicillium geophilum* Oudem. [possibly a synonym of *P. glabrum* (Wehmer) Westling] characteristic of *Carpinus* mycorrhizae, and cultivated a number of unidentified Penicillia from oak. The root-associated Penicillia were found to grow unusually well in media containing tannins, and Peklo suggested that they were favoured in the mantle region by tannins produced by the plant. Later studies (e.g., Foster & Marks 1967, Malajczuk 1979) showed extensive deposits of tannin-like material in the interstices of the mycorrhizal inner mantle; thus Peklo appears to have been first to encounter an interesting feature of mycorrhizosphere biology. The tannin-degrading abilities of Penicillia have since become well-known (Domsch *et al*. 1980).

Hagem (1910), in a study of *Mucoraceae* in Norwegian soils, found *U. ramanniana* to be a characteristic associate of the roots of conifers; this was consistent with the earlier findings of Möller (1903). Also, *Mucor hiemalis* Wehmer was regularly associated with mycorrhizal pine roots, and *M. silvaticus* Hagem was found with spruce roots. In mountainous areas, *Zygorhynchus moelleri* Vuill. and "*Penicillium glaucum* Link" [a *nomen dubium* "frequently used for any green *Penicillium*" (Raper & Thom 1949)] were characteristically isolated from washed pine mycorrhizae. The former species was represented by approximately ten times as many propagules in mycorrhizosphere soils as in control soils, and Penicillia were also much less common in control soils. This appears to be the first demonstration of a rhizosphere effect in association with ectomycorrhizal roots.

Fuchs (1911) attempted to isolate symbionts from washed mycorrhizal roots of pine, spruce and fir, and was able to obtain only *Penicillium* spp., *Verticillium* sp. (*sensu lato*, probably inclusive of the current *Lecanicillium* and perhaps also *Pochonia*), *Fusarium* sp., sterile root fungi, and arthroconidial

Hyphomycetes strongly resembling the anamorphs of wood-decaying *Basidiomycetes*. None of these species formed mycorrhizae, and only *Fusarium* sp. appeared to be pathogenic. Fuchs also tried inoculating seedlings with cultures isolated from basidiocarps of putatively mycorrhizal species. In some cases, [e.g. *Collybia macrooura* (Scop.) Fr., now known as *Xerula radicata* (Relhan: Fr.) Dörfelt] these species are now considered non-mycorrhizal. In other cases, genuinely mycorrhizal species were used, but Fuchs' descriptions suggest that his cultures contained contaminants. In particular, one "*Lactarius deliciosus* (L : Fr.) Gray" strain was a weak pathogen that grew intracellularly in the pine root cortex. The results as a whole caused Fuchs to conclude that ectomycorrhizal fungi were parasitic.

Melin (1923) made considerable progress in bringing ecological modernity to this research area. He tested various fungi isolated from mycorrhizal roots to determine their abilities to form mycorrhizae in pure culture. Unlike his predecessors, he succeeded in isolating mycorrhizal as well as non-mycorrhizal cultures. Included among the cultures considered non-mycorrhiza-forming were *U. ramanniana*, *Penicillium lanosum* Westl., *Chaetomium kunzeanum* Zopf (= *C. globosum* Kunze ex Fr.), *Verticillium* sp. (*sensu lato*), *Acrostalagmus* sp. (probably = *Lecanicillium*, *Pochonia* or *Simplicillium*), *Rhizoctonia silvestris* Melin, and two sterile dark fungi, *Mycelium radicis atrovirens* α and *M. r. atrovirens* β. *Rhizoctonia silvestris*, a fungus about which little is known today (Andersen and Stalpers [1994] noted that no type or authentic materials appeared to have been preserved but that the description appeared to be of an ascomycete), was shown to be a destructive pathogen, while *C. globosum* was shown to be an occasional opportunistic parasite of pine seedlings in pure culture. The two *Mycelium radicis atrovirens* spp., *U. ramanniana*, and "*Verticillium* sp." formed "pseudomycorrhizae." The latter term indicates simply that they invaded root tissues without forming true mycorrhizae, and initiated a gradual decline in seedling vigour usually leading to death. (In addition, the typical "pseudomycorrhiza" had a characteristic appearance resulting from the inhibition of plant root hair formation by the invading fungus). *Penicillium lanosum* and *Acrostalagmus* sp. were harmless saprobes.

In Melin's isolations from roots, he found that *M. r. atrovirens* α was extremely common, and could be cultured even from roots surface-sterilized with mercuric chloride. He deduced that in nature the fungus commonly penetrated mycorrhizal root tissues, and that the colonized mycorrhizae often remained healthy.

Another sterile root fungus was described as a "*Mycelium radicis*" taxon by Bedr Chan (1923) [N.B., Bedr Chan is a German spelling of a surname most commonly rendered Badrkhan or Baderkhan in English, or Bedirxan in the Kurdish from which it most commonly stems; it should not be shortened to "Chan" as was done by Harley (1939) and some others]. The new species, *M. r. fagi*, was commonly associated with beech mycorrhizae. This fungus was later redescribed in detail by Harley (1939), who stated his intention to test its mycorrhiza-forming capabilities. The results of the test were never reported, but a reference to *M. r. fagi* in Harley & Smith (1983) strongly implies that the species was non-mycorrhizal. The one extant isolate with this name, Centraalbureau voor Schimmelcultures 256.48 (CBS; Utrecht, the Netherlands), is a sterile fungus with affinities to *Capronia* (Tata & Summerbell, unpubl. data).

Johann (1932) used two techniques for surface-sterilizing mycorrhizae, and examined the Mucoraceous fungi that grew out on nutrient media. Three tree species were considered: beech, oak, and spruce. Alcohol-disinfected, washed mycorrhizae gave rise to *U. ramanniana*, *Mucor racemosus* Fres., and *Phycomyces nitens* (C. Agardh) Kunze. From roots sterilized with mercuric chloride, only *U. ramanniana* was obtained. Johann concurred with Möller (1903), Hagem (1910) and Melin (1923) that *U. ramanniana* was a typical mycorrhiza-associated saprobe. It was also an extremely common soil fungus in various sorts of forests and at various soil depths.

A number of fungi from rhizosphere soils of beech, pine, and spruce were collected by Jahn (1934, 1936). Unlike many of his predecessors, Jahn actually intended to study rhizosphere organisms, which he believed formed a "peritrophic mycorrhiza" of beneficial saprobes around plant roots. He sampled rhizospheres of trees growing in the two predominant soil types of the Hannoversch-Munden area of Germany: acidic, sandy soils, and neutral-to-alkaline limestone soils. The two soils possessed distinguishable rhizosphere mycotas, although the difference between the two fungal communities was not absolute. *Umbelopsis ramanniana*, *Z. moelleri*, and *Trichoderma* spp. were characteristic of rhizospheres from acidic soils, while *Mucor flavus* Bainier and certain *Penicillium* and *Fusarium* spp. (given numerical designations only) were characteristic of the basic soils. [One can only be uneasy that the more alkaline soils in Jahn's studies yielded a strongly root-associated "*Fusarium* II," while at the same time there was no mention of the somewhat *Fusarium*-like species that would be expected to occur, *Cylindrocarpon destructans* (Zinnsm.) Scholten – e.g., see citation of Kubíková (1965) below under *Mycological mycorrhizosphere studies of the 1960's*]. *Mucor racemosus* and "*Penicillium* I" occurred in both soils. The physiological work Jahn (1936) did with these strains, related to the currently hot topic of rhizosphere

fungi making insoluble nutrients available for plants, will be discussed in a later section of this work (see *Effect of microorganisms on ectomycorrhizosphere pH*).

The above works are discussed in some detail because all of them, except Melin's (1923) classic work, have largely been ignored by subsequent workers on mycorrhizae (Rayner 1927, and Kürbis 1936, are exceptions). Many of the studies are hampered by conceptual problems: e.g., Peklo's belief that Penicillia were mycorrhizal, Fuchs' insistence that mycorrhizal Basidiomycetes were parasitic, and Jahn's heterodox concept of the peritrophic mycorrhiza. Yet comparison with later studies will show that these authors actually assembled a great deal of pertinent information on the taxonomic composition and ecological significance of mycorrhizosphere fungal populations in North European forests.

The studies of Melin (1923) were extended by Lindquist (1939), who isolated mycorrhizal, parasitic, and "indifferent" fungi from mycorrhizal roots of spruce and beech in Scandinavia. The parasitic fungi included *M. r. atrovirens* (α), *U. ramanniana*, and a white sterile mycelium. A dark sterile mycelium proved to be the only "indifferent" fungus among the small group of isolates tested for their effect on seedlings *in vitro*. One of Lindquist's mycorrhizal fungi was unusual: although it formed a Hartig net and a thin mantle on roots, it actively parasitized the shoots of plants in flasks. Its formation of "oidia" (arthroconidia) in culture indicates that it was probably a wood-decay fungus. Although this may seem an unlikely mycorrhizal fungus, its habits of growth and facultative parasitism are analogous to those shown by certain strains of the parasitic wood-decay fungus *Heterobasidion annosum* (Fries) Brefeld (*s.lat.*) that form mycorrhiza-like structures in some tree roots [Kowalski 1970; see also below (*Mycological studies of the mycorrhizosphere: 1970–1985*, subheading *Polish studies*.)].

Facultative root parasites in British heathland soils were extensively studied by Rayner & Neilson-Jones (1944). *Mycelium radicis atrovirens* α was common in these soils, and could occasionally prevail to the point of causing significant damage to seedlings. A fungus similar to Melin's *Rhizoctonia silvestris* was also present, but attacked only one of three ectomycorrhizal conifer species studied. This species, *Picea sitchensis* Carr., was also attacked by a fungus resembling Melin's *M r. atrovirens* β. However, *M. r. atrovirens* β occurred only in experimental pot soils imported by Rayner & Neilson-Jones from the native habitat of *P. sitchensis* at Vancouver Island, Canada.

In British larch stands, How (1942) found *M. r. atrovirens* α to be ubiquitious, but did not report the presence of the other two sterile fungi observed by Rayner and Neilson-Jones.

After the second world war, the emphasis in mycorrhizosphere research changed in several ways. Most striking among these changes was a shift away from studying the effects of individual mycorrhizosphere fungi on tree seedlings *in vitro*. Studies analogous to those of Möller (1903), Fuchs (1911), Melin (1923), and Lindquist (1939) were rarely performed in the period from 1945–1975, excepting the endeavours of a few later students of *M. r. atrovirens* α/*P. fortinii* (e.g, Richard *et al*. 1971). At the same time, several new perspectives were introduced into mycorrhizosphere biology. The perspective of the soil microbiologist was introduced by Manteifel *et al*. (1950) and later workers writing mainly in Russian (occasionally in Ukrainian or Byelorussian). Other Soviet workers, beginning with Mishustin (1951) and Malyshkin (1951) studied the effect of mycorrhizosphere organisms on mycorrhiza formation. Perhaps the most influential works, however, were classic fungal ecology studies conducted by Harley & Waid (1955a, 1955b) on the surface mycota of beech mycorrhizae. The post-war studies will be considered in detail below.

Microbiological analysis of mycorrhizosphere fungi: the 1950's

Throughout the remainder of this review segment, microbiological analyses of rhizosphere fungi will be crudely distinguished from mycological analyses on the basis of two technical factors. Firstly, those studies that stress quantitative estimations of fungal propagule numbers, especially where rhizospheres are compared to control soils, will be accounted as microbiological. Secondly, those studies where specific identification of fungi is de-emphasized in favour of generic or functional categorization will be considered microbiological. In practice, most studies in these first two categories were conducted by microbiologists, and dealt with bacterial as well as fungal groups. Studies emphasizing qualitative or quantitative assessments of the occurrence of identified fungal species will be accounted as mycological. These studies are generally conducted by mycologists *per se*. Borderline cases will be assigned to the tradition from which they appear to derive.

The quantities of fungal propagules in rhizosphere and control soils of oak were studied by Mishustin (1951). The bulk of the roots studied were mycorrhizal. A pronounced rhizosphere effect was found, with fungal propagules being present in quantities 15–20× greater than those found in control soils. In a few soils, the stimulation was reduced or absent. Cellulolytic fungi were assayed separately, and found to be somewhat diminished in numbers in the rhizosphere under most soil conditions.

Samtsevich *et al*. (1952) similarly found a large rhizosphere effect for fungi associated with oaks in arid steppe soil. Compared to control soils, 1–3-yr-old seedlings caused increases in fungal propagule numbers in excess of 400 %. Rhizospheres of 20-yr-old oaks contained approximately 3200 % more microfungal propagules than control soils did. The extremity of these numbers is no doubt due to the aridity of the soil conditions: the tree in such situations is a moisture conduit as well as a source of nutrients.

The studies of Kozlova (1955) on the microorganisms of the oak rhizosphere included a quantitative survey of predominant fungal genera present in the rhizosphere during spring and autumn. In general, members of the genus *Penicillium* were typical of rhizospheres in the spring, although *Mucor* was also prominent at some sites. Numbers of propagules of *Fusarium* and *Alternaria* were greatly increased in the autumn. Although Kozlova did not state that the trees she studied were mycorrhizal, comparison with more explicit antecedent studies (e.g. Manteifel *et al*. 1950) leaves little doubt that most of them were.

The microbiota of the oak rhizosphere in semi-arid steppe sites was studied by Samtsevich (1955). A strong rhizosphere effect was noted, with fungi recorded at 135.3 thousand propagules per gram rhizosphere soil, and only 26 thousand per gram control soil. A more detailed study revealed that *Penicillium* was the major generic category that increased its proportional representation in the rhizosphere. Control soils contained higher percentages of *Cladosporium*, *Aspergillus*, *Trichoderma*, and *Alternaria* propagules. *Fusarium* varied only slightly in proportion between soils. Samtsevich studied the rhizoplane as well as the rhizosphere, and stated that the "thoroughly rinsed" root tips plated out as a rhizoplane sample included both mycorrhizal and non-mycorrhizal roots. More than 70 % of the rhizoplane inhabitants were Penicillia, and the bulk of the remainder was made up of *Fusarium* spp.

Malyshkin (1955) studied oak rhizospheres in the Saratov area of the Volga basin. He found significant increases in numbers of *Aspergillus* spp., *Mucor* spp., *Trichoderma lignorum* (Tode) Harz (in context, probably = *T. viride* Persoon and/or *T. harzianum* Rifai), and *Penicillium purpurogenum* Stoll. in the rhizosphere. *Fusarium* spp. were more common in control soils. In the rhizospheres of older oaks, *T. lignorum* became still more abundant, reaching a level of 67.5 thousand propagules per gram of soil. When mycorrhizal roots were compared to non-mycorrhizal roots, results indicated that the former were associated with relatively high numbers of various unidentified *Aspergillus* spp., while the latter supported relatively high numbers of *P. purpurogenum*, *Fusarium*, *Alternaria*, and two particular *Aspergillus* species, *A. niger* van Tiegh. and *A. sulphureus* (Fres.) Wehmer. *Trichoderma lignorum* did not differ significantly between the two root types. It should be noted that Malyshkin was paying particular attention to *T. lignorum* because he believed that it stimulated mycorrhiza formation (see *Mycorrhizosphere microorganisms as stimulators of mycorrhiza formation*, below).

The microbiota associated with mycorrhizal and non-mycorrhizal pine roots was specifically contrasted by Tribunskaya (1955). The test trees were five-month-old seedlings growing in podzolic soils in or near the Ural Mountains. The results showed that mycorrhizal roots were associated with more than 10× as many mold propagules as non-mycorrhizal roots. Most of the fungi encountered (90–95 %) were assigned to *Penicillium glaucum* Link, (as mentioned above, a nomen dubium). The remaining isolates included a species assigned to *Penicillium luteum* (probably *P. luteum* Zukal = *Talaromyces luteus* (Zukal) C.R. Benj. not *P. luteum* Sopp; in any event, a biverticillate species), plus *Cladosporium herbarum* (Persoon) Link, *Fusarium oxysporum* Schlecht., and *Rhizopus nigricans* Ehrenb.

Samtsevich (1956) studied the rhizosphere and rhizoplane mycotas of unsuberized, assimilative roots of adult oaks, ashes, larches and spruces. These trees grew in forested steppe areas of the Ukraine. The mycorrhizal status of the roots was not specified, but the oaks, larches and spruces can be expected to have had a substantial proportion of ectomycorrhizal roots. In contrast to the planted steppe oaks studied by Samtsevich *et al*. (1952) and Samtsevich (1955), none of the forest trees conspicuously stimulated fungal rhizosphere populations. The microfungal generic composition within rhizospheres was also similar to that of non-rhizosphere soils. Most rhizosphere isolates belonged to the genus *Penicillium*, with *Trichoderma* and *Fusarium* being the next most common genera encountered. All the rhizospheres studied contained *Trichoderma* isolates, even in cases where these fungi were uncommon in corresponding control soils. The generic composition of rhizoplane populations varied drastically from season to season, but ash roots appear to have been less consistently associated with *Trichoderma* spp. than were the other roots. Since ashes (*Fraxinus* spp.) are generally endomycorrhizal, the infrequent isolation of *Trichoderma* from washed roots may have been connected with the absence of ectomycorrhizal structures. Apart from this, there appeared to be little specificity in the rhizosphere and rhizoplane populations of the different tree species.

Kozlova (1958) found an insignificant rhizosphere effect for microfungi associated with both young and mature oaks. This lack of stimulation was found for trees growing in several different subclasses of chestnut loam soils. The sites Kozlova studied were forested,

which may explain why the extreme rhizosphere effects found in planted steppe oaks (Samtsevich *et al*. 1952, Samtsevich 1955) were not observed.

Maliszewska & Moreau (1959), in their studies on the rhizosphere of *Abies alba* Mill. in France, also found a pronounced rhizosphere effect in fungal populations associated with young seedlings. Mature trees, however, had rhizospheres supporting only moderately more fungi than control soils. Weakly-mycorrhizal, suppressed understory trees actually had fewer fungi in the rhizosphere than were found in control soils. Common fungi associated with seedlings and young trees included *Penicillium* spp., *Mortierella* spp. (probably inclusive of the fungi now classed in *Umbelopsis*), and *T. viride*. Mature trees were most commonly associated with *Penicillium* spp. and *Z. moelleri*.

The results of the above studies are not difficult to rationalize with the results of earlier European studies of the mycorrhizosphere. In particular, the abundance of Penicillia seen by Kozlova (1955), Samtsevich (1955), and Tribunskaya (1955) was earlier noted by Hagem (1910) and reflected in the detailed appendices attached to the work of Melin (1923). Penicillia are common soil organisms in general, but in order to fully explain their pre-eminence in the mycorrhizosphere, one must also consider factors specific to that habitat. For this purpose, the observation of Peklo (1909) that tannin-rich extracts of older mycorrhizae served as a semi-selective medium for penicillia becomes important. Tannin production may be one of the means by which mycorrhizal roots are able to select a particular rhizosphere biota. Sylvia & Sinclair (1983) later showed that the mycorrhizal fungus *Laccaria laccata* (Scopoli : Fr.) Berkeley & Broome induces tannin production by Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco] primary roots, and that the tannins produced are inhibitory to *F. oxysporum*. The same sorts of tannins may favour the growth of various Penicillia, which in turn, with their various toxins, may help to create a biochemistry inhibitory to fungal pathogens.

It is interesting to note that aspergilli, which were seldom observed in the early European studies of the mycorrhizosphere, were commonly found in the Soviet studies of the oak rhizosphere. Aspergilli in general are common soil fungi in areas of warm climate, but are very uncommon in northern forests (Söderström & Bååth 1978). It is likely that the studies of Kozlova (1955), Samtsevich (1955), and Malyshkin (1955) were the first examinations of mycorrhizospheres in areas where temperature regimes and soil types favoured the growth of aspergilli. Interestingly, both Kozlova (1955) and Samtsevich (1955) found a smaller proportion of aspergilli in the rhizosphere than in control soils, while Malyshkin (1955) found certain conspicuous *Aspergillus* species more common outside the rhizosphere. It may be that aspergilli in general are less well-adapted to mycorrhizosphere conditions than penicillia are, even where effects due to climate have been ruled out. This point will be considered in more detail later in this review (see *What is the status of Aspergillus in the ectomycorrhizosphere?*)

One conspicuous aspect of the "microbiological" mycorrhizosphere studies reviewed above is the absence of sterile hyphomycetes, e.g., *Mycelium radicis* and *Rhizoctonia* spp. This is connected to the concentration of most of these studies on the rhizosphere, rather than on the microbiota of the mantle and the root interior. As Melin (1923) showed, the number of *M. r. atrovirens* α isolates obtained from roots was greatest when those roots had been surface-sterilized. The less stringent the sterilization procedure was, the higher the proportion of sporulating fungi that was obtained. Samtsevich (1955) did study washed mycorrhizae, but did not specify how thorough the "rinse" procedure applied to these roots was. This sort of methodological vagueness, characteristic of many early rhizosphere and soil fungal surveys, was taken to task by Garrett (1951), and Harley & Waid (1955a). The results of Harley & Waid, discussed in more detail below, indicate that thoroughly-washed mycorrhizae often yield a high proportion of sterile hyphomycetes. It is likely that Samtsevich's washing procedure was not thorough enough to give a similar result. In any case, each type of washing technique roughly adumbrates a microhabitat, and it can be concluded that Samtsevich more-or-less investigated the adherent rhizosphere soil (as defined by Rambelli *et al*. 1972; see *Mycological studies of the mycorrhizosphere: 1970 - 1985. Italian studies*, below) whereas Harley & Waid (1955a) essentially investigated the rhizoplane and root interior.

The results of the above-cited "microbiological" studies have several other interesting aspects, but these will be discussed in the second half of this review in comparison with the results of subsequent studies.

Mycological studies of the mycorrhizosphere: the 1950's

One of the major trends in rhizosphere research in the 1950's was an attempt by Soviet-bloc scientists to provide "biological fertilizers" to crop plants and forest trees. This process included investigations of the abilities of mycorrhizal fungi, nitrogen-fixing bacteria, growth-stimulating bacteria, mycorrhiza-stimulating organisms, and entire beneficial microbial communities to establish themselves after being inoculated into rhizospheres or spermospheres of the appropriate plant associates. Of those studies that are of relevance to the mycorrhizosphere, the majority deal with bacteria or "microbiocoenoses."

Major reviews are given by Voznyakovskaya (1954) and Shemakhanova (1962). The major mycological mycorrhizosphere study conducted in conjunction with this research was that of Malyshkin (1951). Malyshkin examined the rhizospheres of forest oaks in the Saratov area, and found that *T. lignorum* (probably = *T. viride* and/or *T. harzianum*) and *Tieghemella glauca* (Hagem) Naumov (= *Absidia glauca* Hagem) were among the "dominant" fungal species of the root region. He inoculated these fungi and several bacterial species, in various combinations, onto acorns planted in a poor-quality, unforested chernozem (dark prairie-type) soil. Neither *T. lignorum* nor *A. glauca* could be isolated from uninoculated samples of this soil, or from the rhizospheres of uninoculated oaks. Oaks growing from acorns that had been "bacterized" with *T. lignorum* had significant populations of this species in their rhizospheres after five months. Conversely, only a trace of *A. glauca* could be retrieved from rhizospheres of inoculated oaks. Unfortunately, Malyshkin inoculated *A. glauca* in combination with *T. lignorum*, but not separately. Given the tendency of *Trichoderma* spp. to parasitize Mucoralean fungi (Durrell 1968), Malyshkin's methods may have yielded distorted results. Nonetheless, the successful establishment of *T. lignorum* in the rhizosphere is of interest, particularly since it appeared to stimulate mycorrhiza formation. This aspect of its activity will be discussed later in the review section *Mycorrhizosphere microorganisms as stimulators of mycorrhiza formation*, below.

In Britain and the U. S., the major mycorrhizosphere fungi receiving the attention of researchers were sterile root fungi and facultative parasites. Considerable work was also done on damping-off parasites and other virulent pathogens endemic to forest nurseries, but most of this work is outside the scope of this review. In many cases, the very young, artificially cultivated seedlings affected were non-mycorrhizal or probably so. This is the case, for example, with the relatively well-known studies of Warcup (1952) on the occurrence of damping-off pathogens and *Trichoderma* spp. in sitka spruce nurseries.

Levisohn (1954) studied the biology of two fungi causing "aberrant", mycorrhiza-like root infections of pine and spruce in British forest nurseries. One of these was similar to the classic ectendomycorrhizal association of pines (see Harley & Smith 1983). Unlike the true ectendomycorrhizal organism, however, it stunted seedling growth. The other was a deleterious sterile dark hyphomycete that formed a coarse Hartig net-like structure in the root cortex. Levisohn stated that "the predisposing cause of (these) root invasions...is the absence of a mycorrhizal equipment." Mycorrhizal infection, in turn, was inhibited by unfavourable soil conditions, such as those exhaustively analyzed by Rayner & Neilson-Jones (1944). As Brian *et al*. (1945) suggested, microorganisms were probably at least partly responsible for the formation of a "sick" soil inhibitory to mycorrhizal fungi.

Levisohn published further results on sterile dark facultative pathogens in 1960 (Levisohn 1960b). She reported that inoculation of birch seedlings with certain strains of the mycorrhizal symbiont *Boletus scaber* Bull. [= *Leccinum scabrum* (Bull.) Gray] facilitated attack of the root system by *M. r. atrovirens* β. This facilitated attack took place in nature only in certain soils where *M. r. atrovirens* β was prevalent. The *Leccinum* strains that conferred vulnerability to pathogenic attack on birch were from a group of isolates unusual in their "high rhizosphere activity". By the latter expression, Levisohn referred to a facultative saprobic ability exercised by these strains of *L. scabrum*, but not by other strains. It was hypothesized that when the strains with "high rhizosphere activity" were inoculated onto the roots of birch seedlings growing in the field, these strains grew saprobically in the rhizosphere and prevented mycorrhiza formation. This absence of mycorrhizae facilitated the attack by *M. r. atrovirens* β. In soils where *M. r. atrovirens* β was absent, Levisohn found that *M. r. atrovirens* α likewise attacked non-mycorrhizal, *Leccinum*-associated roots. Its effects, however, were much more benign than those of *M. r. atrovirens* β. It should be noted that we have molecularly confirmed CBS 178.46 and 179.46, deposited by Levisohn in 1946 as *M. r. atrovirens*, as *P. fortinii* (Tata & Summerbell, unpubl.). The strains have no α or β designation in the collection records, but are morphologically consistent with the former taxon.

The ecological significance of *M. r. atrovirens* α was further investigated by Robertson (1954). This author confirmed Melin's (1923) findings that *M. r. atrovirens* α could be isolated from healthy pine roots. He also found, however, that approximately 21 % of the short roots collected from the basal regions of long roots were extensively infected by *M. r. atrovirens* α, while only 8 % of short roots collected from the middle regions of long roots were affected. This caused him to suggest that *M. r. atrovirens* α preferentially tended to colonize senescent short roots, which should be concentrated towards the base of individual growing long roots. Robertson found that the short roots nearest the long root apex also had a high frequency of invasion by *M. r. atrovirens* α, a finding that was more difficult to explain. It appeared possible that these short roots, formed in the late autumn (Robertson collected roots in January), were retarded in mycorrhiza formation by seasonal conditions. In the absence of mycorrhizal colonization, the cortical cell layers of these roots soon atrophied and became a suitable substrate for *M. r. atrovirens* α.

Robertson supported these preliminary conclusions with further work on the colonization of mycorrhizal long roots by *M. r. atrovirens* α. He showed that *M. r. atrovirens* could not be isolated from the actively growing apices of the roots, but could be isolated from the basal areas of the growing tips. These areas are regions of cortical senescence, and microscopic examination showed that dark hyphae similar to those of *M. r. atrovirens* α were indeed present in senescent cortical cells. In the apical areas, where only cells in good condition were present, *Pyrenochaeta terrestris* (H.N. Hansen) Gorenz, J.C. Walker & Larson was the chief root surface colonizer. Robertson's use of a very stringent root washing procedure ensured that *P. terrestris*, like *M. r. atrovirens* α, was actually a root-colonizing species. It did not, however, appear to penetrate roots or to colonize the senescent cortex.

Robertson concluded that *M. r. atrovirens* α was essentially a saprobe adapted for colonizing senescent root tissue. Short roots that failed to become colonized by mycorrhizal fungi could undergo an early spontaneous cortical senescence and be converted into "pseudomycorrhizae" by *M. r. atrovirens* α, with concomitant intracellular invasion. Thus, a condition resembling a pathogenic attack could be produced by a fungus whose actual pathogenic ability was decidedly weak. This analysis accounts for the "innocuous" nature (Levisohn 1960b) of *M. r. atrovirens* α under field conditions, but seems to understate the potential pathogenic ability of the fungus as manifested in flask experiments. Under sterile conditions, at least, *M. r. atrovirens* α / *P. fortinii* is capable of killing seedlings (Melin 1923, Richard *et al*. 1971).

In the U. S., Doak (1955) also studied the effect of a sterile root fungus on pine. This fungus proved to be a relatively virulent pathogen in pure culture. Doak did not try to identify the organism, referring to it only as AS 34-3, but he had noted in an earlier abstract (Doak 1934) that it strongly resembled *Rh. silvestris* (Melin 1923) in both colony morphology and mode of infection.

Doak also inoculated *Coprinus micaceus* Fr. and a member of the *Armillaria mellea* (Vahl.) Quel. complex into axenic flasks with pine. He found that the former was an innocuous rhizosphere inhabitant, while the latter was a moderately virulent cortical pathogen. The effect of ectomycorrhizal symbiosis on root colonization by "*A. mellea*" and AS 34-3 was not investigated.

The studies of Doak (1955), Robertson (1954), and Levisohn (1954, 1960b) emphasized the relative importance of the sterile root-inhabiting fungi to ectomycorrhizosphere biology. It could be clearly seen by 1955 that even though species varied from site to site, these fungi as a group were omnipresent in temperate forests. Although different species appeared to possess different degrees of potential pathogenicity, none of these fungi proved to be as destructive as root rots or damping-off pathogens. It appeared likely that the ecological niches occupied by the various sterile root-inhabiting fungi or DSE were fundamentally similar.

The taxonomic and spatial structure of mycorrhizosphere populations was critically studied by Harley & Waid (1955a). These authors introduced a standardized and relatively rigorous procedure for washing surface contamination from roots. The use of this procedure is now a standard practice in rhizosphere biology. In their own use of it, Harley & Waid succeeded in showing that the propagule populations that could be washed off mycorrhizal beech roots differed greatly from the actual fungal populations of the root surface. Dilution plates of mycorrhizosphere soil gave rise to large numbers of isolates of *Penicillium*, *Monilia geophila* Oudem. [= *Geomyces pannorum* (Link) Sigler & J.W. Carmichael], and *Cladosporium*. On unwashed mycorrhizal segments, *Penicillium*, *Hyalopus* (prob. = *Acremonium* or *Pochonia*), *T. viride*, and various members of the *Mucorales* were predominant. Washed mycorrhizae gave rise mainly to sterile mycelia, with *Mucor* sp., *M. ramannianus* (*U. ramanniana*), *Penicillium* sp., and *Cylindrocarpon* sp. also being represented.

Harley & Waid concluded that dilution plating favoured sporulating hyphomycetes and underrepresented soil zygomycetes, while all procedures except root washing obscured the importance of sterile root mycelia. It should be noted that these sterile mycelia, besides including obdurately sterile fungi like the *Mycelium radicis* group, also included "forms of *Fusarium*, *Cylindrocarpon*, and *Gliomastix* (= *Acremonium s.lat. p.p.*, though confusion with *Phialophora*–like organisms cannot be excluded) for instance, which will develop fruiting structures in time." Nonetheless, Harley & Waid found that these sterile fungi made up over 50 % of the isolates from washed roots, while beech petioles washed in the same manner yielded less than 10 % sterile fungi.

Harley & Waid (1955a) also mapped the fungal population of an individual washed beech lateral root, the mycorrhizal status of which was unspecified. Of thirteen fungal species obtained, nine were sterile, with *M. r. atrovirens* (?α) being the most common. Five species were conidial hyphomycetes. The distribution map of these fungi confirmed the conclusion of Robertson (1954) that *M. r. atrovirens* tended not to occur in the actively growing regions of the root. Nonetheless, it occurred just behind these regions, whereas fungi like "*Hyalopus*", *Cylindrocarpon*, and *Rhizoctonia* cf. *sylvestris* were generally restricted to more mature portions of the root.

A second study by the same authors (Harley & Waid 1955b) considered the effect that illumination of the "host" plant might have on mycorrhizosphere populations. They showed that plants grown in the highest of five light intensities tended to support root populations in which *T. viride*, *Gliomastix* (see taxonomic comment two paragraphs above), and a chlamydospore-producing sterile fungus were the most prominent representatives. In the lowest light intensity, roots were associated with *Rhizoctonia* cf. *sylvestris* and a sterile hyaline species. The *Rhizoctonia* caused visible disease lesions. Harley & Waid showed that numbers of *Trichoderma* and *Rhizoctonia* isolates obtained in all treatments were inversely correlated, and speculated that *T. viride* might antagonize or compete with the *Rhizoctonia*. To complicate matters, however, data also showed that roots of well-illuminated plants, besides being high in *Trichoderma* numbers, were also abundantly mycorrhizal. The low-intensity plants beset by *Rhizoctonia* had few mycorrhizae. The authors did not consider the potential positive correlation between mycorrhizal fungi and *Trichoderma*, nor the inverse correlation between mycorrhizal colonization and *Rhizoctonia* pathogenesis.

The first relatively detailed list of fungi isolated from assimilative roots of an ectomycorrhizal host was was published by Sizova & Itakayeva (1956). These authors did dilution plates from rhizosphere soils of birch in the Moscow area. The mycorrhizal status of the trees was not mentioned, but it would normally be expected that most or all were mycorrhizal. Only young "small roots" (*koreshki*) were used as a source of rhizosphere soil. The fungi obtained included 28 species of *Penicillium*, plus several species of *Alternaria* and *Trichoderma*. A few representatives of *Fusarium* were found, as well as a small number of more unusual fungi, like *Stysanus* (= *Doratomyces*) sp. Sizova & Itakayeva established that numbers of fungal propagules in the rhizosphere increased as the birches aged, reaching a maximum in the rhizospheres of 40–50-yr-old trees. In still older trees, the numbers were somewhat lower, although still greatly elevated above the numbers associated with seedlings. The authors also examined the antagonistic properties of the fungi they isolated; these results will be considered later in this review – see *Effect of mycorrhizosphere organisms on root diseases*.

Mańka & Truszkowska (1958) did a detailed floristic study of the fungi growing from surface-disinfected mycorrhizae and suberized roots of *Picea excelsa* (Lamb.) Link [= *P. abies* (L.) Karst.]. The study site was near Poznań, Poland. *Mycelium radicis atrovirens* (α) was by far the most common species obtained from roots of all size classes, but a variety of soil hyphomycetes, *Zygomycetes*, *Ascomycetes*, and sterile mycelia were also obtained. Of these, the most commonly associated with mycorrhizae were *Cephalosporium acremonium* Corda (probably = *Acremonium* sp., based on the description given), *Penicillium waksmanii* Zal., and *Trichoderma koningii* Oudem. Most species declined in frequency as root diameter and suberization increased, although fungi identified as *Geotrichum candidum* Link (a species never confirmed to occur in such habitats; isolates said to be clumped and to become ochraceous on the surface, thus suggesting misidentification of a *Trichosporon*) and *Penicillium commune* Thom appeared to be primarily associated with older roots. A particularly marked association with mycorrhizae themselves was shown by "*C. acremonium*."

As can be seen, the mycorrhizosphere mycota revealed by Mańka & Truszkowska is similar to that revealed by earlier, less taxonomically detailed studies conducted in north temperate forests. The similarity is particularly great when one compares other studies in which roots have been thoroughly washed or mildly surface-disinfected, e.g., Melin (1923) or Harley & Waid (1955a). Clearly, as Harley & Waid (1955a) indicated, isolation technique has a profound effect on the kinds and numbers of fungi isolated. However, even if one compares Mańka & Truszkowska's study to studies where different techniques were used, certain commonalities emerge. One of these, for example, is the scarcity of *Aspergillus* spp. found in northern forest mycorrhizospheres, irrespective of whether fungi are sampled by dilution plating (e.g., Sizova & Itakayeva 1956) or by root disinfection.

Microbiological studies of the mycorrhizosphere: the 1960's

The microbiological mycorrhizosphere studies of the 1960's were often similar in their emphasis to those of the 1950's. In the majority of cases, however, there was a noteworthy conceptual development: that is, more rigorous attention was paid to the precise area of influence of mycorrhizae themselves. The use of whole mycorrhizal root systems, or of "young roots" with a high probability of being mycorrhizal, tended to give way to the use of discrete mycorrhizal and non-mycorrhizal root portions.

This progression can be seen in the studies of Ivarson & Katznelson (1960) and Katznelson *et al*. (1962). These authors worked on rhizospheres of *Betula lutea* Michx. seedlings grown in forest soils from the Ottawa region of Canada. The initial study by Ivarson & Katznelson (1960) showed that roots of yellow birch seedlings supported fungal populations that did not differ quantitatively from those of surrounding soils. (Bacterial studies conducted concurrently are not reviewed here). Ivarson & Katznelson did not specifically examine mycorrhizae, but did state that the root material they used possessed more "mycorrhizal

clusters" than roots seen in other experiments. Their data, then, pertain to whole young root systems bearing a substantial number of mycorrhizal laterals.

The succeeding study (Katznelson *et al*. 1962) compared mycorrhizal to non-mycorrhizal assimilative roots. A significant difference in fungal populations was found between the two, with rhizospheres of non-mycorrhizal roots yielding twice the number of fungal propagules obtained from mycorrhizospheres. The merit of distinguishing the two habitats was clearly demonstrated – as it had been earlier by Tribunskaya (1955).

It should be noted that the data obtained by Ivarson & Katznelson (1960) and Katznelson *et al*. (1962) was markedly different from most data obtained previously for fungi in the rhizospheres of mycorrhizal root systems. Generally, fungal numbers had been found to be increased in the vicinity of mycorrhizal root systems (e.g., see Samtsevich 1955). Also, it had been found that mycorrhizal roots were associated with more mold propagules than were non-mycorrhizal roots (Tribunskaya 1955). In both cases, the results obtained by the Canadian authors contradicted these results. The first discrepancy is easy to rationalize as an artefact of differing control soil conditions, but the second is more problematic. Differences in soil conditions, sampling techniques, plant species, plant health, mycorrhizal species, and the taxonomic composition of rhizosphere populations may all contribute to variability in this sort of data.

Katznelson *et al*. (1962) also examined the generic composition of the mycota associated with serially-washed roots of yellow birch. Mycorrhizal roots were found to support a large number of saprobes, including *Penicillium*, *Paecilomyces*, and *Phialocephala*, in addition to members of the potentially pathogenic genus *Cylindrocarpon*. Non-mycorrhizal roots were mainly associated with potential pathogens, including *Cylindrocarpon*, *Fusarium*, and *Pythium*. The last two genera did not occur on mycorrhizal roots. Many of the saprobes found on mycorrhizae, including *Penicillium*, could not be isolated from non-mycorrhizal roots. The high incidence of potential pathogens on non-mycorrhizal roots eloquently suggests the role of ectomycorrhizae in disease-control. This phenomenon later became recognized as a highly significant aspect ectomycorrhizal biology (Marx 1973).

In light of current knowledge about mycorrhizae and disease control, it is possible to suggest a rationalization of the apparently contradictory quantitative results obtained by Katznelson *et al*. (1962) and Tribunskaya (1955). Tribunskaya, who found relatively few fungal propagules associated with non-mycorrhizal roots, evidently sampled root material that was in good health. Very few potential pathogens were recorded from platings of macerated roots. On the other hand, the non-mycorrhizal roots studied by Katznelson *et al*. (1962) were probably under moderate to severe stress owing to the high number of associated pathogens. The high rhizosphere fungal propagule numbers around these roots may have reflected the reproduction of the pathogenic fungi. Also, other rhizosphere fungi may have been stimulated by the pathogenic attack.

The differences between rhizospheres of diseased and healthy non-mycorrhizal roots of *Pinus contorta* Dougl. seedlings were studied by Timonin (1966). Fungi in general were much more numerous in the rhizospheres of diseased roots (250 000 propagules/ gram soil compared to 68 300 / gr for healthy roots). It is clear that workers comparing rhizospheres of mycorrhizal and non-mycorrhizal roots must pay strict attention to the health of the latter. Non-mycorrhizal roots are often more vulnerable to disease than mycorrhizal roots (Marx 1973), but they may or may not actually be infected at the time microbiological sampling is done.

The rhizosphere effect exerted by ectomycorrhizae of various trees in Italy was studied by Rambelli (1962, 1963, 1965, 1966). In the case of *Eucalyptus camaldulensis* Dehnh. (referred to as *E. grandis* Hill ex Maiden, but corrected in later works), Rambelli (1962) found a clear stimulation of fungi in the mycorrhizosphere. This stimulation was later also found in studies on *Pinus pinea* L. (Rambelli 1963) and *P. radiata* D. Don (Rambelli 1966). With *Populus euramericana* (Dode) Guinier (= *Populus X canadensis* Moench.), however (Rambelli 1965), mycorrhizospheres contained fewer fungi than control soils. Although the control soil sampled in the latter study was relatively high in microbial numbers, the diminution could not be explained in terms of high control soil nutrient content alone. Firstly, bacteria, unlike fungi, were stimulated in poplar mycorrhizospheres. Secondly, the absolute number of fungi in these rhizospheres was much less than the number found in *P. pinea* rhizospheres, even though the pines occurred in a poorer soil. Rambelli (1965) may, then, have observed a genuine inhibition of fungal growth in the poplar mycorrhizosphere.

The taxonomic composition of the rhizosphere fungal populations was studied for both eucalypt (Rambelli 1962) and poplar (Rambelli 1965). In the eucalypt study, several microfungal species found in the mycorrhizosphere and mantle were not found in control soils. These included *Penicillium implicatum* Biourge, *P. sclerotiorum* F.H. Beyma, *Tieghemella spinosa* (Lendner) Naumov (= *Absidia spinosa* Lendner), and *T. koningii*. Other species, like *Penicillium spinulosum* Thom, *P. frequentans* Westl. (= *P. glabrum*), *P. thomii* Maire, and *Gliocladium roseum* Bainier [= *Clonostachys rosea* (Link : Fries) Schroers, Samuels, Seifert & W. Gams] were recorded only from

control soils. The last three *Penicillium* species named are similar in many ecological and morphological respects (see Domsch *et al*. 1980). Some differences were also noted between fungal populations in poplar rhizospheres and control soils. Apart from the usual rhizosphere and soil molds, seven distinct sterile mycelia were isolated in the study, three from the mycorrhizosphere and four from control soils.

The rhizosphere fungi associated with young rootlets of boreal spruces and birches growing in the Vologda region of the USSR were studied by Runov & Zhdannikova (1960). Pronounced rhizosphere effects were seen for filamentous fungi. In general, Runov & Zhdannikova found that the poorer the soil was in the site studied, the higher the r/s (rhizosphere/soil) ratio was. One exception to this rule, however, was found in pure *Sphagnum* bogs. These bogs appeared to have a large number of mold fungi in the control substrate, but rhizospheres nonetheless contained significantly increased numbers. Another intriguing quantitative factor revealed by the study was that birches consistently supported higher numbers of rhizosphere fungi than spruces growing in the same soil type. This pattern was generally true of rhizoplane fungi as well, but there were some exceptions. An auxiliary study comparing spruces and pines within *Sphagnum* bogs showed that the rhizosphere mycota of pines contained many more individuals than the corresponding mycota of spruces. The authors suggested that these figures reflected the superior adaptation of pines to these habitats, which were usually inhibitory to spruce.

Taxonomic studies on birch and spruce rhizosphere fungi showed that the prevailing fungal genera associated with both trees were *Penicillium*, *Umbelopsis* (name applied here in the modern sense to fungi identified under older names), *Mucor*, and *Trichoderma*. In general, higher numbers of Penicillia were associated with birch than spruce. *Umbelopsis*, on the other hand, consistently made up a higher proportion of total isolates from spruce than from birch. *Trichoderma* did not exceed 2–3 % of total isolates in either rhizosphere habitat. Unfortunately, taxonomic breakdowns of rhizosphere fungi were only done for two of the four soil types the authors examined. Podzols and peaty-humus soils were included, while *Sphagnum* bogs and grassy bog lowlands were omitted.

Further quantitative microbiological studies on the ectomycorrhizosphere were carried out by Neal *et al*. (1964), Neal *et al*. (1968), and De Leval & Remacle (1969). Neal *et al*. (1964) found a reduction in mold propagule numbers in the Douglas-fir mycorrhizosphere, as compared to control soils. One mycorrhizal type, "yellow mycorrhiza" (probably formed by *Piloderma fallax* (Libert) Stalpers or a related fungus) was associated with unusually small numbers of molds. Despite its loosely-woven, rhizomorphic morphology, it yielded only 25 % of the mold numbers found in the control.

Neal *et al*. (1964) observed an interesting distribution of yeasts in the mycorrhizosphere of Douglas-fir in Oregon. Yeasts associated with ectomycorrhizal roots had previously received very little study. Of the soils these authors examined, only those from the rhizospheres of yellow and grey mycorrhizae appeared to contain yeasts. Control soils and soils from around suberized roots and white mycorrhizae yielded no yeasts whatsoever. No numerical data were given, but the possibility of a specific stimulation of yeasts by the mycobionts forming yellow (*Piloderma*-type) and grey mycorrhizae must be acknowledged. It should be noted that a small number of yeast species in the genus *Rhodotorula* are among the few stimulants that can induce the basidiospores of certain mycorrhizal fungi to germinate in pure culture (Fries 1943, 1977, 1978, 1980). It is possible that such yeasts have important, specific associations with ectomycorrhizal basidiomycetes in nature.

Neal *et al*. (1968) compared *Alnus rubra* Bong. mycorrhizospheres to those of Douglas-fir. The study was conducted in northern Oregon, U.S.A. Both trees showed a stimulation of mold numbers in the mycorrhizosphere, but the alder mycorrhizosphere was significantly more stimulatory than that of Douglas-fir. The suberized roots of both species had similar numbers of associated molds. In this case, Douglas-fir mycorrhizae were formed by a known mycobiont, *Cenococcum geophilum* Fr. *In vitro* studies showed that the *C. geophilum* mycorrhizae contained compounds inhibitory to microbial respiration. This may explain in part why alder mycorrhizae were more stimulatory than the Douglas-fir × *C. geophilum* mycorrhizae. Also, however, the relatively high nitrogen content of the actinorrhizal alder roots must be taken into consideration.

DeLeval & Remacle (1969), working in Belgian poplar forests, found that the length of fungal hyphae per gram dry soil did not differ between trees in ectomycorrhizal and non-ectomycorrhizal stands. However, the ectomycorrhizal stand differed from five non-ectomycorrhizal stands in two qualitative respects. Firstly, its rhizospheres yielded significantly more sterile mycelia than did those of the non-ectomycorrhizal stands. Secondly, it conspicuously lacked *Trichoderma* spp., which were plentiful elsewhere. Sterile mycelia were isolated in relatively high numbers at all sites, perhaps because the authors used a soil-washing technique for sampling rhizosphere fungi. Unfortunately, they did not attempt to determine whether the sterile mycelia isolated in the ectomycorrhizal stand included ectomycorrhizal fungi. To the present author, this seems unlikely, given the growth media and techniques used. The observed

sterile mycelia are likely to have been saprobic *Ascomycetes* and *Basidiomycetes*.

Marletto (1969) found that yeasts were not detectably stimulated in soils proximal to fruiting bodies of *Tuber* spp. in the Italian Piedmont. Since roots were also reported to be present in the soil samples examined, it may be assumed that *Tuber* mycorrhizae also do not dramatically stimulate yeast growth. The truffle-influenced soils, like control soils, contained typical yeasts associated with temperate soils and plant surfaces. Species prominently represented included the phyllosphere-and litter-inhabiting *Aureobasidium pullulans* (de Bary) G. Arnaud, and the typical soil-inhabitants *Hansenula saturnus* (Klöcker) Sydow & P. Sydow [now *Williopsis saturnus* (Klöcker) Zender], *Cryptococcus albidus* (Saito) C.E. Skinner *et al*., and members of what is now called the *Trichosporon cutaneum* (Beurmann, Gougerot & Vaucher) M. Ota complex.

The extent to which an ectomycorrhizal fungus could potentially influence the soil mycota was graphically demonstrated by Ohara & Hamada (1969) as part of a series of studies of the "shiro" of *Tricholoma matsutake* (S.Ito & S.Imai) Singer. The term "shiro," Japanese for "castle" or "fortress," referred to a visible soil region delimited by a zone of conspicuous white fungal hyphae; it is thus the first and best mycological term for the three-dimensional equivalent of a fairy ring and is here proposed for adoption into English as a mycological technical term. The *T. matsutake* shiro could be divided into several distinct subzones (Ogawa 1976a). Two of them contained active mycorrhizae. A zone containing mature mycorrhizae was characterized by the formation of a thick white mycelial mat near the soil surface. In an adjacent zone containing senescing mycorrhizae, this mat became pulverulent and rendered the nearby soil "desiccated and impermeable to water" (Ogawa 1976a). Within the zone of mature mycorrhizae, bacteria and actinomycetes were often completely absent (Ohara & Hamada 1967). Ohara & Hamada showed that within the shiro of *T. matsutake*, fungal populations were drastically reduced in diversity. Indeed, in the most active regions of the shiro, only one species, a "*Mortierella* sp.", could be isolated. Outside the shiro, a normal microbiota occurred. An unusually intimate relationship between *T. matsutake* and *Mortierella vinacea* Dixon-Stewart [= *Umbelopsis vinacea* (Dixon-Stewart) Arx] had earlier been shown by Tominanga (1963). This author regularly isolated *U. vinacea* from both mycorrhizae and fruiting bodies formed by *T. matsutake*. There seems little doubt that this was also the *Mortierella* sp. referred to by Ohara & Hamada.

In general, the microbiological mycorrhizosphere studies of the 1960's confirmed that ectomycorrhizal symbionts exercised a profound selective influence over the mycota of their rhizospheres. In the absence of these symbionts, cortical and damping-off pathogens tended to proliferate. Although fungal numbers were generally stimulated in the mycorrhizosphere compared to control soils, this was not always the case. Moreover, comparisons of mycorrhizal and non-mycorrhizal roots showed that the latter were often more stimulatory than the former. All this information was of particular interest to mycologists and forest pathologists interested in the role of mycorrhizae in the control of root diseases.

Mycological mycorrhizosphere studies of the 1960's

A large and relatively poorly-known corpus of work was produced in the 1960's by Polish workers investigating rhizosphere and soil communities in relation to forest pathology. One of the early studies in this series (Mańka & Truszkowska 1958) was mentioned earlier in this review. Mańka (1960) studied various aspects of the distribution of *M. r. atrovirens* in Polish forests. Unlike many previous authors, he did not distinguish *M. r. atrovirens* α and *M. r. atrovirens* β, but his descriptions indicate that he primarily worked with the former. *M. r. atrovirens* occurred abundantly on suberized roots of *Picea abies*, *Pinus sylvestris* L., and *Quercus robur* L. It could not, however, be isolated from roots of *Salix americana* Hoedt. When Mańka compared suberized roots of spruce to mycorrhizae, he found that over 25 % of surface-disinfected suberized root sections yielded *M. r. atrovirens*, while only 19 % of mycorrhizae did. The largest numbers of *M. r. atrovirens* isolates were obtained from suberized roots less than 1 mm in diameter occurring in the humus layer of the soil profile. Larger roots or roots from deeper soil horizons were less likely to harbour inoculum of the fungus.

Mańka also noticed that *M. r. atrovirens* numbers on fine roots seemed to be inversely correlated with the numbers of a potential pathogen, *Cylindrocarpon destructans* (the current correct name for a species often referred to in older literature as *C. radicicola* Wollenw.). This suggested that the former fungus tended to preempt a niche on the roots that would otherwise be occupied by the latter fungus. Mańka concluded that except in the case of a few deleterious "races," *M. r. atrovirens* was a beneficial organism. However, he also showed that a number of *M. r. atrovirens* strains acted to stimulate rhizomorph production in the root pathogen *A. mellea*. Since this fungus generally forms rhizomorphs before invading root tissue (Mańka 1953, Doak 1955), the stimulation exerted by *M. r. atrovirens* might serve to precipitate attacks on fine roots.

Mańka & Rząsa (1961) examined surface-disinfected young long-root sections (probably non-mycorrhizal, since they were over 1 mm in diam) of pine, oak, and spruce. Their data make an interesting

comparison to related studies where mycorrhizae were examined. These authors confirmed that *M. r. atrovirens* was more-or-less restricted to roots growing in the upper soil layers. It was commonly accompanied by a *Mortierella* species ("*Mortierella pusilla*," a nomen confusum, probably in this case referring to various members of the genus *Umbelopsis* – see Truszkowska 1961). *Cylindrocarpon destructans* was again ubiquitous on roots at lower soil depths (110 cm depth and below), but did not appear to be actively pathogenic. Mańka & Rząsa also studied the sere of fungi developing on detached root portions immersed in forest soil, and showed that the typical fungi of the living roots – *M. r. atrovirens* and *C. destructans* – were rapidly displaced by saprobes. Mańka (1960) had already shown that *M. r. atrovirens* and *C. destructans* were associated with mycorrhizae to about the same degree as they were associated with other portions of the assimilative root system.

A similar study was conducted by Mańka & Gierczak (1961) on long-roots of pine. In this case, however, an exhaustive list of fungal colonizers was compiled for both healthy and severed, decaying roots. Healthy roots were predominantly associated with *M. r. atrovirens* and *Mortierella alba* Mańka & Gierczak [= *Umbelopsis nana* (Linnem.) Arx]. Few isolates of *C. destructans* were found in this study, but two other potential pathogens, *Cylindrocarpon didymum* (Hartig) Wollenw. and *Rh. sylvestris* Melin, were commonly isolated from roots in the deeper soil layers. Common invaders of severed roots included *Trichoderma* spp. and *Zygorhynchus vuilleminii* Namysl. (= *Z. moelleri* Vuill.).

Another thorough mycological study was carried out by Truszkowska (1961) on mycorrhizae and fine roots of "*Populus euramericana marilandica* Bosc." (= *Populus* × *canadensis*). Since Truszkowska studied trees on plantations, and since many of the plantations were on previously-cultivated or cleared land, very unusual populations of fungi were obtained from the roots. *Fusarium* spp., especially the potential pathogen *F. solani* (Mart.) Sacc. (now known to be a species complex), constituted the largest component of the mycota on roots of all size classes. By comparison, Mańka & Gierczak (1961) found no *Fusarium* spp. whatsoever on healthy roots of pine. It should be pointed out that both the pines and poplars studied were growing in the same general area, the Poznań district of Poland. The general scarcity of *Fusarium* spp. in coniferous forest soils later became well documented (Mishustin *et al*. 1966, Schisler & Linderman 1984).

Other common fungi on poplar mycorrhizae included *Hormodendrum resinae* Lindau (= *Hormoconis resinae* (Lindau) Arx & de Vries) and *Fusidium viride* Grove [possibly = *Acremonium luzulae* (Fuck.) W. Gams]. Both these species are rarely found in mycorrhizosphere studies of trees growing in forest soils. *Mycelium radicis atrovirens* was uncommon; in fact, only two of 156 isolates from mycorrhizae were representatives of this taxon.

Besides documenting unusual fungal communities, Truszkowska also established that the greatest diversity of fungal species occurred on mycorrhizae and roots under 0.5 mm diam. Older roots yielded fewer species of fungi. Also, distinct differences were shown to occur in roots of all size classes when fungal populations from the four sites were compared to one another.

The major contribution of the above-cited Polish studies is to show the dependence of rhizosphere fungal community structure on root age, tree species, site history, soil depth, and root condition. The studies also make the suggestion, taken up in later Polish work, that *M. r. atrovirens* (α) is an indicator of favourable conditions for root growth. In soils where it is absent or rare, Nectriaceous pathogens – *Cylindrocarpon* and *Fusarium* – tend to predominate on roots.

Sizova & Vasin (1961) added two further factors influencing rhizosphere populations: tree age and plant species diversity within a stand. These authors did dilution plates of rhizosphere soils around "young roots" of oaks from the Moscow region. Oaks of various ages from both pure stands and mixed forest stands were sampled. There was a limited amount of specificity attributable to tree age: for example, a species identified as *Penicillium expansum* Link appeared to be specific to trees over 50-yr-old, and this was true in both pure and mixed stands. With regard to stand composition, there was an almost fourfold increase in the percentage of *Alternaria* spp. in the rhizospheres of oaks in mixed stands as compared to pure stands. Other fungi, including *Penicillium* spp., *Aspergillus* spp., and *Trichoderma* spp., seemed to be little affected by stand composition.

Sizova & Vasin (1961) also found that although the general quantity of fungal propagules was greater in the rhizosphere than in control soils, certain fungal genera were found in much higher proportion in the control. *Trichoderma* and *Aspergillus* were the most clearly affected. On the other hand, *Penicillium* spp. were significantly more abundant in the rhizosphere. Perhaps because of the media and techniques used, no *Zygomycetes* or sterile mycelia were recorded for either soil type. Sizova & Vasin stated that when their techniques were used, the rhizosphere mycoflora of Moscow-region oaks was typified by *Trichoderma koningii* Oud. (in the taxonomy of the day, this taxon included *T. koningii sensu stricto* and several other *Trichoderma* species with green, elliptical conidia), *Penicillium paxilli* Bain., *P. nigricans* (Bain.) Thom, and *Aspergillus clavatus* Desm. By comparison, birch rhizospheres typically contained *P. martensii* Biourge (= *P. aurantiogriseum* Dierckx), *T. koningii*,

P. nigricans, and *P. paxilli*. Spruce from the same region was associated with *Penicillium fuscum* Sopp, *Penicillium* sp., *T. lignorum* (= *T. viride* and/or *T. harzianum*), and *M. ramannianus* (*U. ramanniana*). Sizova and Vasin regarded these microbial specificities as possible factors predisposing different species of trees to have differing abilities to resist root pathogens. Their attempts to assess the antifungal antibiotics produced by the rhizosphere mycota will be mentioned later in this review – see *Effect of mycorrhizosphere organisms on root diseases*.

A brief report included in the work of Shemakhanova (1962) mentions that this author found *Fusarium* spp. and *Trichoderma* spp. to be characteristic of non-mycorrhizal roots of pine seedlings and adult oaks in the Moscow region. Both genera were less common on mycorrhizal roots.

Chastukhin & Nikolayevskaya (1962) compared the fungi growing in the rhizospheres of oak root tips with those colonizing decaying woody oak roots. This study was conducted in the Voronezh area of the Don Valley, U.S.S.R. Both natural oak stands and oaks planted in steppe chernozem (black prairie-type) soils were considered. The authors noted that in all habitats, rhizospheres of healthy oaks contained greater quantities of fungal propagules than control soils. Mature oaks had a more abundant rhizosphere mycota than young oaks. When mycorrhizal and non-mycorrhizal roots of young oaks from steppe soils were contrasted, the former were found to have more associated mold propagules than the latter in the autumn, but to have approximately equal numbers in the spring.

Chastukhin & Nikolayevskaya noted that the specific composition of the rhizosphere mycota did not differ greatly from that of the control soil mycota. In steppe chernozems, *Aspergillus oryzae* (Ahlburg) Cohn (= *A. flavus* Link in this habitat type) and other Aspergilli were prominent, as well as *R. nigricans*. In woodland soils, *Mucorales* [e.g., *Tieghemella tieghemi* (K.N. Deckenb.) Naumov (= *Absidia coerulea* Bain.), *M. silvaticus* Hagem, *U. ramanniana*], penicillia (*P. luteum* Zuk. = *T. lutea*, *P. biourgenianum* Zal. = *P. brevicompactum* Dierckx, *P. granulatum* Bain.), *Trichoderma lignorum* (= *T. viride* and/or *T. harzianum*) and *Scopulariopsis brevicaulis* (Sacc.) Bain. were common. The major difference between rhizosphere and control soils in woodland was that Penicillia predominated in the rhizosphere, whereas Mucoraceous fungi predominated in the controls.

Decaying roots of 1-yr-old stumps tended to be colonized by *Fusarium* spp., especially *F. oxysporum*, which caused conspicuous "pustules" of intense decay. More advanced decay was brought about by various Basidiomycetes [e.g., *Psathyrella candolleana* (Fr. : Fr.) Maire, *Hypholoma fasciculare* (Hudson : Fr.) P. Kummer, *Mycena polygramma* (Bull. : Fr.) S.F. Gray], the hyphae of which intermingled with those of *T. viride* and *T. koningii*. In the final stages of decay, *A. coerulea* and *U. ramanniana* were often recovered. It is clear that these fungal decay communities are quite different from rhizosphere communities. However, the results of this study make possible the following prediction: that mycological studies on woodland rhizospheres containing a high proportion of decaying or declining roots will yield exaggerated numbers of *Fusarium* or *Trichoderma* propagules.

Sizova & Suprun (1962) compiled a detailed list of fungi isolated from fine-root rhizospheres of four ectomycorrhizal species: *P. abies*, *Betula pendula* Koth., *B. pubescens* Ehrh., and *Tilia cordata* Mill. Since sampling was done by dilution plating, *Penicillium* spp. greatly predominated in the list. Some species, e.g., *P. fuscum* Sopp, were common in rhizospheres and in non-rhizosphere soils, while others were present only in the rhizosphere. *Penicillium vinaceum* J.C. Gilman & E.V. Abbott, for example, was found only in the spruce rhizosphere. Certain species, e.g., *Aspergillus fumigatus* Fres., evidently tended to be suppressed in rhizospheres. Each tree species had a distinctive assemblage of rhizosphere associates. Interestingly, *Aspergillus* spp. were strongly represented in the rhizosphere of *T. cordata*, but were uncommon in the other rhizospheres. Control soils from *T. cordata* stands contained relatively few Aspergilli, and were comparable to control soils from spruce and birch stands.

A study of the general abundance of fungal propagules in the rhizosphere provided Sizova & Suprun (1962) with some intriguing data. They found that fungal numbers were greatly enhanced in the rhizospheres of *Betula* and *Tilia*, but were suppressed to less than one-fifth of control soil levels in the *Picea* rhizosphere. This suppression was ascribed to the low pH and low nutrient status of the rhizosphere, but the involvement of unfavourable root exudates and resins was also suggested. The potential role of antagonistic mycobionts was not considered. The congruence of these data with those of Runov & Zhdannikova (1960) for boreal spruce should not be overlooked. Spruce rhizospheres in general may be relatively inhibitory towards filamentous fungi.

A very unusual study of the surface mycota of tree roots was conducted by Baxter & Middleton (1961). These authors studied the microfungi associated with "fibrous roots" of willows, poplars, alders, spruces and hemlocks occupying a sere at the margin of a retreating glacier in Alaska. It is likely that a large proportion of the root material used in isolations was non-mycorrhizal, suberized material. Evidently, however, some mycorrhizae were included. The authors isolated a large number of clamp-connection-bearing

Basidiomycetes from their samples, and suggested that some of these might be mycorrhizal fungi. Given the nature of the isolation medium used (water agar mixed with gas-sterilized legume straw or corn kernels), it is more likely that the Basidiomycetes were cellulolytic saprobes.

Baxter & Middleton found that the pioneer plant community (small willows, alders and spruce) was associated with few fungi. The isolates obtained from roots consisted mainly of *Pythium*, *Fusarium*, and *Mortierella* spp. As stand age and diversity increased, fungal diversity also increased, and genera such as *Trichoderma*, *Cephalosporium* (probably = *Acremonium*, *Lecanicillium*, *Simplicillium* or *Pochonia*) and *Melanospora* were found in more mature hemlock-spruce stands. Interestingly, the number of *Fusarium* species also increased with stand maturity. This represents one of the few instances on record where substantial numbers of Fusaria were found in conifer rhizospheres in established northern forest stands.

In the course of a study on "stand-opening disease" of white spruce [*Picea glauca* (Moench) Voss.], Whitney (1962) surface-sterilized various portions of the root system and attempted to isolate pathogenic fungi from them. The primary agent of the disease, *Polyporus tomentosus* Fr. [= *Onnia tomentosa* (Fr.) P. Karsten], was isolated from older, woody roots, but was completely absent from mycorrhizae. The most common fungus isolated from younger suberized roots on both healthy and diseased trees was a sterile dark fungus referred to as DRP. According to Whitney, it was "close to the *M. r. atrovirens* group." Other common fungi included *U. ramanniana*, various sterile species, and *Hyalostachybotrys* (= *Stachybotrys*) sp. Both DRP and *Stachybotrys* sp. were found to be weak facultative pathogens in agar culture with white spruce seedlings. Since many of the fungi Whitney isolated from moribund suberized roots are similar to those isolated by Melin (1923) from mycorrhizae, it is likely that the fungal species and pathogenic interactions Whitney studied are of significance within the mycorrhizosphere.

The majority of conifer rhizosphere studies conducted by forest pathologists in the 1960's will not be reviewed here. Most such studies (e.g., Salt 1965, Bloomberg 1966, Vaartaja & Salisbury 1965) dealt mainly with pathogens of nursery-grown, probably non-mycorrhizal plants. It should be noted, however, that Nectriaceous pathogens, especially *C. destructans* and *Fusarium* spp., were abundant on both healthy and diseased nursery-grown seedlings sampled in these studies. Bloomberg (1966) also found *M. r. atrovirens* (probably α) to be a common nursery-inhabiting species in British Columbia, Canada.

Another perspective brought to bear on mycorrhizosphere fungi during the 1960's was that of the root developmental physiologist. Turner (1962) screened culture filtrates of a number of soil fungi isolated from "root tips or dichotomous roots" of *Pinus sylvestris* for the ability to cause morphogenetic changes in excised pine roots. It is to be expected that the majority of isolations were made from mycorrhizal root segments, particularly where dichotomous roots were sampled.

Turner found that certain of the root isolates were able to stimulate or repress the elongation of excised radicles. Stimulatory fungi included *F. oxysporum*, *Mortierella bainieri* Costantin, *U. ramanniana*, and *M. r. atrovirens*. *Botrytis cinerea* Pers. and *T. viride* were strongly inhibitory. The formation of lateral roots was inhibited by *Calcarisporium arbuscula* Preuss., *Cylindrocarpon destructans*, and "*Gliocladium* sp." The induction of root dichotomy, a process presumed to be hormonally controlled, was effected by *Gliocladium deliquescens* Sopp (= *G. viride* Matr.), and *Mucor spinosus* (= *M. plumbeus*). One clear trend distinguishable in these and other data presented by Turner is that *Zygomycetes* generally appeared to be benign or stimulatory to roots. Other significant features of Turner's results will be further discussed in a subsequent portion of this review (*Phytohormonal relations among roots, mycorrhizal fungi, and mycorrhizosphere organisms*).

The occurrence of *M. r. atrovirens* (α) on mycorrhizae of *Abies alba* in the French Jura mountains and the Savoyan Prealps was studied by Gams (1963). This author found that samples of surface-sterilized mycorrhizae could often yield up to 25 % *M. r. atrovirens*, despite frequent overgrowth of the slow-growing colonies by other fungi on artificial media. Gams essayed various taxonomic studies, and succeeding in inducing a few strains to produce conidia he identified as *Phialocephala dimorphospora* Kendrick; in hindsight, these seem very likely to have been *P. fortinii*. The sporulating strains, however, failed to anastomose in culture with other *M. r. atrovirens* strains. The non-sporulating strains also appeared to be a diverse grouping. All, however, formed sclerotia, indicating that they represented Melin's *M. r. atrovirens* α, not the asclerotial *M. r. atrovirens* β (Melin 1923). Gams's studies indicated that *M. r. atrovirens* α was probably heterogeneous. Currently, over 40 years later, it is known that there are indeed a number of lineages in this complex (Piercey *et al*. 2004), some corresponding to *P. fortinii* and at least one common group corresponding to the genetically well distinguished "type 1" isolates of Grünig *et al*. (2001, 2002), very recently described as a separate taxon (Grünig & Sieber 2005). Also, it has been shown recently that even in closely genetically related subgroups within *P. fortinii*, anastomosis

may be unreliable (Sieber 2002), suggesting that this species or species-complex has a very complex system regulating vegetative compatibility. The diversity of *M. r. atrovirens* types will be referred to again later in this review (in most detail in the section *What was included in the designation M. r. atrovirens and to what extent did the name indicate organisms found to be harmful?*).

The most ambitious survey of mycorrhizosphere fungi published during the 1960's was that of Kubíková (1965). Kubíková took a novel approach: she used the techniques of plant synecology to elaborate a taxonomy of rhizosphere fungal communities. Various ectomycorrhizal and endomycorrhizal trees, shrubs, and herbs were sampled in forest ecosystems in Czechia. Kubíková used the serial washing techniques prescribed by Harley & Waid (1955a). The resulting collections of fungal cultures were grouped according to emergent patterns in fungal communities from different plant species, forest communities, and soil types. Ectomycorrhizal plant species sampled included *Quercus sessilis* Salisb. [= *Q. petraea* (Matt.) Liebl.] , *Carpinus betulus* L., *Fagus silvatica* L., *Alnus glutinosa* (L.) Gaertner, and others. In the end, ten microfungal "synusias", or synecologically distinct associations, were delimited. In general, these synusias were based on patterns in the occurrence of fungal genera, as opposed to species. One particularly prominent species, *C. destructans*, was given exceptional treatment.

Of the delimited synusias, only four were characteristic of ectomycorrhizal root tips. These were "union *Penicillium* + *Cylindrocarpon radicicola* (= *C. destructans*)", "union *Penicillium*", "union Mycelia sterilia + *Penicillium*", and "union Mycelia sterilia + *Penicillium* + *Cylindrocarpon radicicola*." [The nomenclature is by analogy with that applied to plant synecological taxa, e.g. "*Querco-Ulmetum carpinetosum* (Pass. 1953) Mez. & Samek 1954"]. As can be seen, the four associations spanned a continuum of rhizosphere communities dominated by *Penicillium* spp. and sterile mycelia, but secondarily associated with *C. destructans* and other fungi. Endomycorrhizal roots tended to be associated with *C. destructans*-dominated communities, often with a strong representation of *Absidia* and *Mucor* spp. These results are very similar to those of Katznelson *et al*. (1962) for ectomycorrhizal and non-ectomycorrhizal birch roots. The same criticism, in fact, can be applied to both studies: that is, the potential influence of the ectomycorrhizal mantle in trapping conidia and other particulate propagules is not ruled out. There is no doubt, however, that the results of both studies are significant.

Kubíková pointed out that *C. destructans* showed a preference for alkaline conditions, tending to be excluded from acidic forest biogeocoenoses and to be replaced by *Fusarium* spp. in acidic agricultural biogeocoenoses. This aspect of the biology of *Cylindrocarpon* spp. was also demonstrated by Matturi & Stenton (1964) in Great Britain. Kubíková, like Kürbis (1936), found that *C. destructans* was also specifically associated with roots, and was uncommon from non-rhizosphere soil.

According to Kubíková (1965), the fungal communities on typical ectomycorrhizal roots in her study area followed a succession. First, the mantles were colonized by *Penicillium* spp. and *C. destructans*. This stage corresponded to "un. *Penicillium* + *C. radicicola*." Later, the mantles became colonized by various hyphomycetes, including *Trichoderma* spp., *Cladosporium herbarum*, and *Verticillium* sp. (*ss. lat.*) This stage corresponded to "un. *Penicillium*", and was still dominated by members of that genus.

Another important floristic study of the mycorrhizosphere was conducted by Fontana & Luppi Mosca (1966). These authors identified numerous soil fungi isolated during attempts to obtain mycorrhizal symbionts in pure culture. Six ectomycorrhizal tree species from Italian forests were sampled; four of these species were associated with known fungal symbionts. The isolation technique used was unusual: roots were surface-sterilized with silver nitrate, a compound whose selective effect on fungi is little known. The isolation medium contained casein hydrolysate (essentially a mixture of amino acids) as its sole source of carbon.

The vast majority of isolates was obtained from one tree species, *Pinus strobus* L. The fungus most frequently obtained from pine mycorrhizae was the symbiont, *Suillus luteus* (L.: Fr.) Gray, but *M. r. atrovirens* (prob. α) was also common. The balance of fungi consisted of various Penicillia, Trichodermas, and an unusual variety of homothallically ascosporulating *Ascomycetes*. These same *Ascomycetes – Gymnoascus* spp., *Chaetomium* spp. and others – were also found in association with other ectomycorrhizal trees. No *Zygomycetes* whatsoever were obtained, but a total of fourteen unnamed sterile mycelia were included in the listings. The unusual composition of this list of species probably reflects the isolation techniques used, as Rambelli *et al*. (1972), using more conventional techniques, obtained quite different fungi from pine mycorrhizae in Italy. The Gymnoascaceous species, especially, may have been favoured by the casein hydrolysate medium. Many members of this family tend to be proteolytic and keratinophilic organisms (Domsch *et al*. 1980).

Fontana & Luppi-Mosca concluded that different mycorrhizal types tended to be associated with different mycorrhizosphere communities, but that the soil biology of the rhizosphere also influenced community composition. The latter factor may explain why two larch species with the same mycorrhizal

symbiont [*Boletus elegans* Schum. = *Suillus grevillei* (Klotzsch:Fr.) Singer] appeared to be associated with substantially different fungal populations.

An electron microscopic study conducted by Marks & Foster (1967) showed that mycorrhizal mantle hyphae were often intimately interwoven with granule-covered "alien hyphae" strongly resembling those of *M. r. atrovirens*. Even when the mantle was composed of pseudoparenchymatous tissue, alien hyphae were still closely interwoven with the mycorrhizal hyphae. Marks & Foster (1967) also observed that soil fungi often formed localized or extended superficial layers on the surfaces of mycorrhizae. In many cases, these layers were formed by "dark brown mycelia of unknown identity." These observations apparently corroborate those of Jahn (1934), who based his concept of the "peritrophic mycorrhiza" on similarly-disposed saprobic fungal sheaths.

An interesting study on succession in the rhizosphere was done by Smith (1967). This author transplanted *Pinus lambertiana* Dougl. seedlings from forest nurseries in California to field sites on forest soils. The mycorrhizal status of the seedlings was not examined at any time, but it must be assumed that those that survived in the field became mycorrhizal if they were not so already. Smith showed that the pathogen-rich nursery rhizosphere communities, typified by the presence of *F. oxysporum*, were drastically altered after transplanted seedlings had spent 2-3 growing seasons under field conditions. At the end of the fourth growing season in the field, *F. oxysporum* could not be found in association with the roots. It was also absent at all times from direct-seeded and natural regeneration in the same area. Two possible explanations for the exclusion of *F. oxysporum* can be suggested. One is that the mycorrhizal fungi colonizing *P. lambertiana* in the field were inhibitory to the pathogen. The other is that soil conditions in field sites favoured other fungal species in competition for the rhizosphere.

Richard (1969) studied "pseudomycorrhizae" formed by sterile dark facultative pathogens, and gave criteria for distinguishing these structures from those formed by true mutualistic symbioses. He stated that pseudomycorrhiza-forming fungi like *M. r. atrovirens* (α) tended to colonize significant numbers of root tips in "certain unfavourable situations, such as excessively humid soils." Richard's studies were conducted in Québec and France, where pseudomycorrhizae were routinely found on spruces and pines.

The ecology of *M. r. atrovirens* (α) or a similar fungus received further scrutiny in the studies of Parkinson & Crouch (1969). These authors studied the root fungi associated with Corsican pine, *Pinus nigra* Arnold var. *laricio* Poiret [= *P. nigra* subsp. *laricio* (Poiret) Maire], in Lancashire, England. *Mycelium radicis atrovirens* was only tentatively identified (the taxon was otherwise designated sterile dark fungus, "SDF"), but there seems little doubt that the identification was correct. It predominated on suberized roots, increasing in dominance as the roots grew older. Parkinson & Crouch noted that by contrast, *Penicillium* spp. generally became less abundant on older roots, while *Zygomycetes* and *Trichoderma* remained in approximately the same proportions.

Although Parkinson & Crouch did not attempt to determine the mycorrhizal status of their "young roots", it seems likely that "upper lateral roots" and young "lower vertical roots" examined by these authors possessed at least a proportion of mycorrhizal tips. Examinations showed that young roots in upper soil layers were associated with a high proportion of *M. r. atrovirens* strains, while in lower soil layers *C. destructans*, *C. cylindroides* Wollenw., and the sterile dark fungus SDA (not to be confused with the aforementioned SDF) began to predominate. These results are similar to those obtained by Mańka & Rząsa (1961) and Mańka & Gierczak (1961).

Parkinson & Crouch did root-dissection studies on suberized roots, and found that *M. r. atrovirens* could often be isolated from the root stele, especially in younger plants. Other sterile fungi, including *Basidiomycetes* and a sterile dark species, could also be isolated from this region. Dissected cortical tissue gave rise to a much higher diversity of fungi, including many Penicillia. These findings are very similar to those obtained by Waid (1957) with dissected ryegrass roots. A partial explanation for all such results was provided by Waid (1962), who showed that sterile mycelia isolated from root interior tissues generally had an unusual ability to withstand low oxygen concentrations. It is likely that *M. r. atrovirens* α possesses this attribute, in contradistinction to most other fungi commonly isolated from ectomycorrhizae. It can be routinely seen in the laboratory to grow much deeper into agar media than most fungi are able to do (personal observation).

Two studies on mycorrhizosphere fungi associated with *Pinus taeda* L. in fumigated nursery soils were conducted by Danielson (1966) and Danielson & Davey (1969). In the first study, three forms of mycorrhizae (probably representing three mycobionts) were surface-sterilized and plated out. *Fusarium* spp. were found to be regularly associated with only one of the three mycorrhizal types. This same type was also regularly associated with two *Chaetomium* species. The observed specificity was similar to that seen by Neal *et al*. (1964). Interestingly, *Trichoderma* spp. were uncommon on all mycorrhizae studied.

The later study (Danielson & Davey 1969) contrasted surface-disinfected mycorrhizae from fumigated and unfumigated nursery soils. Both soils were treated with a pine needle mulch from a nearby

forest immediately after seeding with trees took place. In mycorrhizal roots harvested from seedlings on unfumigated soils, sterile mycelia (of various kinds, including hyaline, dark, and clamped), *Fusarium* spp., *Phoma* sp., and two *Chaetomium* species predominated. The two *Chaetomium* species were strictly associated with root surfaces, and were not found in rhizosphere soils. Mycorrhizae in fumigated soils tended to be associated with the two main soil-recolonizing fungi, *Penicillium piscarium* Westling [= *P. simplicissimum* (Oudem.) Thom] and *Trichoderma* spp., plus sterile dark fungi and *Botrytis* sp. The last-named fungus, a potential pathogen, was specific to root surfaces in fumigated soils.

It is interesting to note that various soil fungi common in unfumigated soils were seldom or never isolated from surface-disinfected mycorrhizae. Most conspicuously absent were *Aspergillus* spp., but *Zygomycetes* (*Cunninghamella*, *Mucor*, *Z. moelleri*) were also affected. In fumigated soils, *Trichoderma* spp. became increasingly uncommon in the rhizosphere as seedlings grew older. Their decline in the rhizosphere was much more abrupt than their decline in non-rhizosphere soil. As might be expected, however, *Penicillium* spp. became predominant in the rhizosphere within 100 days of seed germination.

The fungal communities documented by Danielson & Davey (1969) share many of the common attributes of forest nursery communities (e.g., a high representation of *Fusarium* spp.) and of warm-temperate soil communities (e.g., the high number of aspergilli, and perhaps also the high number of *Chaetomium* spp.). The populations associated with surface-sterilized mycorrhizae have some unique attributes: for example, one mycorrhizal type, "dark mycorrhizae", had a very high degree of association with a *Phoma* species. This *Phoma* species, by contrast, was uncommonly obtained from "coralloid mycorrhizae", and was absent from "normal mycorrhizae." This result, and others comparable to it, once again suggests that individual mycobionts have considerable ability to influence mycorrhizosphere populations.

Microbiological studies of the mycorrhizosphere: 1970–1985

Surprisingly few "microbiological" studies of the mycorrhizosphere were conducted in this fifteen-year period. Most of those that were published concerned bacteria only. In a few cases, however, valuable information on fungi was made available.

The microbiology of mycorrhizal *P. taeda* trees in kaolin spoils (strip-mined kaolin wastelands) in the American state of Georgia was investigated by Otrosina (1977). This author found that the predominant rhizosphere fungal genera were identical to the predominant genera in control soils. Chief among them were *Penicillium*, *Oidiodendron*, *Trichoderma*, and *Gongronella*. The last-named is a Zygomycete typical of subtropical regions, but found in warm, open forest sites in the temperate zone (Domsch *et al*. 1980). Numbers of propagules of these fungal genera were several orders of magnitude higher in the rhizosphere than in control soils. Rhizosphere soils in an undisturbed kaolin area were similar to those on mining spoils, except that the former soils contained substantial populations of the genus *Verticillium* (*ss. lat.*).

In a study related to the Marletto (1969) study cited above on yeasts associated with truffle-producing oaks, Ozino Marletto & Sartoris (1978) examined the yeast biota of the "burnt areas" produced by allelopathic activity of *Tuber melanosporum* Vitt. These areas did not differ significantly from control soils in yeast population. Given the profound effect that the "burnt zone" allelopathy has against bacteria (Chalvignac *et al*. 1959) and competing plants (Fasolo-Bonfante *et al*. 1971), yeasts may be unusual in their imperviousness. The most common species found were all soil-inhabiting types: "*Torulopsis* sp." (uninterpretable in modern context, most likely either *Candida* sp. among the ascomycetous yeasts or *Cryptococcus* or *Rhodotorula* among the basidiomycetous yeasts), *Cryptococcus albidus* var. *aerius* (Saito) Phaff & Fell, *Lipomyces lipofer* Lodder & Kreger ex Slooff, and *L. kononenkoae* Nieuwdorp, P. Bos & Slooff.

Kilbertus *et al*. (1978) studied microorganisms associated with mycorrhizal and non-mycorrhizal seedlings of *Picea abies* in laboratory pot experiments. Seedlings in the mycorrhizal test group were infected with *Hebeloma crustuliniforme* (Bull.) Quel. inoculum previous to being planted in pots. The pot soils were obtained from a spruce plantation in the Jura mountains of France. The authors stated that the most common soil fungal genera – *Penicillium*, *Chrysosporium*, and *Trichoderma* – were found in all of the habitats studied (control soils, the rhizosphere of non-mycorrhizal roots, and the mycorrhizosphere), as was "a white sterile mycelium." (N.B., the *Chrysosporium* species seen were not characterized, but the habitat and the abundance data strongly suggest species currently placed in *Geomyces*). *Oidiodendron griseum* Robak [a name which at the time was also sometimes applied to isolates of *O. maius* G.L. Barron; see Sigler & Gibas (2005–this volume)] and *Paecilomyces* sp. were unique to control soils; *Cladosporium*, *Cephalosporium* (probably = *Acremonium*, *Lecanicillium*, *Simplicillium* or *Pochonia*), and *Rhizopus* to the rhizosphere of non-mycorrhizal roots; and *Gliomastix* (probably = *Acremonium* subg. *Gliomastix*) and *Rhinocladiella* to the mycorrhizosphere. The significance of these results is difficult to assess, since the authors did not report the numbers of isolates they examined.

Malajczuk & McComb (1979) found a positive rhizosphere effect for fungi associated with two ectomycorrhizal *Eucalyptus* species in Australia. Both mycorrhizae and unsuberized non-mycorrhizal root portions were probably included in their samples. For one eucalypt, *E. marginata* Donn ex Sm., an especially pronounced fungal rhizosphere effect was found in soils suppressive to a root disease caused by *Phytophthora cinnamomi* Rands. The same species had been shown in previous studies to produce greater quantities of root exudates than *Phytophthora*-resistant eucalypts (Malajczuk & McComb 1977).

The same authors also studied the composition of fungal populations in the rhizospheres of eucalypts on several soil types. Fungi were identified to genus, and then informally grouped according to morphological characteristics. The resulting groups approximated species. Fungal populations were shown to vary considerably between soil types and between tree species, but there were few discrete differences between disease-suppressive and -conducive soils, or between the rhizospheres of susceptible and unsusceptible trees. Penicillia were abundant in the "rhizoplane" (including mycorrhizal mantles) of washed roots, indicating that they were probably active as mycelia on root surfaces. *Mucor*, unlike most other genera found, was restricted to rhizosphere soils. Other common genera represented were *Ulocladium*, *Chaetomium*, *Aspergillus*, and *Trichoderma*. A dematiaceous fungus common in the rhizosphere of *Eucalyptus calophylla* R. Br. was regarded as a sterile mycelium at first, but eventually produced conidia resembling those of *Drechslera* spp.

As can be seen, the fungal populations revealed in the above study combine the features of mycorrhizospheres in warm-temperate soils (relatively high *Aspergillus* and *Chaetomium* counts) and of studies using dilution-plating techniques (many dry-spored hyphomycetes; few *Zygomycetes*). Malajczuk and McComb found that eucalypts actually infected by *P. cinnamomi* were associated with more *Penicillium* and *Trichoderma* propagules than were healthy plants, but concluded that this merely reflected colonization of moribund root tissue. Overall, no likely role in disease-suppression or disease-facilitation could be ascribed to mycorrhizosphere fungi.

Mycological studies of the mycorrhizosphere: 1970-1985

Most of the mycological mycorrhizosphere studies in the 1970's derived from one of several distinct schools of scientific thought. Many of these "schools" were representative of a single region or nation, and communication between the delimited groups of researchers was slight. For this reason, a completely chronological evaluation of the results of these studies is less coherent than one that treats each school of thought as the semi-separate entity it actually was.

North American research: Went (1971) appears to have been the first author to consider the role of mycorrhizosphere fungi in nutrient cycling within forest ecosystems. This author attempted to find the microorganisms responsible for nutrient transfer between leaf litter and mycorrhizae in a *Pinus murrayana* Grev. & Balf. [= *Pinus contorta* Dougl. ex Loud. var. *murrayana* (Grev. & Balf.) Engelm.] forest in Nevada, U.S.A. He isolated a number of microfungi from unwashed mycorrhizae, rhizomorphs, and litter fragments. *Mucor hiemalis*, *Mortierella* sp., and *Penicillium terrestre* Jensen (a species now synonymized with *P. crustosum* Thom – see Samson & Frisvad 2004) made up 90 % of the isolates from all three substrates. Went proposed that these fungi served to "connect litter with roots, decomposing the cell wall materials and transferring the released nutrients by way of the rhizomorphs to the roots." Although the situation in reality is probably more complex than Went suggested (for example, the *Mortierella* component of the system may be decomposing fungal hyphae as well as litter, or instead of it), the importance of mycorrhizosphere organisms in nutrient cycling is beyond doubt. Mycorrhizal fungi can be expected to be the beneficiaries of a substantial portion of this activity.

The exemplary work of Vozzo & Hacskaylo (1971) on the reasons for failure of non-mycorrhizal *Pinus caribaea* Morelet plantations in Puerto Rico contained a few observations on mycorrhizosphere fungi. Successful pine seedlings, all of which had been inoculated with forest soils, were shown to have a characteristic non-mycorrhiza-forming root surface associate. This fungus was a hyaline sterile mycelium that grew on and around short roots but did not penetrate them. Surface-sterilized mycorrhizae mainly gave rise to this fungus and to a *Thelephora*-like mycorrhizal mycelium.

Vaartaja & Agnihotri (1970) investigated rhizospheres of *Picea glauca* seedlings planted in fumigated and unfumigated forest nursery beds in Ontario, Canada. They did not separate mycorrhizal from non-mycorrhizal roots, but noted that mycorrhizae made up approximately 66 % of root tips in fumigated nursery beds, and 82 % of root tips in unfumigated beds. Common species growing from unwashed root tips (mycorrhizal and non-) included *T. viride*, *Penicillium janthinellum* Biourge, *Fusarium* spp. (mainly the pathogen *F. oxysporum*), and *Mortierella* spp. *sensu lato* [*M. alpina*, *Micromucor longicollis* (Dixon-Stewart) Arx, *U. ramanniana*, *U. nana*]. [Note that the true *Mortierella* (*Micromucor*) *longicollis* Dixon-Stewart is only known from its Australian type isolate; thus it is more likely that Vaartaja and Agnihotri isolated

the similar *Umbelopsis vinacea*, which is common in Ontario forests]. *Cylindrocarpon destructans* was also occasionally isolated from mycorrhizae. Fusaria were less common in fumigated than unfumigated soils. By contrast with similar studies conducted by Danielson & Davey (1969) in North Carolina, there were no Chaetomia or Aspergilli reported.

Richard & Fortin (1974) isolated fungi from surface-sterilized pseudomycorrhizal roots of *Picea mariana* [Mill.] BSP in Québec, Canada. From these roots four sterile hyphomycetes were regularly isolated, the least abundant of which was *M. r. atrovirens* (α) / *P. fortinii*. The other three assemblages of similar isolates were referred to as "groups" X, B, and N. Group X was hyaline, while N was melanized; the pigmentation of B cannot be discerned from the photograph provided. Group X, known to be heterogeneous, was by far the most abundant taxon. Both it and group B were found only in natural spruce stands. *Mycelium radicis atrovirens* α was obtained only from nurseries, while group N occurred in both nurseries and forests. Richard & Fortin (1970) had previously isolated *M. r. atrovirens* α from surface-sterilized mycorrhizae in natural spruce stands. It should be noted in relation to groups X and B that Summerbell (1989), also isolating from *P. mariana* ectomycorrhizae in a similar forest type in the adjacent Canadian province of Ontario, obtained large numbers of both hyaline and dark sterile fungi that have transpired, after recent molecular analysis, to be *Meliniomyces variabilis* Hambleton & Sigler (Hambleton & Sigler 2005–this volume). The photos of groups X and B in Richard & Fortin (1974) appear compatible with this species.

Richard & Fortin went on to study the biology of *M. r. atrovirens* α / *P. fortinii* in detail, and showed that its ability to colonise non-mycorrhizal root tips was a serious problem in nurseries where soils had been fumigated. They also showed that *M. r. atrovirens* α produced toxins that caused considerable damage to excised tomato shoots *in vitro*. This result supported those of Lindquist (1939), who showed that culture filtrates of *M. r. atrovirens* (α) were inhibitory to axenically grown spruce seedlings. Richard & Fortin confirmed the results of Gams (1963) by showing that a proportion of *M. r. atrovirens* alpha strains could be induced to sporulate as a *Phialocephala* species (Richard & Fortin 1973) initially (mis-)identified as *P. dimorphospora*.

When the pathogenic ability of *M. r. atrovirens* α *in vitro* was examined, the fungus was found to cause stunting and discoloration in spruce, and to cause damping-off in pine (Richard *et al*. 1971). Both root and hypocotyl tissues were invaded. These results were similar to those of Melin (1923) and others. The mycorrhizal fungus *Suillus granulatus* (L.) Kuntze could prevent damage due to *M. r. atrovirens* α in both spruce (Richard *et al*. 1971) and pine (Richard & Fortin 1975).

Wang & Wilcox (1985) induced sporulation of several fungi they considered to be representative of *M. r. atrovirens*, though their concept was relatively broad. Pseudomycorrhiza-forming strains, representing *M. r. atrovirens* α *sensu* Melin, produced conidiogenous structures typical of the genus *Phialocephala*, as shown by Gams (1963) and Richard & Fortin (1973). Wang & Wilcox described their strains as a new species, *P. fortinii*. Other strains difficult to distinguish from *M. r. atrovirens* α produced true mycorrhizae. These fungi could be induced to differentiate conidial structures typical of other dematiaceous hyphomycete genera. One group of strains was described as *Chloridium paucisporum* C.J.K. Wang & H.E. Wilcox, the other as *Phialophora finlandia* C.J.K. Wang & H.E. Wilcox [now *Cadophora finlandica* (C.J.K. Wang & H.E. Wilcox) T.C. Harrington & McNew]. Similar mycorrhiza-forming strains of " *M. r. atrovirens* " were reported by Kowalski (1973) and Pachlewski & Pachlewska (1974). These results made it clear that not all "sterile dark" fungi or even sporulating ascomycetous fungi isolated from mycorrhizae could be assumed to be non-mycorrhizal.

Italian research: The mycorrhizosphere mycota of *Suillus granulatus* mycorrhizae on *Pinus radiata* in Italy was studied by Rambelli *et al*. (1972). These authors isolated fungi both from the "proximal rhizosphere," consisting of the material washed from excised mycorrhizal tips, and the "adherent rhizosphere," represented by serially-washed mycorrhizae pulverized in a mortar. The great majority of fungi isolated from the proximal rhizosphere were Penicillia, but small numbers of *Spicaria* (= *Paecilomyces*), *Aspergillus*, sterile mycelial, and other isolates were also obtained. The adherent rhizosphere material yielded only *Penicillium* spp., particularly *P. corylophilum* Dierckx. The more-or-less conventional techniques used by Rambelli *et al*. did not yield a diversity of teleomorphic *Ascomycetes* comparable to that previously obtained from silver-nitrate-sterilized pine mycorrhizae by Fontana & Luppi Mosca (1966).

Soil fungi in "burnt zones" and other soils strongly influenced by *Tuber* spp. were studied by Luppi Mosca *et al*. (1970) and Luppi Mosca (1972). The former study considered *Tuber magnatum* Pico sites in the Italian Piedmont district, while the latter considered *T. melanosporum* sites in France. The characteristic fungal species of the truffle zones included *Mortierella alpina* Peyronel, various sterile mycelia, *Penicillium lilacinum* Thom [= *Paecilomyces lilacinus* (Thom) Sams.], *Aspergillus niger*, *F. oxysporum*, and an unidentified *Acremonium* sp. Some of these species (e.g., *M. alpina*) had previously shown to be characteristic of mildly alkaline forest soils (Bhatt 1970).

Further studies on the microfungi associated with *T. magnatum* mycorrhizae were conducted by Luppi Mosca (1973). In this case, rhizosphere soils and pulverized mycorrhizal roots were examined, rather than "burnt zone" soils in general. Based on the results, Luppi Mosca suggested that the following fungal species were characteristic of truffle soils and rhizospheres: *Paecilomyces lilacinus*, *Gliocladium roseum* (= *Clonostachys rosea*), *M. alpina*, *Humicola fuscoatra* Traaen var. *fusco-atra*, and *Penicillium thomii*. She also noted that several species typically found in "burnt zone" soils were lacking or rare in the *Tuber* mycorrhizosphere. These species included *Paecilomyces marquandii* (Massee) Hughes and *Botryotrichum piluliferum* Sacc. et March. A surprisingly small number and diversity of sterile mycelia was associated with *Tuber* mycorrhizae, an anomaly that Luppi Mosca herself found "difficult to interpret." These sterile mycelia were among the most common colonizers of truffle-associated non-rhizosphere soils (Luppi Mosca *et al*. 1970, Luppi Mosca 1972).

Luppi Mosca & Fontana (1982) used a modification of the techniques of Fontana & Luppi Mosca (1966) to study the mycota associated with ectomycorrhizae of *A. alba* in Piedmont. The mycorrhizal tips were serially-washed and surface-sterilized with silver nitrate. They were then plated out on media with a simple carbon source. A surprisingly high number of plectomycetous *Ascomycetes* were obtained by means of this procedure. Prominent among these species were *Pseudogymnoascus roseus* Raillo, *Eurotium amstelodami* (Mang.) Thom & Church, and *Talaromyces flavus* (Klöcker) Stolk & Samson. More conventional rhizosphere fungi – Penicillia, Trichodermas, sterile mycelia – were also regularly isolated.

Given these data, it appears likely that silver nitrate surface-sterilization, like some other sterilizing procedures (e.g., ethanol-washing), does not significantly affect ascospores, leading to an unusually heavy outgrowth of ascosporulating species in isolation studies. Luppi Mosca & Fontana, however, did not consider this possibility in their discussion, and stated that their data indicated "the possibility of a particular adaptation of these (Plectomycetous) fungi to the innermost layers of the mycochlaena." ("Mycochlaena" was a term mainly used in Italian mycorrhizosphere research: it referred to the interstices of the ectomycorrhizal mantle as a rhizosphere habit). Whether or not any specialized adaptations exist, it is certainly true that cleistothecial *Ascomycetes* can be isolated in relatively high numbers from washed mycorrhizae in some areas. It seems likely that *Plectomycetes* are characteristic mycorrhizosphere inhabitants at least in the forest zones studied by Luppi Mosca & Fontana (1982) and Fontana & Luppi Mosca (1966). The only other pre-1985 author to find comparable fungi regularly associated with conifer roots was Whitney (1962), who found *P. roseus* to be a common colonizer of decaying white spruce roots in Saskatchewan, Canada. More recent authors like Summerbell (1989), have also found these fungi in association with ectomycorrhizae; Summerbell (2005–this volume) concluded that his own findings and those of previous studies on soil fungi indicated that *P. roseus* was mainly associated with mineral soil horizons in forest soils, and that ectomycorrhizae occurring in mineral soils might yield such isolates.

Polish studies. The work of Polish researcher Stefan Kowalski on mycorrhizosphere communities in relation to conifer root diseases was perhaps the most ambitious contribution to mycorrhizosphere research in the 1970's. In the early stages of this work, Kowalski showed that two fungi more commonly thought of as root pathogens were sometimes capable of forming mycorrhizae. These fungi were *Fomes annosus* (Fr.) P. Karst. (= *Heterobasidion annosum*) (Kowalski 1970) and *M. r. atrovirens* (Kowalski 1973). The former fungus appeared to be a facultative and atypical mycorrhiza-former on *P. sylvestris* in axenic culture. The seemingly harmless infection was characterized by a thin mantle bearing conidium-producing funiculi, and by a "slightly but distinctly developed" Hartig net. A few cellular penetrations were observed within the cortex, leading Kowalski to suggest that the association might degenerate into a "pseudomycorrhiza" over time. The study indicated that this mycorrhiza-forming ability might serve as a reservoir for *H. annosum* in young stands of pine. When the trees were weakened or reached a certain stage of woody growth, the more destructive abilities of the wood-decaying pathogen might be unleashed.

This unusual relationship of *H. annosum* and pines had previously been observed in the field by Orlos & Dominik (1960). These authors classed the *H. annosum* mycorrhizae they collected as genus "Aa" in the Dominik mycorrhiza recognition system. The situation of *H. annosum* as a conidium-producing root-associated fungus forming mycorrhiza-like associations that might serve as a reservoir for pathogenic attacks is similar to that of the slow-growing, "oidium"-producing "parasitic and mycorrhiza-building" fungus (Mycelium 19f) isolated by Lindquist (1939). It is possible that 19f is identical to *H. annosum*; however, modern studies in which such isolates are molecularly characterized are needed to ascertain how many similar species are involved in these unusual associations.

With regard to *M. r. atrovirens*, Kowalski (1973) showed that strains fell into two categories: classic pseudomycorrhiza-forming strains, and superficially similar mycorrhiza-forming strains. Only the former category corresponds to *M. r. atrovirens* α as described

by Melin. The latter category consists of a group of fungi probably unknown to previous users of the name *M. r. atrovirens*. The further clarification of the taxonomy of these fungi by Wang & Wilcox (1985) has been mentioned above.

The hypothesis that soil fungal communities might be conducive or suppressive to *H. annosum* was investigated by Kowalski (1974a). Fungi were obtained from two *Pinus sylvestris* stands, one heavily infected by *H. annosum*, and one disease-free. Rhizosphere and control soils, litter, suberized roots, and surface-sterilized, washed mycorrhizae were sampled. A technique outlined by Mańka (1974), the "biotic series," was used to assess the composite ability of fungal communities from the two sites to suppress *H. annosum*. Implicit in Mańka's procedure are two assumptions: firstly, that the collection of fungal isolates obtained in pure culture from a site adequately represents the true fungal population of the site; and secondly, that the inhibitory actions exerted against *H. annosum* by soil fungi grown in agar culture reflect actual inhibition of *H. annosum* in nature. Empirical evidence that these assumptions (both of which would be considered highly suspect by many modern researchers) tend overall to be justified in the aggregate for whole fungal communities is provided by Mańka (1968, 1974). The results Kowalski obtained using the "biotic series" technique led him to conclude that fungal communities from the disease-free pine stand were considerably more "resistant to the development of *H. annosum*" than were fungi from the diseased stand.

The actual isolates obtained from washed and surface-sterilized mycorrhizae by Kowalski (1974a, 1974b) included both mycorrhiza-forming and non-mycorrhizal strains. Among the latter, "*Hormodendrum*" spp. (*Cladosporium* and possibly other blastosporic dark hyphomycetes), *Mortierella humilis* Linnemann ex W. Gams, and *M. r. atrovirens* α were prominent. Several other non-sporulating hyphomycetes were also commonly obtained. Rhizosphere soils typically contained *Fusidium terricola* Mill., Gidd. & Fost. [= *Acremonium implicatum* (J.C. Gilman & E.V. Abbott) W. Gams], *Aspergillus versicolor* (Vuill.) Tir., and *Hormodendrum microsporioides* Mańka & Truszk (*nom. inval.*, Article 37.1 International Code of Botanical Nomenclature, a minimally described *Cladosporium*–like isolate type of uncertain identity). *Penicillium*, represented by 26 species, was also extremely abundant. Suberized root surfaces were characterized by an overwhelming predominance of *M. r. atrovirens* α.

Using the same fungal collections, Kowalski (1974a) concluded that the diseased and disease-free pine stands differed strongly in the composition of their fungal communities. The greatest quantitative and qualitative divergence between stands was shown by rhizosphere isolates; the smallest divergence was shown by the populations isolated from washed and surface-sterilized mycorrhizae. Different mycorrhizal "genera", classified by the Dominik system (Dominik 1956), gave rise to different collections of fungal isolates, but there was a large degree of overlap between populations from the various mycorrhizal types.

The influence of fungal communities on forest regeneration by *Abies alba* was considered by Kowalski (1980a–d). A brief English synopsis of the results of these studies is given by Kowalski (1982). Over 8000 fungal isolates from *A. alba* mycorrhizae, suberized roots, rhizosphere soils, and non-rhizosphere soils were characterized by Kowalski (1980a). Predominant associates of washed, surface-sterilized mycorrhizae included *M. r. atrovirens* α, *Cylindrocarpon destructans*, *Mortierella parvispora* Linnem., and *Thysanophora penicillioides* (Roum.) Kendr. *Mycelium radicis atrovirens* α was more common in areas of good natural fir regeneration than in poor areas, while the reverse was true for *C. destructans*. The same inverse relationship was true for suberized roots as well.

Kowalski (1980a) observed that the fungal populations isolated from suberized roots, mycorrhizae, and rhizosphere soil were distinctly different from one another. The same specificity had earlier been noted with fungal populations isolated from *P. sylvestris* stands (Kowalski 1974a, b). Although some of this specificity may have been due to different treatments of the substrates (e.g., both suberized roots and mycorrhizae were serially washed, but only the latter were alcohol-disinfected), some of it could only be ascribed to habitat differences. For instance, a strong association of *M. r. atrovirens* α with older and/or suberized roots had previously been noted by Robertson (1954), Mańka (1960), and Parkinson & Crouch (1969), among others. Kowalski (1980a) found the same relationship occurring in *A. alba* stands.

The negative correlation between *C. destructans* and *M. r. atrovirens* α in *A. alba* stands was further explored by Kowalski (1980b). Kowalski found that *C. destructans*, a potential damping-off pathogen, was the chief agent responsible for poor natural regeneration of *A. alba*. *Mycelium radicis atrovirens* α, although nominally a weak pathogen, appeared to be an indicator both of sites of good natural regeneration, and of sites where *C. destructans* was uncommon. Since *M. r. atrovirens* α was not directly inhibitory to *C. destructans* (Kowalski 1980d), a likely explanation for the inverse relationship was that both organisms were favoured by different soil pH's. Highly acid sites (av. pH 3.9) favoured *A. alba* and *M. r. atrovirens* α; less acid sites (av. pH 5.3) favoured the pathogen.

A further study (Kowalski 1980c) showed that mycorrhiza formation was also inhibited at the sites of higher pH. Whether this was due to pH alone or to microbial interactions was not investigated, but a contribution of the latter factor must be considered. Many mycorrhizal fungi have pH optima in the vicinity of 5–5.5 (Harley & Smith 1983). A slowing of mycorrhiza formation on neutral soils (especially calcareous soils) is not uncommonly observed (e.g., see Tserling 1960, Theodorou & Bowen 1969), but an inhibition in mildly acid forest sites is unusual.

A list of fungal species isolated from various mycorrhizal types was presented by Kowalski (1980c). The list showed little or no specificity of individual mycorrhizosphere species for individual mycorrhizal types.

The final segment of Kowalski's work on *A. alba* regeneration (Kowalski 1980d) concerned the abilities of soil and mycorrhizosphere communities to inhibit *C. destructans in vitro*. Once again, the "biotic series" assay technique (Mańka 1968, 1974) was used. Numerical inhibition values obtained by means of this technique rated the fungal populations of good sites four times as inhibitory to *C. destructans* as the fungal populations of poor sites. Interestingly, many individual fungal species found in both types of sites showed intraspecific variation in their reactions to *C. destructans*. In almost all cases, isolates from the *Cylindrocarpon*-rich "poor" sites inhibited *C. destructans* much less in agar plate inhibition studies than did conspecific isolates from "good" sites. Apparently, the degree of mutual adaptation of members of saprobic mycorrhizosphere communities is high, and is manifested at the strain level as well as at the species level. It should be mentioned, though, that it is well known that microbial interactions as witnessed on artificial media may sometimes be drastically different than those observed between the same taxa under more natural circumstances (Bowen 1980).

Some of the fungi isolated from pine mycorrhizae by Kowalski (1974a, b) were tested for their ability to form auxins (Strzelczyk *et al*. 1977) and cytokinins (Kampert & Strzelczyk 1978) *in vitro*. Many of the organisms tested could produce auxins, particularly if supplied typtophan or indole precursors. An unnamed sterile hyphomycete and *M. r. atrovirens* α were especially good producers of auxins from tryptophan. Another root associate, *Cephalosporium acremonium* (= *Acremonium* sp. or possibly a species of *Pochonia*, *Lecanicillium* or *Simplicillium*) was able to produce trace quantities of auxins in tryptophan-free medium. *Mycelium radicis atrovirens* α and "*C. acremonium*" were also capable of producing cytokinins.

According to Strzelczyk *et al*. (1977), the investigated strains of *M. r. atrovirens* α and *C. acremonium* were both root-invading fungi. The former formed typical pseudomycorrhizae on pine, while the latter produced a non-pathogenic invasion resembling the classic ectendomycorrhiza (see Harley & Smith 1983). Another auxin-synthesizing fungus, *Cephalosporium glutineum* Kamyschko (an uninterpretable *nomen nudum fide* Gams 1971) also formed these ectendomycorrhiza-like invasions. Possibly, then, the production of hormones served to facilitate the invasion of roots.

In toto, the Polish studies of the 1970's and very early 1980's present an unusually clear and detailed picture of mycorrhizosphere population structures. The populations of fungi that can be isolated from surface-disinfected, washed mycorrhizae contain a high proportion of root-invading species, many of which are weak pathogens or apparently harmless endophytes. Rhizosphere soils, by contrast, contain a great diversity of heavily-sporulating saprobes. In the forests investigated by Kowalski (1974b, 1980a) many of the typical rhizosphere-inhabitants are in the genera *Mortierella*, *Penicillium*, and *Trichoderma*. These fungi are typical of mycorrhizospheres in cooler northern soils. Fungi from suberized roots and non-rhizosphere soils differ little at the generic level from those isolated from rhizosphere soils, but distinct differences exist in the species composition of populations and in the relative abundance of individual species.

As well, these studies show that in at least some sites, the abilities of different mycorrhizal mycobionts to select taxonomically distinct mycorrhizosphere associates may be minimal. However, entire regions (in this case, forest stands) may be colonized by rhizosphere and soil fungal communities that act more-or-less in concert to favour the growth of some potential associates and to inhibit others. Underlying these complex community structures are certain chemical and physical factors, such as pH and moisture content. Within an individual fungal species obtained from two or more sites, strains may be found that are adapted to the biotic and abiotic conditions of only a single site. For ecological or phytopathological predictive purposes, therefore, merely knowing the qualitative and quantitative species composition of a site may not be sufficient. The relevant physiological attributes of the fungi found within a site or habitat must be independently characterized. Such factors are important to consider in mycorrhizosphere studies, since the ability of mycorrhizal mycobionts to protect roots from disease and the ability of these fungi to colonize roots may both be influenced by the nature of the associated rhizosphere communities.

Indian studies: Mishra & Kanaujia (1973) studied rhizosphere fungi associated with seven gymnosperm species growing in a botanical garden at Gorakhpur in Uttar Pradesh (the area is in the Ganges basin not far

from the Himalayan foothills). Of these species, three were conifers, three were cycads, and one was a *Ginkgo*. Only one species, *Pinus longifolia* Roxb. ex Lamb., can be expected to have had ectomycorrhizal roots. These roots were not examined in direct microscopy, however; nor were ages given for the plants. Except in the unlikely event that only very young seedlings were examined, the influence of mycorrhizal associations can safely be presumed to be reflected in the data.

The data showed that the rhizosphere mycota of each of the seven species was distinct to some degree. The pine differed from all the other gymnosperms by lacking *T. viride* in its rhizosphere. It also lacked *Fusarium* associates, an attribute shared only by the non-ectomycorrhizal species *Cupressus sempervirens* L. The greatest part of the diversity of fungi associated with pine roots was made up of *Aspergillus* spp., of which seven were found. By contrast, only two *Penicillium* species were recorded. This preponderance of Aspergilli was likewise reflected in the rhizospheres of the other plants.

A completely contrasting situation was found by Sharma (1981) working with *Pinus kesiya* Royle seedlings in the Khasi Hills near Shillong, Assam. No Aspergilli at all were found in the rhizospheres of the young seedlings examined, either before or after mycorrhiza formation. Instead, Penicillia were the most common inhabitants of the mycorrhizosphere, followed by fungi identified as *Verticillium* spp. Young germinant seedlings favoured the growth of *Verticillium* spp. (*ss. lat.*), "*Verticilliastrum* sp." (= *Trichoderma* sp.), and *F. oxysporum* in their rhizospheres, but did not stimulate Penicillia. When mycorrhiza formation took place on the majority of roots, *F. oxysporum* and "*Verticilliastrum* sp." were excluded from the rhizosphere.

The differences between the studies of Mishra & Kanaujia (1973) and Sharma (1981) are probably accounted for in large part by the difference in elevation between the two study sites. The latter study was conducted at 1500 m. above sea level, while the former was conducted at an elevation below 100 m. (The official elevation of Gorakhpur is 77 m). Moreover, the latter study was conducted in forest soil, whereas the former was conducted in garden soil. The results, then, correlate well with previous data showing *Aspergillus* spp. becoming predominant in warmer areas and on cultivated or grassland soils.

It is interesting to note that in both study sites, the growth of *Fusarium* spp. was inhibited in the rhizosphere of ectomycorrhizal plants. Although an inhibition of *Fusarium* is common in forest soils (e.g., Schisler & Linderman 1984), the finding of such an inhibition is unusual in cultivated soils, particularly those planted with seedling trees. The absence of *Fusarium* from the *P. longifolia* rhizosphere at Gorakhpur may be an ectomycorrhiza-mediated effect. That this sort of exclusion can occur, even in cultivated soil, has previously been shown by Danielson (1966), who found that two out of three mycorrhizal types on *Pinus taeda* appeared to select against Fusaria in the mycorrhizosphere. Sylvia & Sinclair (1983) later showed a similar effect with *Laccaria laccata* mycorrhizae on Douglas-fir.

Soviet studies: Soviet studies on assimilative-root rhizospheres of ectomycorrhizal hosts in the 1970's concentrated on the disease-suppressing aspects of microfungal populations. Enikeyeva *et al*. (1970) isolated rhizosphere fungi from "young roots" of pines growing in four different stands. Considerable differences in microfungal populations existed between stands, but some species occurred in all cases. Most prominent among these were *P. thomii*, *T. koningii* (in the broad sense), and *T. viride*. Other fungi, like *Penicillium miczynskii* Zal., were restricted to specific sites. Since dilution plating was used to obtain the fungi, Penicillia predominated. However, sterile mycelia were represented in 50 % of the individual samples. In a subsequent study on the antibiotic properties of the pine rhizosphere isolates (Enikeyeva *et al*. 1972), various penicillia, trichodermas, and sterile mycelia showed a high degree of antagonism towards potential root pathogens and wood-rotting fungi. *Heterobasidion annosum* and *Peniophora gigantea* (Fries) Massee [= *Phlebiopsis gigantea* (Fries) Jülich] were inhibited *in vitro* by 77 % of the rhizosphere isolates tested. The inherent problems of this type of testing have been mentioned above.

Karimbayeva & Sizova (1976) conducted a similar series of isolations from young-root rhizospheres of *Quercus robur*, *Betula pendula*, *Picea abies*, and *Pinus sylvestris*. These studies, like the above-mentioned ones, were conducted in the Moscow area. Isolates were collected in both 1970 and 1972. The resulting isolations varied as much from year to year within a species as they did between species in a given year. Nonetheless, some definite species-specific interactions were observed. For example, *Penicillium simplicissimum* was frequently found in high numbers in spruce and pine rhizospheres, but was seldom found in association with birch or oak. *Trichoderma viride*, *Aspergillus fumigatus*, and some others tended to associate with the angiosperm species. [N.B., however, that Enikeyeva *et al*. (1970) had found *T. viride* to be common in the pine rhizosphere]. *Penicillium daleae* K.M. Zalessky was abundant in the rhizospheres of pine, birch, and oak, but was very uncommon in the spruce rhizosphere. Karimbayeva & Sizova (1976, 1977) subsequently conducted physiological studies in an attempt to determine the basis of these species-specific interactions. They found that isolates obtained

from the rhizosphere of a particular tree species were often conspicuously stimulated by root exudates of that species. Other tree species were generally less stimulatory or, in some cases, inhibitory. Thus, each tree species exercised a selective effect. Such findings are discussed in greater detail later in this review (see *Ectomycorrhizal phytobionts as regulators of rhizosphere populations*). It is interesting to note, however, that if these data are accepted, then the selective effect of the tree root exudates must be exerted regardless of mycorrhizal colonization. Unfortunately, as mentioned above, none of the available 1970's Soviet studies on the rhizosphere mycota of ectomycorrhizal trees acknowledged the potential importance or even the existence of mycorrhizae.

The overall take-home message of the 1970's Soviet studies was that individual tree species are able to stimulate a particular rhizosphere mycota possessing a high degree of antagonism towards root pathogens. For a brief review of this work, see Sizova (1977).

North and Central European studies: The ability of mycorrhizosphere fungi to assist in preventing *H. annosum* attacks on conifers was investigated in Germany and in Scandinavia. Bücking (1976) isolated fungi from hydrogen peroxide-disinfected mycorrhizae of *Picea abies* and identified those able to inhibit the pathogen *in vitro* (In this case, the species involved may have been the recent segregate *Heterobasidion parviporum* Niemelä & Korhonen, which mainly parasitizes *P. abies* – see Korhonen *et al*. 1998). In over 250 mycorrhizosphere isolates, only 21 *Heterobasidion* antagonists were found. Most of these were *Scopulariopsis* and *Cephalosporium* (probably = *Acremonium*, *Lecanicillium*, *Simplicillium* or *Pochonia*) isolates, not identified to species. Such antagonists were predominantly isolated from mycorrhizae collected in sites with calcareous soils.

Rhizosphere fungi of both *Alnus incana* (L.) Moench and *P. abies* were investigated for their ability to inhibit *H. annosum* by Johansson & Marklund (1980). The study site was in central Sweden. *Trichoderma*, *Penicillium*, and *Paecilomyces* species were commonly encountered in both types of rhizospheres, and were generally inhibitory to the pathogen. On the other hand, *Mortierella* species, which made up 20–40 % of total isolates, had no inhibitory properties – at least, not on artificial media. Strongly antagonistic isolates from alder and spruce rhizospheres included *Aphanocladium* sp. (probably = *Lecanicillium aphanocladii* Zare & W. Gams), *Chalara* spp., and a sterile mycelium thought to be basidiomycetous.

The rhizospheres and rhizoplanes of both *A. incana* and *P. abies* supported fewer *Trichoderma* strains than did control soils. This was true for both forest-grown and field-grown plants. It is likely that these data reflect both mycorrhizosphere colonization and the colonization of suberized root surfaces, with emphasis on the latter.

The potential contribution of mycorrhizosphere fungi to the pollution-mediated tree decline of German forests was investigated by Blaschke (1981). This author's studies were conducted on *A. alba* stands growing near Munich, Bavaria. Blaschke showed that roots in mineral soil tended to have ectendomycorrhizal infections, rather than the classic ectomycorrhizal infections found in the litter and humus layers of the soil. Whether these infections represented the presence of symbiotic ectendomycorrhizal fungi (Harley & Smith 1983) or of pathogens with a similar mode of infection (Levisohn 1954) was not determined. The roots from mineral soil were afflicted by various intracellular infections caused by Oomycetes and by unidentified *Mortierella* spp. (*ss. lato*, i.e., generic concept not excluding *Umbelopsis*). Ectomycorrhizal roots also occasionally showed oomycete-like infections, but these were less frequent than infections in "pseudomycorrhizae" or other non-ectomycorrhizal roots. Blaschke concluded that the scarcity of true ectomycorrhizae in the mineral soil was contributory to the high degree of pathogenic root infection found there. In a subsequent study, Blaschke (1982) determined that *Phytophthora* spp. were responsible for many of the infections occurring on declining *A. alba*.

The contribution of *M. r. atrovirens* α to forest decline was assessed by Livingston & Blaschke (1984). The species was isolated in large numbers from both long-root sections and sodium hypochlorite-disinfected mycorrhizae of *P. abies* from Bavaria. Although the fungus was isolated more often from senescent, "inactive" mycorrhizae than from healthy mycorrhizae, it did not appear to be responsible for the decline of root systems. Neither did *Cylindrocarpon destructans*, which was routinely isolated from long-roots in the single alkaline forest site included in the study. Like many other researchers, Livingston & Blaschke found *M. r. atrovirens* α to be more common on long roots than on mycorrhizae.

Japanese studies: Most of the 1970's Japanese mycorrhizosphere studies came from the oeuvre of Makoto Ogawa and co-workers, and mainly concern the shiro of *T. matsutake* and related fungi. Some earlier studies in this series were discussed above (see *Microbiological studies of the mycorrhizosphere: the 1960's*). Since the import of many of these studies is similar, no attempt will be made here to summarize each one individually. In general, however, *T. matsutake* has a profound effect on soil fungi in the area surrounding the fairy-ring-like zone of root colonization. Most soil fungal species are eliminated,

and only a few characteristic taxa remain. Healthy "mycorrhizae" (actually an unusual, hypertrophied infection of uncertain symbiotic status) are particularly antagonistic to other fungi, and if plated out on fungal medium often yield no surface mycota whatsoever (Ogawa 1976a).

In *Pinus densiflora* forest, a typical *T. matsutake* shiro could be divided into several functional zones (Ohara & Hamada 1967, Ogawa 1976a, 1977a). In the outermost zone, colonized by advancing mycelium of the mushroom, strains of *Trichoderma* sp. and *Mortierella* sp. *s.lat.* (probably *Umbelopsis* as mentioned above under *Microbiological studies of the mycorrhizosphere: the 1960's*) were typically found (Ogawa 1977a). In the adjacent zone of young, healthy colonized roots, these fungi disappeared, and only a small number of sterile root fungi were isolated. These fungi were designated R-I and R-II. Occasionally, a few strains of "*Mortierella* sp." could also be isolated from zone of young colonized roots. In the next zone, the zone at which fruiting bodies form, "*Mortierella* sp." increased in number and was joined by *Oidiodendron* sp. and a higher number of R-I and R-II isolates. In distal regions of the shiro where senescent colonized roots occurred, "*Mortierella* sp." and the sterile root fungi were often abundant. Ogawa (1977a) gave evidence that the former fungus was able to decay senescing hyphae of *T. matsutake*, while the sterile fungi were lignolytic and cellulolytic organisms capable of decaying senescing plant parts. In the most distal regions of the shiro, Penicillia, Aspergilli, and other common soil fungi could again be isolated.

From washed colonized roots themselves, Ogawa (1977a) found that only sterile dark root fungi (R-I, R-II, R-III) could be isolated from mycorrhizae collected at their most vigorous stages of growth. When decline began to occur, however, "*Mortierella* sp.," *Trichoderma* spp., and *Pachybasium* sp. [= a white-spored *Trichoderma*, prob. *T. polysporum* (Link) Rifai] colonized the mycorrhizae immediately.

The same pattern was essentially adhered to when *T. matsutake* infected other conifer species (Ogawa 1976a, 1976b, 1977b, 1977c). In some forest types, e.g. *Picea glehnii* (Fr. Schmidt) Mast. forests (Ogawa 1976b), "*Mortierella* sp." is replaced by *M.* (= *Umbelopsis*) *nana*. When species related to *T. matsutake* were examined [*T. fulvocastaneum* Hongo, *T. bakamatsutake* Hongo, *T. caligatum* (Viv.) Rick.], similar patterns of soil fungal development were observed (Ogawa 1977d, 1978, Ogawa & Ohara 1978, Ohara & Ogawa 1982). In most cases, however, the observed inhibition of the soil microbiota was less dramatic than it was with *T. matsutake* itself. In Algerian forests where *Cedrus libanotica* Link (= *Cedrus libani* A. Richard) is colonized by *T. caligatum*, *Mortierella* spp. (inclusive of the modern *Umbelopsis*) were not found, but *Penicillium janthinellum* was similarly characteristic of the inhibited shiro area. Throughout all the studies on *T. matsutake* and relatives, the identity of the common "*Mortierella* sp." of shiro habitats remained undisclosed; as mentioned above, however, the studies of Tominanga (1963) suggest that the species may in fact be *U. vinacea* or a close relative.

RECURRING QUESTIONS AND RUNNING THEMES IN EARLY STUDIES OF FUNGI IN THE ECTOMYCORRHIZOSPHERE

It will have become apparent that the pre-1985 studies on fungi in the mycorrhizosphere tended to focus around certain recurring themes. For example, many authors attempted to determine whether fungal populations in general were stimulated or repressed around ectomycorrhizae or ectomycorrhizal root systems. A brief synthesis of results pertaining to several of these recurring themes and questions is given below.

Are fungal populations quantitatively stimulated by ectomycorrhizae or ectomycorrhizal root systems? The rhizospheres of young assimilative root systems significantly modified by the presence of ectomycorrhizal fungi have been examined by numerous authors. For some such studies, I have inferred the presence of ectomycorrhizae even though they are not mentioned. This is because of the extreme unlikelihood of the trees examined being in a normal, healthy condition except under the influence of ectomycorrhizal fungi (see Vozzo & Hacskaylo 1971). The studies showing a positive rhizosphere effect for fungi in the ectomycorrhizal symbiorhizosphere (for definition of this term, see Summerbell, 2005–this volume) include those of Hagem (1910), Samtsevich (1955, 1956), Runov & Zhdannikova (1960), Sizova & Vasin (1961), Chastukhin & Nikolayevskaya (1962), Otrosina (1977), and Malajczuk & McComb (1979). On the other hand, Ivarson & Katznelson (1961) and De Leval & Remacle (1969) found an insignificant difference between rhizosphere and non-rhizosphere soils. Similar results were obtained for a non-ectomycorrhizal forest tree, *Liriodendron tulipifera* L., by Shipman (1957). For ectomycorrhizae themselves, distinguished from adjacent portions of the young assimilative root system, a positive relative stimulation was recorded by Tribunskaya (1955), Rambelli (1962, 1963, 1966), and Neal *et al*. (1968). A possible inhibitory effect of ectomycorrhizae on soil fungal population numbers was noted by Katznelson *et al*. (1962), Rambelli (1965), and Neal *et al*. (1964). A much greater inhibition appeared to be conferred by some ectomycorrhizal mycobionts than

by others (Neal *et al*. 1964, Ohara & Hamada 1967, Ogawa 1976a). The generally stimulatory effect of ectomycorrhizal root systems appeared to be modified by the species-specific nature of exudation by different trees (Malajczuk & McComb 1979), by the nutrient content of non-rhizosphere soil conditions (Runov & Zhdannikova 1960), or by the presence of root infections (Malajczuk & McComb 1979).

To what degree do different ectomycorrhizal mycobiont species modify the mycota of the mycorrhizosphere?

Only a few pre-1985 authors examined this question. Such an examination was rendered difficult during this period by the lack of dependable techniques for reliably identifying mycobionts occurring *in situ* on mycorrhizae. Neal *et al*. (1964), using mycorrhizal types distinguished by morphology and colour, found that some types were much more inhibitory than others to fungal population numbers. Whether each of these types represented a single mycobiont is not clear. The same question underlies the morphological classification used by Danielson & Davey (1969). These authors found distinct species compositions for fungal populations associated with "normal", "dark", and "coralloid" mycorrhizae. These different root populations could almost certainly not be selected strictly as a result of differences in mycorrhizal surface morphology. It seemed likely, therefore, that at least some of the specific properties ascribed to mycorrhizal types by Neal *et al*. (1964) and by Danielson & Davey (1969) reflected genuine ecological differences between the mycorrhizospheres of different mycobionts.

The relatively sophisticated but often-criticized Dominik system of mycorrhizal classification (Dominik 1956 and subsequent), forerunner of the much more detailed systems of Agerer (1987-1998), was used to distinguish mycorrhizosphere populations by Kowalski (1974b, 1980c). In these studies, the differences in mantle-colonizing mycotas associated with different mycorrhizal "genera" appeared to be insignificant. An independent mycorrhizal classification system used by Luppi Mosca & Fontana (1982) in ectomycorrhizosphere studies yielded results of uncertain significance.

Since some mycorrhizal fungi were known to inhibit saprobic rhizosphere fungi *in vitro* (e.g., see Park 1970), and to inhibit pathogenic fungi *in vitro* and *in vivo* (Marx 1973), a regulatory effect of individual mycobionts on mycorrhizosphere populations was widely expected. To 1985, however, no named mycobiont species other than *T. matsutake* and its close relatives (Ohara & Hamada 1967, Ogawa 1976a, 1977a and other studies discussed above under *Mycological studies of the mycorrhizosphere: 1970–1985. Japanese studies*) had been shown to have a specific effect on mycorrhizosphere fungal populations *in vivo*. Kilbertus *et al*. (1978) did study the mycorrhizosphere of a known mycobiont, *H. crustuliniforme*, but did not attempt a comparison with any other mycobiont species.

What was included in the designation *Mycelium radicis atrovirens* and to what extent did the name indicate organisms found to be harmful?

Overall, the name *M. r. atrovirens* in the pre-1985 period appears to have been most commonly comfortably applied to fungi that we now know as a genetically diverse assemblage of *P. fortinii* isolates (probably qualifying as several cryptic species – see Grünig 2004) and perhaps also by some people to Grünig's "type 1" (Grünig *et al*. 2001, 2002), recently described as *Acephala applanata* Grünig & Sieber (Grünig & Sieber 2005), a species closely related to *P. fortinii* but forming only sparse aerial mycelium in culture. As intimated above, however (see *Mycological studies of the mycorrhizosphere: 1970–1985. North American research*), various historical individuals have certainly had broader concepts and some have probably had narrower concepts.

Mycelium radicis atrovirens was originally conceived by Melin (1921) as a single entity. In 1923, however, he expanded the scope of the name to include two distinct entities, *M. r. atrovirens* α (the original bearer of the name) and *M. r. atrovirens* β. This expansion was consistent with Melin's nomenclature for other sterile cultures: for example, distinct mycorrhizal symbionts isolated from *P. sylvestris* roots were referred to as *Mycelium radicis silvestris* α, *M. r. silvestris* β, and so on (Melin 1921). The name *M. r. atrovirens*, then, for all its length, was very roughly analogous to a generic name; species-like entities were denoted by a Greek letter.

Mycelium radicis atrovirens α was clearly described by Melin (1921, 1923). Auxiliary descriptions were given by Linhell (1939) and Mańka (1960). Further features, particularly those characteristic of the species' morphology when in contact with native cellulose (summarized in the fifth and sixth paragraphs following this one), were delineated by Levisohn (1954, 1963), Gams (1963), and Richard & Fortin (1974). According to Gams (1963), most *M. r. atrovirens* α strains from different provenances were highly similar to one another. Hyphal anastomosis might or might not occur between isolates, and "incomplete" anastomoses were also seen (Linhell 1939, Gams 1963). The strains isolated by Levisohn from British forest nurseries differed from most others by a much narrower hyphal diameter (Gams 1963). [N.B. that our own recent (unpubl.) studies have revealed the two Levisohn strains in the CBS collection to be

compatible with *P. fortinii*]. These strains were studied both by Gams and by Richard & Fortin). Richard & Fortin (1973) induced *M. r. atrovirens* α strains from Canada, Finland, Denmark, and Poland to sporulate as the anamorph soon to be named *P. fortinii*. A number of Levisohn strains, as well as various other strains of more prototypical hyphal morphology, did not sporulate.

Mycelium radicis atrovirens α could, then, be seen by 1985 to be a heterogeneous group of organisms, but it, like many other heterogeneous fungal anamorph taxa of the era (e.g., *Trichoderma viride*, *Rhodotorula glutinis*) contained biologically similar isolates difficult or next to impossible to segregate phenotypically into dependably distinguishable groups. The morphological characters it produced during lysis of cellulose fibres were well-described, and there was probably no reason for any cautious investigator to confuse it with the mycorrhiza-forming strains placed into the form-genus *M. r. atrovirens* by Kowalski (1973), Pachlewski & Pachlewska (1974), and Wang & Wilcox (1985). In most trials, *M. r. atrovirens* α was also characterized by its formation of pseudomycorrhizae or intracellular infections in conifer seedlings grown *in vitro* (Melin 1923, Wang & Wilcox 1985, Wilcox & Wang 1985).

With regard to the degree of harm caused by *M. r. atrovirens* α, an interesting pattern is perceptible in the pre-1985 studies. A potential for pathogenicity was established beyond doubt: such isolates proved to be harmful or lethal to many conifer species *in vitro* (Melin 1923, Hatch 1934, Lindquist 1939, Linhell 1939, Robertson 1954, Richard & Fortin 1974, Schönhar 1984). At the same time, they were consistently correlated with microbiologically "healthy" soils, as opposed to "sick" soils (Levisohn 1960b, Mańka *et al*. 1968a, 1968b, Kowalski 1980c, 1982). In forest nurseries beset by seedling diseases, they were found to be more common on healthy than on diseased roots (Bloomberg & Sutherland 1971). Where they were scarce or absent on ectomycorrhizal root systems in temperate soils, the dominant fungal colonizers tend to be potentially destructive *Fusarium* or *Cylindrocarpon* spp. (Mańka 1960, Mańka & Gierczak 1961, Truszkowska 1961, Kowalski 1980c). Generally, they infected and formed pseudomycorrhizae only with senescing non-mycorrhizal roots (Robertson 1954). They were, however, found to create problems by colonizing roots in forest nurseries artificially deprived of mycorrhizal inoculum (Richard & Fortin 1974). Generally harmless strains, when transferred from their native soils to foreign soils, could also cause an unusual degree of damage to tree seedlings (Rayner & Levisohn 1943). These last two effects appeared to be mediated by a release of the fungus from normal competition.

In short, *M. r. atrovirens* α was found to be potentially harmful, but under normal circumstances appeared to be well adapted to growing on senescent (Robertson 1954, Livingston & Blaschke 1984) and suberized (Mańka 1960, Parkinson & Crouch 1969, Kowalski 1980a) root material without harming its plant associates. Even when the fungus was isolated from within steles of living roots (Parkinson & Crouch 1969), damage was not detectable (In this work, see isolates labelled "SDF," which are likely to represent *M. r. atrovirens* α). The presence of mycorrhizal mycobionts is probably instrumental in keeping *M. r. atrovirens* α in check in some situations, preventing a deleterious effect on vulnerable host seedlings (Richard *et al*. 1971, Richard & Fortin 1975).

Mycelium radicis atrovirens β, by contrast, is a relatively virulent pathogen (Melin 1923, Levisohn 1960b). As no isolates appear to have been preserved, its identity in modern systematics has not yet been rediscovered, though Melin's descriptions of cultures and patterns of pathogenicity should be adequate to allow this. Since its description, *M. r. atrovirens* β has been observed infrequently. Generally, it is associated with "sick" soils unmistakeably harmful to the growth of conifer seedlings (Rayner & Neilson-Jones 1944, Levisohn 1960b).

Mycorrhizal strains historically attributed to *M. r. atrovirens* are difficult to distinguish from *M. r. atrovirens* α in agar culture, although their growth rate may be slower (Kowalski 1974b). Whether they form the microsclerotia typical of *M. r. atrovirens* α in culture (Melin 1923) or the characteristic "rooting branches" (Gams 1963) and "nets" (Levisohn 1954) typical of *M. r. atrovirens* α on cellulose has not been explicitly recorded, but coincidental formation of all these various, relatively distinctive structures by what are now known to be mostly relatively distantly related fungi seems unlikely.

Sieber (2002) has recently illustrated the morphology of *P. fortinii* growing in and on cellulose sheets: the sheets tend to be vertically penetrated by microhyphae, while spreading, often lobed "plate hyphae" [very similar to the structures referred to as 'frondose hyphae' in dermatophytes and *Fusarium* species penetrating nail keratin (see Zaias 1966, 1972)] form on surfaces in the space between two overlaid sheets. Currah & Tsuneda (1993) have given details of the extensive multi-hyphal strand formation by *P. fortinii* on cellulose nitrate filters, and have also given electron microscopic details of the relatively simple sclerotia formed by this species. Neither Sieber nor Currah & Tsuneda, however, dealt in similar detail with the structures formed by other *M. r. atrovirens*-like fungi. Practical identification of *P. fortinii* and similar species at the modern level of resolution is more or less obligately done via sequencing. Nonetheless, the

more recent studies do support the idea that careful pre-1985 researchers could probably successfully identify *P. fortinii* per se as *M. r. atrovirens* α without confusing it with a variety of other DSE types. This conclusion facilitates the interpretation of some older data.

Recent review information on the still unfolding biosystematic and ecological complexities of *P. fortinii* and the *M. r. atrovirens* complex (now sometimes extremely broadly conceived as encompassing all dark sterile endophytes) is provided by Jumpponen and Trappe (1998), Jumpponen (2001), Sieber (2002) and Mandyam and Jumpponen (2005–this volume).

Is the growth of *Trichoderma* spp. favoured in the ectomycorrhizosphere?

Trichoderma spp. are variously cited as potential pathogens of mycorrhizal fungi (Summerbell 1987), pathogens of young seedlings (Galaaen & Venn 1977, Schönhar 1984) helpers of mycorrhiza formation (Malyshkin 1951, Mishustin 1951, Shemakhanova 1962) and even as organisms parasitized by mycorrhizal fungi (Werner *et al*. 2002, Zadworny *et al*. 2004). In the pre-1985 period, they were mainly thought of as potentially useful organisms, and the topic of their rhizosphere competence was frequently revisited. Davey (1970), in his review on the subject of mycorrhizosphere organisms, states that *Trichoderma* spp. were "mildly or strongly rhizophobic". He cited the study of Danielson (1966), who isolated only a small number of *Trichoderma* strains from loblolly pine mycorrhizae in the nursery. Of the other studies available on the subject, one reported an enhanced number of *Trichoderma* isolates in the rhizosphere of ectomycorrhizal trees (Malyshkin 1955) while various others showed the genus forming a highly significant proportion of the rhizosphere population (Malyshkin 1951, Harley & Waid 1955a, b). Many studies, on the other hand, reported a greater number or proportion of *Trichoderma* isolates from non-rhizosphere soils (Samtsevich 1955, Sizova & Vasin 1961, Danielson & Davey 1969, Johannsen & Marklund 1980) or from non-ectomycorrhizal roots (Shemakhanova 1962, De Leval & Remacle 1969, Mishra & Kanaujia 1973). Even where *Trichoderma* was reduced in proportion around roots of ectomycorrhizal trees, however, the rhizospheres investigated could still contain characteristic and significant *Trichoderma* populations (Sizova & Vasin 1961).

The prevalence of *Trichoderma* spp. in the mycorrhizosphere was shown to be contingent on physical factors in at least some cases. Harley & Waid (1955b) found that *Trichoderma* was strongly favoured by good illumination of the plant associate; poorly illuminated plants were associated with few isolates. Ecological factors, such as the organic composition of the soil layer from which mycorrhizae are sampled, were also proposed as being important. Kowalski (1974a) found that when litter, non-rhizosphere soil, rhizosphere soil, and washed suberized roots were sampled, by far the greatest number of *Trichoderma* isolates was obtained from litter. *Trichoderma* numbers from washed roots were next largest, followed by rhizosphere and non-rhizosphere soil. Since mycorrhizae often form in the lower litter layers or immediately beneath them (e.g., see Went 1971) as well as in mineral soil, the number of *Trichoderma* isolates in the mycorrhizosphere may vary considerably when samples are taken from different soil layers.

One general finding was that any process in which mycorrhizae were rigorously washed or surface-sterilized tended to eliminate the isolation of *Trichoderma* spp. (Harley & Waid 1955a, Danielson & Davey 1969, Kowalski 1974b, 1980a). Members of the genus clearly seldom penetrated living roots, and also did not tend to associate intrinsically with mantle hyphae. In studies connected with forest decline in central Europe and Scandinavia, root penetration and pathogenic attacks by *Trichoderma* spp. were observed in young conifer seedlings *in vitro* (Galaaen & Venn 1977, Schönhar 1984). The broad applicability of these findings was clearly questionable at the time, however, since various experiments had shown *Trichoderma* to be non-pathogenic (Salt 1965, Sinclair *et al*. 1982, Nylund & Unestam 1982) or even stimulatory (Yatazawa *et al*. 1960) to ectomycorrhizal tree hosts. In overview, it was apparent that *Trichoderma* spp. were usually sufficiently "rhizophobic" not to penetrate healthy mycorrhizal or non-mycorrhizal roots in nature. The habitat in which they are most often found in association with mycorrhizae was the proximal rhizosphere soil. Even larger numbers were associated with adjacent suberized root surfaces in some habitats (Kowalski 1974a, 1980a).

Various investigators found that when roots began to decay, either after logging (Chastukhin & Nikolayevskaya 1962), after excision (Mańka & Gierczak 1961), during late senescence (Ogawa 1977a), or after infection by pathogens (Malajczuk & McComb 1979), *Trichoderma* isolates tend to be found in large numbers.

What is the status of *Aspergillus* in the ecto-mycorrhizosphere?

The common association of *Aspergillus* spp. with warm climatic regions and with cultivated and steppe soils has been mentioned previously. Many northern forest soils conspicuously lack aspergilli (Söderström 1975, Söderström & Bååth 1978). Even in zones where *Aspergillus* is found, however, pre-1985 studies most often found it to be more common in non-rhizosphere soils than in the mycorrhizosphere or on mycorrhizae (Kozlova 1955, Samtsevich 1955, Sizova & Vasin

1961, Danielson & Davey 1969). Likewise, it was found to be more common in the proximal rhizosphere than in close association with the mantle (Rambelli *et al*. 1972). Occasionally, it or a related teleomorph was reported as a predominant fungus in the rhizosphere of ectomycorrhizal plants (Chastukhin & Nikolayevskaya 1962, Mishra & Kanaujia 1973, Luppi Mosca & Fontana 1982). Malyshkin (1955) found that some species were more common on mycorrhizae than on non-mycorrhizal roots, while others showed the reverse pattern. Sizova & Suprun (1962) found that one ectomycorrhizal tree species, *Tilia cordata*, appeared to stimulate *Aspergillus* spp. in the rhizosphere. Other ectomycorrhizal phytobiont species in the same study appeared to suppress *Aspergillus* spp. Kowalski (1974a) found a single *Aspergillus* species, *A. versicolor*, to be typical of the rhizosphere of ectomycorrhizal pine. This species was much less common in litter or in non-rhizosphere soil than in the rhizosphere. Runov & Zhdannikova (1960) did not find *Aspergillus* spp. in large numbers when they sampled spruce roots in *Sphagnum* bogs, but pointed out that in those habitats any Aspergilli they found were invariably associated with roots. None occurred in *Sphagnum* material sampled outside the rhizosphere.

This rather fragmented pattern showed two things. Firstly, the consideration of the genus *Aspergillus* as a single ecological entity, as was done in numerous early studies, is ill-advised; species must be considered individually. Secondly, even though the mycorrhizosphere appeared not to be as favourable a habitat for most *Aspergillus* spp. as it was for many *Penicillium* spp., it could still support significant populations. Exactly how these populations were supported was not investigated. No specific ecological role such as degradation of tannins and phenolics (as per *Penicillium*) was suggested for *Aspergillus* in the mycorrhizosphere. They, like *Trichoderma* spp., could at least safely be said not normally to penetrate roots or to commingle intimately with mycorrhizal mantles.

Mineral nutrient interchanges between decomposers and ectomycorrhizal fungi

Ectomycorrhizal fungi were shown early on generally not to decompose macromolecules (Harley & Smith 1983) and to have only a limited ability to mobilize rock phosphate (Wilde 1954, Harley & Smith 1983), or nitrogen bound in clay, polyphenolic materials, or humic complexes (Loll & Bollag 1983). It therefore appeared that ectomycorrhizal fungi growing in soils with low levels of soluble mineral nutrients must depend on the nutrient-solubilizing activities of other microorganisms.

One of the most valuable features of ectomycorrhizal fungi to their plant hosts is their ability to increase uptake of phosphates (Harley & Smith 1983, Barea & Azcón-Aguilar 1983). By 1985, it was well known that much of the total phosphorus content of most soils is present in insoluble mineral forms (Kucey 1983) or refractory organic forms (Greenwood & Lewis 1977). Insoluble mineral phosphates may be brought into solution by microorganisms that secrete large quantities of organic acids (Kucey 1983). The abilities of ectomycorrhizal fungi to secrete acids are unremarkable, at least in pure culture (Harley & Smith 1983). Although at least one ectomycorrhizal fungus, *Boletus felleus* Bulliard [= *Tylopilus felleus* (Bulliard : Fries) P. Karsten], was shown to render rock phosphates available to plants (Rosendahl 1942, Wilde 1954), this appeared to be an exceptional case (Wilde 1954). Some experiments on mycorrhizae vs. inorganic phosphates (Stone 1950, Bowen & Theodorou 1967) showed some breakdown of the phosphates in the presence of mycorrhizal roots. In these studies, however, contaminating microorganisms may have been responsible for the effects observed (Harley & Smith 1983).

Among the organisms best adapted to dissolving inorganic phosphates are certain bacteria, *Penicillium* spp., and *Aspergillus* spp. (Kucey 1983). Phosphate-solubilizing bacteria were shown to occur in the symbiorhizosphere of *Pinus contorta* (Dangerfield *et al*. 1978). The occurrence of aspergilli and penicillia in mycorrhizospheres has been discussed above (see sections labelled *Microbiological analysis of mycorrhizosphere fungi: the 1950's* and *What is the status of Aspergillus in the ectomycorrhizosphere?*). It was clear by the mid-1980's that the marked tendency of ectomycorrhizae to stimulate the growth of *Penicillium* spp. could be predicted to have a significant effect on the availability of phosphorus from poorly soluble inorganic sources.

Refractory organic sources of phosphorus, like ferric and calcium phytates, are broken down by a variety of microorganisms possessing the requisite phytase or phosphatase enzymes (Greenwood & Lewis 1977, Dighton 1983). High levels of acid phosphatases were shown to be associated with mycorrhizae in nature (Blaschke 1980). Some ectomycorrhizal fungi were demonstrated to possess phosphatases and phytases, and to be able to mobilize significant quantities of organic phosphorus (Theodorou 1971, Dighton 1983). Thus, it appeared that many of these fungi do not depend on saprobes to perform this function. It is possible that the ability of ectomycorrhizal fungi to compete for organic phosphorus partially explains the repression of litter decomposition that occurs in some ectomycorrhizal forests (Romell 1939, Gadgil & Gadgil 1975). It has been suggested that litter-decomposing microorganisms are restricted in their uptake of mineral nutrients in these habitats (Gadgil & Gadgil 1975). This matter is discussed in more detail below (see *Disseminated effect of mycorrhizal fungi on soil microbial populations*).

Much less investigation was done by early mycorrhizosphere researchers into the prospective role of mycorrhizosphere organisms in rendering refractory nitrogen available to mycorrhizae. Ectomycorrhizal fungi were seen often not to be proteolytic (Harley & Smith 1983), but studies compiling lists of known proteolytic microorganisms (Loll & Bollag 1983) indicated that many common mycorrhizosphere organisms probably perform this function. Ammonifying and proteolytic bacteria in the mycorrhizosphere were extensively studied (Rambelli 1973). Many *Penicillium* species were shown to degrade proteins (Domsch *et al*. 1980). The cleistothecial *Ascomycetes* obtained in large numbers from pine and fir mycorrhizae by Fontana & Luppi Mosca (1966) and Luppi Mosca & Fontana (1982) were mostly from genera well known to be proteolytic (Loll & Bollag 1983). Loll & Bollag (1983) also listed *Trichoderma*, *Paecilomyces*, *Aspergillus*, and *Cephalosporium* (probably = *Acremonium*, *Lecanicillium*, *Simplicillium* or *Pochonia*) as containing proteolytic species. These are all common mycorrhizosphere or mantle-inhabiting genera or generic complexes.

Another mineral nutrient that was shown to transact between mycorrhizal and mycorrhizosphere organisms is iron. Many mycorrhizal fungi were shown to produce hydroxamate siderophores that chelated soil iron and thus aided in obviating iron limitations to phytobiont growth (Szaniszlo *et al*. 1981). Similar siderophores produced by bacteria were proposed as inhibitors of the growth of various microorganisms, including pathogenic rhizobacteria (Kloepper *et al*. 1980) and *Trichoderma hamatum* (Hubbard *et al*. 1983). On the other hand, the ability of some bacteria to respond positively to siderophores provided a standard bioassay for the presence of these compounds (Szaniszlo *et al*. 1981). Thus, it appeared that siderophores produced by ectomycorrhizal fungi might have a selective effect on mycorrhizosphere inhabitants, repressing some and stimulating others. Recent studies have shown that *Phialocephala fortinii* forms a number of hydroxamate siderophores (Bartholdy *et al*. 2001).

Apart from these nutrient-specific interactions, a general nutrient transfer effect between soil fungi and mycorrhizal fungi was suggested by Went (1971). Although it may seem elementary that a nutrient flux should occur in this direction, little work was done in the pre-1985 period to determine the quantities and the exact natures of the substances transferred. Akhromeiko & Shestakova (1958), however, showed that labelled phosphorus could be transferred from leaf litter to tree seedlings through the agency of soil microorganisms.

Some pre-1985 authors suggested that a release of nutrients from senescing rhizosphere microbes might be important in the nutrition of trees. Tribunskaya (1955) recorded the existence in the pine rhizosphere of bacteria capable of an efficient lysis of mould hyphae. She suggested that this might contribute to the nitrogen nutrition of the pines. Akhromeiko & Shestakova (1958) suggested the existence of a cycle in which rhizosphere bacteria absorbed nutrients from the roots, and then released them again upon senescence. A substantial fraction of the mineral nutrient lost to microorganisms was later reclaimed by the plant. In addition, the microorganisms took up and sequestered mineral nutrients released by litter decay processes. The proliferation of organisms in the rhizosphere was suggested to aid plants by retaining mineral nutrients in the root zone over extended periods of time.

Effect of microorganisms on ectomycorrhizosphere pH

As mentioned above, many soil organisms were shown in early soil microbiology research to secrete organic acids. The potential importance to plant nutrition of this facility was first suggested by Kunze (1906). Later on, *Aspergillus niger* received much attention as a phosphate-liberating soil organism (Lohmann 1931) that was able to aid in the nutrition of (non-ectomycorrhizal) elm seedlings in pot experiments (Rosendahl 1942). The lack of enzymatic intervention in the acid-mediated process by which rock phosphate was solubilized was well known. Besides dissolving phosphates directly, however, organic acids could also chelate calcium ions, thus leading to an indirect solubilization of phosphates (Katznelson & Bose 1959).

Jahn (1936) suggested that moulds in the proximal rhizosphere tended to maintain a pH optimal for providing newly solubilized mineral salts to plant roots. He studied the production of acids by a small number of fungi isolated from the rhizospheres of ectomycorrhizal trees. The trees occurred both in acidic soils and in neutral-to-alkaline, calcareous soils. In laboratory tests, the fungi isolated from calcareous soils tended to depress the pH of their growth medium more than did those from naturally acidic soils. This appeared to confirm Jahn's prediction that the rhizosphere fungi of calcareous soils would secrete sufficient acid to maintain the solubilization of essential minerals, despite the tendency of the prevailing soil pH to suppress those reactions. Unfortunately, Jahn's sample size was very small. The degree to which acid-producing mycorrhizosphere organisms contribute to tree nutrition in forests remained poorly known in subsequent decades.

That the acid-secreting abilities of mycorrhizal and rhizosphere organisms could aid tree nutrition in the nursery was shown by Wilde & Rosendahl (1945), and Wilde (1946). These authors successfully grew both ecto- and endomycorrhizal tree seedlings with rock

phosphate and potassium feldspar as mineral nutrient sources.

The production of basic compounds in the mycorrhizosphere received some attention. Ammonifying organisms, including both bacteria and fungi, will secrete ammonia as a byproduct when using amino acids as a principal carbon source. This in turn will give rise to basic conditions, at least temporarily. (However, many fungi that take up and metabolize the ammonium ions arising in this way will then secrete acid). Most microbiologists investigating the mycorrhizosphere recorded relatively high numbers of ammonifying organisms (Rambelli 1973), but actual ammonifying activity, which can often be repressed by simple sugars, was generally not measured. Tribunskaya (1955) ascribed the poor growth of pine seedlings fertilized with albuminous substances to "the appearance in the soil of a high quantity of ammonia, on account of the activity of putrefying bacteria." However, no actual measurement of ammonia quantity or pH was given.

In the first 80 years of ectomycorrhizosphere research, few direct measurements were made of the pH of mycorrhizospheres in nature. Peña-Cabriales & Valdes (1975), however, measured the pH of the rhizosphere soils they worked with. In their study, soil associated with *Abies religiosa* (HBK.) Schltdl. & Cham. roots had a pH of 6.3. Non-rhizosphere control soil had a minimally distinguished pH of 6.4. Dangerfield *et al*. (1978) found indirect evidence that the lodgepole pine symbiorhizosphere was possibly more alkaline than the surrounding soil. In their studies, rhizoplane bacterial populations were significantly more inhibited by acidic conditions *in vitro* than were bacterial populations from control soil. Direct measurements of pH on the rhizoplane were not done.

In general, the pH of rhizospheres is expected to be strongly influenced by the overall conditions of soil microbial activity and soil chemistry. Most pre-1985 studies conducted in forest soils showed the upper soil layers to be much more acidic than the lower horizons (e.g., Ivarson & Katznelson 1960, Kowalski 1974b). It was rationalized that if this was principally due to the high microbial activity in the litter and humus layers, the acidification might be even more pronounced in the highly microbially active mycorrhizosphere. This could be expected, at least, wherever a positive rhizosphere effect was observed and where microorganisms producing basic substances did not prevail. However, it was clear that any acidifying effect of rhizosphere organisms was not strong enough to counteract the tendency of acid-intolerant fungi, like *Cylindrocarpon destructans*, to colonize roots in the more alkaline lower soil horizons (Mańka & Rząsa 1961, Parkinson & Crouch 1969). The extensive production of acids in the rhizosphere appeared to depend on an input of organic matter beyond that supplied by root exudation alone.

Effect of mycorrhizosphere organisms on plant growth

Another early finding was that when the effects of individual nonpathogenic microorganisms on plant growth were studied, interesting effects were often found. Plants appear to be stimulated by some microorganisms and inhibited by others (Bowen and Rovira 1961, Domsch 1963). Organism groups like *Fusarium* spp. and *Rhizoctonia solani*, considered pathogenic under some conditions, were stimulatory under others (Bilai 1955, Katayev & Koloshina 1955). Significant interactions in field- or pot-grown plants were attributed to a variety of causes. Among these were nutritional stimulation by nitrogen-fixing (Balandreau & Knowles 1978) or mineral-solubilizing organisms (Azcón *et al*. 1976), the production of organic compounds directly stimulatory or inhibitory to plant growth (Bowen & Rovira 1961), the inhibition of pathogens (Fedorinchik & Vanderflaas 1954, Elad *et al*. 1980), and the inhibition of unfavourable non-pathogens or breakdown of their harmful metabolites (Broadbent *et al*. 1977).

A small proportion of the work in this field was addressed to the effects of microorganisms on ectomycorrhizal phytobionts. Lindquist (1939) found that culture fluids in which the facultative root invaders *M. r. atrovirens* (prob. α) and *U. ramanniana* had been grown produced an inhibitory effect on the growth of both roots and shoots of spruce. Mycorrhizal strains and a "parasitic and mycorrhiza-building fungus" labelled "Mycelium 19f" produced stimulatory extracts. Mycelium 19f may be *Heterobasidion annosum*, as discussed above under *Mycological studies of the mycorrhizosphere: 1970–1985*. According to a re-evaluation by Harley (1948), the differences shown in Lindquist's data were statistically significant. Richard & Fortin (1974) confirmed the production of plant growth inhibitors *in vitro* by *M. r. atrovirens* α, inclusive of isolates later shown to be *P. fortinii*.

Bowen & Rovira (1961) assayed the effect of soil microbial populations on the growth of *Pinus radiata* roots in sterile sand and in plant nutrient agar. They found that roots inoculated with dilute soil suspensions invariably experienced a stunting of root growth compared to sterile control roots. The stunting appeared to be caused by specific soil microorganisms, but these were not isolated individually. A similar experiment conducted by Kampert & Strzelczyk (1975b) gave similar results. In this case, a census of the microbes proliferating around stunted pine roots in agar tubes showed that coryneform bacteria were predominant. Various soil fungi were also present, but

the composition of their populations varied greatly with the dilution of the soil used as an inoculum. This and the rather profound differences between microbial populations of the original soil and those found around roots in the tubes were considered to show the general unsuitability of agar media for such experiments.

A great many *Penicillium* species were shown to produce metabolites that could be shown *in vitro* to be toxic to plants (Berestetskii & Borovkov 1977, Domsch *et al*. 1980). Generally, only agricultural crop plants were subjected to tests for *Penicillium* phytotoxicity. Culture filtrates of isolates identified by the ambiguous name *Penicillium cyclopium* Westl. were found by Manturovskaya & Sizova (1967) to be stimulatory to spruce seedlings. Culture filtrates attributed to the same species are toxic to wheat and barley (see Domsch *et al*. 1980). Several members of *Penicillium* subgenus *Penicillium*, all with different toxin spectra, might have been identified with this frequently misused name (Samson & Frisvad 2004). Pine seedlings with roots colonized only by coryneform bacteria and *Penicillium* spp. did not show any growth inhibition compared to sterile controls (Kampert & Strzelczyk 1975b). No inhibition of the growth of ectomycorrhizal host plants by Penicillia was shown, but it was suggested that the growth of these plants could be inhibited when certain soil Penicillia contributed to the chemistry of soils inhibitory to the growth of mycorrhizal symbionts (see Brian *et al*. 1945).

Much more numerous than *in vitro* studies with ectomycorrhizal phytobionts and microbes were plant growth simulation/suppression studies conducted with pot-or field-grown plants. A review of many studies of this sort conducted before 1960 has been published by Shemakhanova (1962). Many of these publications are very difficult to access in the original.

Various pre-1985 authors found that a superior growth stimulation of ectomycorrhizal tree seedlings was obtained when mycorrhizal inoculum was combined with other components of the soil microbiota. Some authors simply found that forest soils containing mycorrhizal inoculum gave better stimulation than pure mycorrhizal cultures (e.g. Sobotka 1956). This effect may, however, have been due at least in part to the superiority of mycorrhizal inoculum in forest soil. Moser (1956, 1963) isolated various nonpathogenic soil fungi ("penicillia, aspergilli, *Mucoraceae*") and combined them with pure mycorrhizal cultures in inoculations of tree seedlings. Such "half-pure-culture"-inoculated seedlings, upon being outplanted into alpine afforestation sites, generally showed better height growth than seedlings inoculated with pure mycorrhizal cultures alone. Unfortunately, the data given by Moser (1963) as evidence of this stimulation were not strongly detailed.

An unequivocal stimulation of tree growth by soil organisms was observed by Rayner & Neilson-Jones (1944). These authors used organic composts and humus amendments to render phytotoxic and fungitoxic heathland soils suitable for tree growth and mycorrhiza formation. The general stimulation provided by composting appeared to alter the balance of microbial activities in the toxic soils. Although the nature of this change was complicated, it appeared to depend on at least three factors. One was the breakdown of the toxic compound itself; this breakdown was accomplished by the newly-stimulated microbiota. A second was the elimination of the toxin-producing organism or organisms through competition. The third was the salutary influence of the nutrients added with the composting material itself.

When microbial activity had altered the toxic soil, the mycorrhizal inoculum already resident in the soil was able to make an effective colonization of seedling roots. The stimulation of tree growth seen in this series of experiments was due both to mycorrhiza formation and to the establishment of a beneficial microbiota in the soil. As for the toxicity of the original unamended heathland soil, it was variously ascribed to the influence of toxin-producing Penicillia (Brian *et al*. 1945) and to the ericoid mycorrhizal mycobionts of the *Calluna* heath vegetation (Handley 1963, Robinson 1972).

The effects on tree growth brought about by the nitrogen-fixing bacterium *Azotobacter chroococcum* Beijerinck were assayed by a number of Soviet workers in the 1950's and 1960's. Growth stimulation was recorded for oak (Malyshkin 1951, Vedenyapina 1955, Voznyakovskaya 1954, Shemakhanova 1962), pine (Vavulo & Yanushkevich 1953, Vavulo & Ponomareva 1955, Mishustin & Pushkinskaya 1961, Shemakhanova 1962) and Siberian larch (Ponomareva & Pron'ko 1955). Vavulo & Yanushkevich (1953) obtained only a small, insignificant stimulation with spruce. In many of the studies showing stimulation, the persistence of *Azotobacter* on roots was not studied. However, a positive effect on growth was sometimes perceptible several years after seedlings had been "bacterized" (Shemakhanova 1962). At least in some cases, this may have been due to a stimulation of spontaneous mycorrhiza formation following bacterial inoculation (Vedenyapina 1955, Mishustin & Pushkinskaya 1961, Shemakhanova 1962). As might be expected, the acid-intolerant bacterium persisted longer in neutral conditions (Shemakhanova 1962) than in acidic conditions.

Trichoderma lignorum (= one or more *Trichoderma* species with globose or subglobose, green conidia, most likely *T. viride* but also possibly *T. harzianum* or *T. asperellum* Samuels, Lieckfeldt & Nirenberg) also received considerable attention as a stimulator of plant growth. In part, this was because of its already well-

known ability to inhibit root disease fungi (Weidling 1932, 1934, Fedorinchik & Vanderflaas 1954). Also, however, the fungus was known to produce volatile and water-soluble antibiotics inhibitory to bacteria as well as fungi (Bilai 1955, 1956). *Trichoderma lignorum*, like *A. chroococcum*, was shown to increase the formation of mycorrhizae on field-grown tree seedlings (Malyshkin 1951, 1955, Mishustin and Pushkinskaya 1961, Shemakhanova 1962). These results will be discussed later in this review under the heading *Mycorrhizosphere microorganisms as stimulators of mycorrhiza formation*. Most studies measuring an effect of *Trichoderma* on plant growth did not attempt to isolate effects due to stimulation of mycorrhiza formation from other effects such as pathogen control; nor was there generally any attempt to establish the direct effect of *Trichoderma* isolates on plants themselves.

Trichoderma viride or closely similar species often did produce a significant stimulation of plant growth, even in cases where mycorrhiza formation was not significantly stimulated. In data given by Shemakhanova (1962: fig. 30), a pronounced growth stimulation was frequently evinced after *T. viride* inoculation of pine seedlings, even though the level of mycorrhiza formation was similar to or less than that found in control plants. In most studies, however, the positive effect of *Trichoderma* inoculation could not be separated from a positive effect on mycorrhiza formation (Malyshkin 1951, 1955, Mishustin & Pushkinskaya 1961). Not all studies showed a positive effect: equivocal or negative results were obtained under some conditions by Vavulo & Yanushkevich (1953) and Shemakhanova (1962). In Sweden, marginally positive effects due to *T. viride* inoculation were recorded in pine and spruce nursery beds (Ingestad & Nilsson 1964). These effects were statistically significant under some conditions and not under others. Mycorrhiza formation was not examined. In recent years, the reputation of *Trichoderma* species, especially *T. viride*, as pathogens of fine roots in *Picea abies* (Galaaen & Venn 1977, Schönhar 1984) has been supported by additional study (e.g., Schönhar 1991), but these species appears to be weak and fortuitous pathogens (Kattner 1992). Possibly positive effects due to their mycoparasitism or other microbial interactions may prevail over negative effects due to root invasiveness in various situations.

Ingestad & Nilsson (1964) investigated the effects of *Umbelopsis ramanniana* rhizosphere inoculations on spruce seedlings in the nursery. Seedlings growing in both fumigated and unfumigated soil were examined. A small but significant positive effect due to inoculation was registered after the first season of seedling growth on fumigated soil, but this stimulation fell into insignificance in 18-mo-old seedlings. Ingestad & Nilsson, in their discussion, did not mention the facultatively pathogenic attributes earlier ascribed to *U. ramanniana* (Melin 1923, Lindquist 1939) and did not appear to find the slight stimulation they observed surprising. They hypothesized that *U. ramanniana*, like *T. viride*, might temporarily prevent more deleterious organisms from colonizing the rhizospheres of seedlings in fumigated soil.

According to Mishustin & Pushkinskaya (1961), "bacterization" with a phosphorus-liberating *Bacillus* strain produced a significant growth effect in planted pines. Once again, this effect was confounded by a positive effect on mycorrhiza formation. A similar concurrent stimulation of plant growth and mycorrhiza formation was recorded by Katayev & Koloshina (1955) with isolates identified as *Rhizoctonia solani* (*s. lat.*) on oak seedlings in Moldavia (now Moldova). The same *R. solani* strains were destructively parasitic on young potato plants. The hyphal "nets" formed by *R. solani* on parasitized potatoes could also be observed on roots and root collars of the stimulated oak seedlings. The authors did not suggest a mechanism that might explain the stimulation they observed.

An elaborate experiment conducted by Shemakhanova (1961, also summarized by Shemakhanova 1962) showed that forest soil microbial communities had a beneficial effect on pine and oak seedlings even when mycorrhiza formation was precluded. Paper-filtered extracts of forest soil were more stimulatory to the growth of (near-) axenically-grown pines and oaks than were Seitz-filtered extracts of the same soil. The former type of extract contained inoculum of most spore-forming and particulate soil organisms, while the latter contained soil leachates but no microorganisms. No mycorrhizae were formed by plants treated with paper-filtered extracts, although forest soil itself, when inoculated directly into pots with seedlings, did lead to mycorrhiza formation. The stimulatory effect of mycorrhiza formation on growth was considerably greater than the stimulatory effect of other soil microorganisms.

The suggestion that the role of mycorrhizal fungi might be partially or wholly supplanted by saprobic microorganisms in certain soils was repeatedly, independently made by various authors across the decades, including Jahn (1934, 1936), Wilde (1954), Malajczuk & McComb (1979) and Malajczuk (1979). Wilde (1954) maintained that ectomycorrhizal phytobiont seedlings raised in forest soils could "continue to grow satisfactorily in prairie soils even though their root systems lacked mycorrhizal short roots." (By contrast, seedlings planted directly into prairie soils did very poorly.) Shemakhanova's experiments (Shemakhanova 1962) were among the more influential demonstrations that although forest soil saprobes are not entirely without benefit to ectomycorrhizal phytobiont seedlings, the formation

of mycorrhizae is of primary importance in conferring good growth and nutrition on the plants.

An anomalous indirect effect of soil organisms on the growth of ectomycorrhizal phytobionts was suggested by Bokor (1956). This author found that the germination of tree seeds was often repressed in forest soils and old forest nursery soils. He hypothesized the production of seed-suppressing antibiotics by ectomycorrhizal fungi. To provide support for this idea, he showed that culture metabolites of mycorrhizal fungi were inhibitory to seed germination of two pine species *in vitro*. *Pluteus cervinus* (Schaeff.) Kumm., a non-mycorrhizal basidiomycete used for comparison, produced metabolites that were much less inhibitory. Growing *Penicillium* or *Aspergillus* spp. in the same vessels as the mycorrhizal fungi sometimes reduced the degree of seed inhibition shown by the culture filtrates. Bokor therefore suggested that soil saprobes, the activity of which may be suppressed in mature ectomycorrhizal forests (Romell 1939, Gadgil & Gadgil 1975 – see *Disseminated effect of mycorrhizal fungi on soil microbial populations section below*), were capable of breaking down the antibiotics and of facilitating seed germination. Bokor's observations on the suppressive nature of forest soils are curiously parallel to those of Romell (1939). This author, however, blamed the soil suppressiveness on the high efficiency of mycorrhizal competition for mineral nutrients.

No other pre-1985 author attempted to confirm or elaborate upon Bokor's findings. Marx *et al*. (1984) did, however, observe that coating seeds of various southeastern U.S. pine species relatively heavily with basidiospores of the mycorrhizal fungus *Pisolithus tinctorius* (Pers.) Coker decreased seedling establishment by up to 60 %, even though the symbiont in general was highly beneficial to the same pine species. In another study on seed germination, a somewhat inconsistent stimulation of this process was shown for pine and spruce seeds treated with isolates of *Azotobacter* and *Trichoderma* (Vavulo & Yanushkevich 1953).

Ectomycorrhizal phytobionts as regulators of rhizosphere populations

Ectomycorrhizal phytobionts were known by 1985 to produce compounds of an unknown nature that stimulated and oriented the growth of ectomycorrhizal fungal mycelia (Melin 1963) and that initiated the germination of mycobiont basidiospores (Birraux & Fries 1981). These compounds were collectively referred to as M-factors. It was also shown (Bowen & Theodorou 1973) that plants other than ectomycorrhizal phytobionts also produce compounds that mimic at least some of these stimulatory effects.

The effect of such compounds on mycorrhizosphere inhabitants was tested by Nylund & Unestam (1982). These authors found that radicles of spruce seedlings in agar culture caused a directional stimulation of the growth of the ectomycorrhizal mycobiont *Piloderma croceum* Erikss. & Hjortst. On the other hand, *M. r. atrovirens* (probably α), *Heterobasidion annosum*, three *Penicillium* spp. (not named) and *Mortierella* sp. (possibly *Umbelopsis* or *Mortierella s. str*.) were not stimulated. A second spruce-associated mycobiont, *Suillus bovinus* (L. Fr.) Kuntze, also evinced no stimulation of growth. A conspicuous weakness of Nylund & Unestam's experiment was that it used radicles rather than short roots: the former, unlike the latter, are not susceptible to mycorrhizal infection. The compounds released into the surrounding medium by seedling radicles may be considerably different from those released by short roots. Nonetheless, compounds released by radicles do possess some classic "M-factor" properties and often stimulate mycobionts.

Sylvia & Sinclair (1983) showed that the presence of mycorrhizal or soil-inhabiting organisms around axenically-grown radicles could result in a stimulation of the production of defensive compounds by those radicles. The mycobiont *Laccaria laccata* or its culture filtrates induced the production of phenolic compounds in Douglas-fir radicles. These phenolic compounds in turn greatly inhibited the root pathogen *Fusarium oxysporum*. *Fusarium oxysporum* itself did not stimulate the production of these compounds, even when invading the radicle. These results explained the prior observations of Stack & Sinclair (1975) and Sinclair *et al*. (1975) that *L. laccata* could prevent seedling mortality due to *F. oxysporum*, even at a stage when seedlings were not yet able to initiate mycorrhiza formation. In the experiments of Sylvia & Sinclair (1983), the soil-inhabiting saprobes *Trichoderma harzianum* and *Pseudomonas cepacia* Burkh. were likewise found to elicit the production of phenolic compounds in radicles. *Epicoccum purpurascens* Ehrenb. and the mycorrhizal fungus *Cenococcum geophilum* caused only a partial stimulation of phenol accumulation. Even though Sylvia & Sinclair made no attempt to investigate the reactions of mature roots, their results suggested that some rhizosphere organisms were able to change root chemistry in ways that inhibited the growth of other saprobes in the rhizosphere. They also suggested that mycorrhizal fungi could alter root chemistry in ways that fundamentally alter the rhizosphere as a habitat.

The stimulation of growth of some root-associated organisms by ectomycorrhizal phytobiont root secretions or root extracts was shown by a small number of authors. Harley (1939) found that the sterile fungus *Mycelium radicis fagi*, a common colonizer of beech mycorrhizae, was greatly stimulated *in vitro* by

beech root extracts. Karimbayeva & Sizova (1977) grew various rhizosphere fungi on agar media along with pine and spruce germinants. They found that the presence of the germinants increased the growth rate of some rhizosphere fungi compared to fungus-only controls, but inhibited or failed to stimulate others. Of strains originally isolated from pine rhizospheres, 61 % were significantly stimulated by pine germinants *in vitro*. Only 33 % of isolates from originally from spruce rhizospheres were similarly stimulated by pine germinants. On the other hand, spruce germinants stimulated 67 % of the spruce-derived isolates, and only 25 % of the pine-derived isolates. Spruce germinants inhibited the growth of the majority of pine-derived fungi, while pine germinants had the same effect on most spruce-derived fungi. These differences were observed even when the pine- and spruce-derived strains belonged to the same species, e.g., *Penicillium simplicissimum*.

Karimbayeva & Sizova subjected a number of *P. simplicissimum* strains to an experiment in which they were grown on artificial media amended with seedling root exudates. Considerable differences were shown in the degree of growth stimulation obtained with different isolates. For example, of 14 *P. simplicissimum* isolates originally from pine rhizospheres, four were inhibited by the presence of pine exudates and ten were stimulated. The experiments as a whole indicated that root exudates were selectively stimulatory to rhizosphere fungal strains, but that this selection was not consistent at the (morpho)species level.

The experiments of Karimbayeva & Sizova (1977) had the same deficiency as those of Nylund & Unestam (1982): that is, they treated the seedling radicle as an analogue of the mature root system. Also, Karimbayeva & Sizova studied the effects of non-mycorrhizal root exudates on fungi isolated from the ectomycorrhizal symbiorhizosphere, a habitat likely to be distinct from the rhizospheres of newly emerged radicles or of non-mycorrhizal roots. Nonetheless, the experiments did suggest that despite the presence of mycorrhizal fungi on the roots of mature trees, the exudates released by the roots themselves could have a significant influence on the composition of the symbiorhizosphere population.

In a later experiment, Karimbayeva & Sizova (1978; experiment summarized in English by Hanso 1981) attempted to determine whether amino and organic acids known to be components of pine root exudates were responsible for the differential stimulation of rhizosphere fungi. Not surprisingly, no individual compound was found that possessed stimulatory or inhibitory effects identical to those of total root exudates. The degree of stimulation or inhibition experienced by a fungal strain exposed to a given compound depended greatly on the concentration of that compound. For example, a *Penicillium nigricans* K.M. Zalessky strain clearly inhibited by 0.06 mg/mL malic acid in Czapek's agar was slightly stimulated by a 0.2 mg/mL amendment of the same acid. Karimbayeva & Sizova concluded that the concentration in which root exudates appeared in the rhizosphere might be as important an influence on rhizosphere fungi as was the actual chemical constitution of the exudates.

It should be noted that researchers studying agricultural crops had already long known that different plant species favoured different rhizosphere populations, and even that different races or genotypes within a single plant species could stimulate markedly different rhizosphere populations (Timonin 1941, Neal *et al*. 1973). It is therefore not surprising that different tree species were found to have distinctive stimulatory effects on rhizosphere organisms.

Most pre-1985 floristic studies comparing the rhizosphere populations of different ectomycorrhizal tree species occurring in nature found some qualitative or quantitative differences in population structure. These studies, although relevant to this topic, will not be discussed in this section, and in any case are discussed above under "*Elucidating the microfungal species and assemblages associated with ectomycorrhizal roots.*" In such studies, the differential effect due to plant exudations cannot be distinguished from the effects due to differences in mycobiont colonization.

Phytohormonal relations among roots, mycorrhizal fungi, and mycorrhizosphere organisms

In one of the major trends in the pre-1985 literature, especially studies done in central Europe, many mycorrhizosphere-inhabiting organisms were shown to produce plant growth substances. Auxins were shown to be produced *in vitro* by various mycorrhizosphere filamentous fungi (Kampert & Strzelczyk 1975a, Strzelczyk *et al*. 1977, Strzelczyk & Pokojska-Burdziej 1982), yeasts (Haselwandter 1973), eubacteria (Haselwandter 1973, Kampert *et al*. 1975a, Strzelczyk & Pokojska-Burdziej 1984) and actinomycetes (Strzelczyk & Pokojska-Burdziej 1984). Other mycorrhizosphere organisms that did not produce auxins themselves were shown to modify those produced by mycorrhizal fungi in mixed culture *in vitro* (Moser 1959, Horak 1963). Mycorrhizal fungi likewise were shown to alter the auxins produced by mycorrhizosphere organisms (Haselwandter 1973).

The production by mycorrhizosphere organisms of gibberellin-like substances (Kampert *et al*. 1975b, Strzelczyk & Pokojska-Burdziej 1982, 1984) and cytokinins (Kampert & Strzelczyk 1978) was also shown. Soil-inhabiting species known to occur in the mycorrhizosphere were shown to produce another hormonal substance, ethylene (Lynch 1972, Lynch & Harper 1974). The conifer root pathogen *Fusarium*

oxysporum was demonstrated to produce this bioactive gas (Graham & Linderman 1979).

The potential consequences of the production of these compounds in the rhizosphere remained unclear. Speculations on why root-associated microorganisms might synthesize plant growth substances fell into four categories:

• Proposals that microbial hormone-production altered the plant's internal resource allocation in a way that provided better nutrition to the microorganisms,
• Proposals that hormone-production stimulated the plants in general, and therefore indirectly elicited a rich nutrient medium for the microorganism.
• Proposals that hormone-production induced gross or microscopic morphological changes in the plant in a way benefiting the microorganism.
• Proposals that hormone-production elicited the synthesis by the plant of defensive compounds selectively suppressive to competitors of the hormone-producing microorganism.

The possibility that production of plant hormones by mycorrhizal fungi might contribute to general plant vigour, thus enhancing the value of the mycorrhizal partner, was suggested by Miller (1971) and Slankis (1973). It was clear to many of the authors cited above that the same relationship might also apply in the case of non-symbiotic root associates. *In vitro* experiments with corn coleoptiles demonstrated that auxins produced by epiphytic bacteria could be taken up and accumulated by plants (Libbert & Silhengst 1970). It was clear that if such compounds were produced in appropriate quantities in the mycorrhizosphere, and if they were absorbed into the plant, a mutually beneficial stimulation of phytobiont metabolism might occur.

Moser (1959) suggested that the production of auxins by mycorrhizal fungi might engender a favourable change in the nature or quantity of root exudations. Miller (1971) suggested a similar role for cytokinins. Non-symbiotic organisms intimately associated with plant roots might derive a similar advantage from auxin or cytokinin production. In keeping with this idea, Haselwandter (1973) suggested that the production of auxins by rhizosphere organisms might improve the nutritional status of the root system, thus effectively increasing the chance of mycorrhizal infection. He suggested that Shemakhanova's (1962) observations on the favourable effect of *Trichoderma*, *Azotobacter*, and other mycorrhizosphere organisms on mycorrhiza formation could be explained in this way.

Meyer (1962, 1967) found that ectomycorrhizal roots "of equal mycorrhiza-frequency" growing in different soil horizons contained sugar levels proportional to the level of microbial activity in nearby soils. Roots in the "very microbially active" humus layer had a higher soluble (reducing-) carbohydrate content than roots in less-active, deeper soil horizons. Although various ecological and physiological factors might explain these results, growth substances produced by the microbiota may have been at least partly responsible.

Turner (1962) found that various filamentous fungal saprobes isolated from mycorrhizae could exert morphogenetic effects on pine root growth. Many of these effects duplicated those known to be caused *in vitro* by exogenous plant growth substances (Slankis 1973). The ecological significance of such abilities remained unclear. The one activity examined that might directly benefit rhizosphere organisms – the stimulation of lateral root production, which inevitably entails leakage from the site of rupture of the mother-root cortex – was not stimulated by any of the rhizosphere isolates tested.

Various authors (e.g., Crafts & Miller 1974) suggested that the production of plant growth substances might bring about changes in cell morphology or cell division that facilitated entry by fungal hyphae into ectomycorrhizal phytobiont roots. Kampert & Strzelczyk (1978) established that root-penetrating species such as *M. r. atrovirens* α and a fungus identified as *Cephalosporium acremonium* (= *Acremonium* sp.?) could produce cytokinins. This study was somewhat uncontrolled, however, in that rhizosphere organisms that did not penetrate roots were not examined for parallel cytokinin production. Kampert & Strzelczyk also found one competent root-penetrating fungus, "*Cephalosporium glutineum*" (a *nomen nudum fide* Gams 1971, thus an uninterpretable name though probably indicating an *Acremonium*-like fungus), that produced no detectable cytokinins.

Situations of similar complexity were found when other hormones were examined in relation to root penetration or pathogenic ability. For example, Strzelczyk & Pokojska-Burdziej (1982) found no correlation between the abilities of various *Cylindrocarpon destructans* isolates to synthesize auxins and gibberellin-like substances vis-à-vis relative virulence against roots of *Abies alba* seedlings. Pathogenic *Fusarium oxysporum* f. sp. *pini* strains examined by Graham & Linderman (1979) produced small amounts of ethylene *in vitro*, but also appeared to induce the production of far higher levels of ethylene by the Douglas-fir roots they invaded. Increased ethylene levels in the rhizosphere facilitated root invasion by *F. oxysporum* f. sp. *pini*, but not by the mycorrhizal fungus *Hebeloma crustuliniforme* (Graham & Linderman 1981).

Crafts & Miller (1974) suggested that cytokinins produced by mycorrhizal fungi might promote the formation of phenolic compounds by the phytobiont. Cytokinin production by other root-penetrating fungi

should clearly have the same effect. Crafts & Miller's suggestion was partly based on the observation by Miller (1969) of a stimulation of phenolics elicited by cytokinins in soybean tissue. In mycorrhizal roots, it was suggested, an analogous response to cytokinin might prevent the invasion of roots by organisms intolerant of phenolic defense compounds. The same response might also supply phenolics to organisms capable of using these compounds as a carbon source. Similar ecological conditions would exist, however, if the production of phenolic compounds were stimulated by factors other than cytokinins. *Laccaria laccata*, *Trichoderma harzianum*, and *Pseudomonas cepacia* were shown by Sylvia & Sinclair (1983) to elicit phenolic production by Douglas-fir seedling radicles, but no cytokinin or other hormonal mediation was demonstrated or suggested.

Gibberellins were often suggested to influence the abilities of different fungi to penetrate roots. Levisohn (1960a) found that introducing gibberellin-synthesizing strains of the rice pathogen *Gibberella fujikuroi* (Sawada) Wollenweber into pine rhizospheres stimulated root-pathogenic fungi and repressed the development of mycorrhizae. In a related experiment, Levisohn (1960b) found that exposing potted pines to small quantities of gibberellic acid resulted in a complete suppression of mycorrhizal and other root infections. Soil fungi and bacteria did not seem to be affected. However, microalgae in the pots were repressed. Such microalgae may play a significant role in the rhizosphere biology of ectomycorrhizal trees (Danielson 1966, Davey 1970, Aleksakhina 1972). Levisohn's studies did not clarify what if any advantage might accrue to a rhizosphere organism able to synthesize gibberellins. Some later evidence, however, indicated that a root pathogen able to synthesize these compounds in the rhizosphere might repress the development of competing root infections. Ectomycorrhizal basidiomycetes were shown to be inhibited by exogenous gibberellins *in vitro* (Santoro & Casida 1962), and it is possible that these symbionts may experience direct competition from gibberellin-secreting root pathogens in nature.

As mentioned by Harley & Smith (1983), the early literature on mycorrhizal fungi and hormones was prone to speculation; the same thing can be said about parallel literature on mycorrhizosphere organisms. Many such organisms were certainly shown to produce plant growth substances, but many of the effects attributed to this could also have been induced by other stimuli.

Effect of mycorrhizosphere organisms on root diseases

Although some pre-1985 investigators were cautious about suggestions that mycorrhizosphere organisms might influence the occurrence of feeder root diseases (e.g., Marx & Krupa 1978), there was already considerable evidence that this caution was unwarranted. Competitive interactions between saprobes and pathogens in some cases took the form of "exploitation competition" [direct competition for resources in the rhizosphere (Wicklow 1981)], while in other cases, "interference competition" (e.g., competition mediated by antibiotic-production or mycoparasitism) occurred. Root pathogens might encounter both mycoparasitic fungi and mycolytic bacteria in the rhizosphere (Mangenot & Diem 1979).

Perhaps the first investigators to assay the pathogen-inhibiting capabilities of organisms from the ectomycorrhizal symbiorhizosphere were Abraamova *et al*. (1953). These authors found that the rhizospheres of various ectomycorrhizal trees did not differ significantly from non-rhizosphere soils in their content of microorganisms able to inhibit potential fungal pathogens. Inhibition was measured *in vitro* in agar culture – a method already subjected to much criticism (see Zogg 1951, Bowen 1980). Also, the fungal pathogens investigated were of agricultural origin, and may not have represented tree root pathogens adequately.

Vörös (1954) investigated the abilities of soil bacteria, actinomycetes, and molds to inhibit pine root pathogens in the genus *Fusarium*. Only one *Bacillus* strain and an actinomycete possessed significant inhibitory ability *in vitro*, and only the *Bacillus* was able to exert significant inhibition in greenhouse trials. It did not, however, eliminate disease entirely. A similar, earlier study by Krasil'nikov & Raznitsina (1946) had also shown that pine damping-off could be reduced by bacterial inoculations.

Sizova & Itakayeva (1956) showed that numerous *Penicillium* spp. obtained from the rhizosphere of birch were able to inhibit disease-producing bacteria *in vitro*. Putrefactive bacterial pathogens, e.g. *Bacillus carotovora* Jones [long classified in *Erwinia*; currently *Pectobacterium carotovorum* (Jones) Waldee], were inhibited by a large proportion of the investigated fungal strains. *Bacillus tumefaciens* Smith & Townsend [= *Agrobacterium tumefaciens* (Smith & Townsend) Conn] was inhibited by fewer strains, and the saprobe *B. coli* Migula [= *Escherichia coli* (Migula) Castellani & Chalmers] was inhibited by still fewer. Fewer fungi antagonistic to these bacteria were found in the rhizospheres of mature trees than in the rhizospheres of young trees. The significance of these results may reside entirely in analogy, since none of the bacteria tested are significant pathogens of birch. Apparently, these bacteria were used as test organisms simply because they were regarded as representative bacterial plant pathogens or suitable control non-pathogens.

A similar study conducted by Sizova & Vasin (1961) established that oak rhizospheres contained considerably more fungi with pathogen-inhibiting capabilities than non-rhizosphere control soils did. These results, then, were contrary to those of Abraamova *et al*. (1953). The pathogens used as test isolates in this study were *Fusarium sporotrichiella* Bilai (= *F. sporotrichioides* Sherb.), *Erwinia* (*Pectobacterium*) *carotovora* (Jones) Holland, and *E. aroideae* (Townsend) Bergey *et al*. (= *P. carotovorum*). Of the rhizosphere isolates found to possess antibiotic ability active against one or more of these pathogens, 78.7 % were *Penicillium* spp. Trees under ten years of age had greater numbers of antibiotic-producing rhizosphere associates than older trees had.

In a later study from the same group of researchers, Enikeyeva *et al*. (1972) found that 77 % of isolates from the rhizosphere of pine were antagonistic to one or more wood-decay or wood-staining fungi. Pathogens, like *Fomitopsis annosa* (Fr.) P. Karsten (= *Heterobasidion annosum*) were inhibited by large numbers of rhizosphere fungi, while saprobes tended to have few antagonists. The most powerful antagonistic rhizosphere fungi were members of the genera *Penicillium* and *Trichoderma*. The authors proposed that the presence of these fungi in the rhizosphere formed a sort of natural barrier to infection by wood-decaying pathogens.

Vasiliauskas & Kazhemekene (1977) found that this natural barrier was much attenuated in the vicinity of pines growing in former agricultural soil. Only pines growing in forests with a well-formed humus layer had a full complement of associated soil organisms antagonistic to *H. annosum*. Pathogenesis by *H. annosum*, as might be expected, was a particular problem in afforested, formerly-agricultural land. Severe problems with *H. annosum* on such lands had previously been noted by other researchers, e.g., Orlos & Dominik (1960).

Vaartaja *et al*. (1961) and Vaartaja & Salisbury (1965) found that saprobic microorganisms isolated from forest nurseries and from tree rhizospheres were able to inhibit various damping-off pathogens *in vitro*. Particularly strong antagonists included *Streptomyces* spp., certain bacteria, *Penicillium* spp., and *Trichoderma viride*. Of the potential damping-off pathogens, *Fusarium* and *Cylindrocarpon* spp. tended to be rather insensitive to antagonistic organisms, while many *Pythium*, *Phytophthora*, and *Rhizoctonia* spp. were relatively sensitive. The saprobic microorganisms of nursery soils were unable to prevent damping-off, but tended to reduce seedling mortality to levels far below those found in axenic, *in vitro* damping-off trials.

The activity of rhizosphere and other soil organisms against oomycetous root pathogens was further investigated by various Australian researchers (Malajczuk & McComb 1979, Malajczuk 1979, Keast & Tonkin 1983). Malajczuk & McComb (1979) and Malajczuk (1979) suggested that correlations existed between the microbiotas of various soils and the activity of *Phytophthora cinnamomi* in those soils. Malajczuk (1979) also suggested that the specific populations of microorganisms associated with mantles of different mycorrhizal types might exert specific suppressive activities. According to Malajczuk & McComb (1979), eucalypt rhizospheres in soils suppressive to *P. cinnamomi* contained more Actinomycetes, fungi, and bacteria in general than did rhizospheres in conducive soils. Malajczuk (1979) found that bacteria and actinomycetes were present in far greater numbers in mycorrhizospheres than in the rhizospheres of non-mycorrhizal roots, and proposed that this quantitative effect might also adversely affect the pathogen. Keast & Tonkin (1983) found that *Pinus radiata* rhizospheres contained relatively high numbers of actinomycetes inhibitory to *P. cinnamomi* and related species. They thought this association might partially explain the high tolerance of *P. radiata* to *Phytophthora*-infested soils.

The root-invading *Heterobasidion annosum* [*s. lat.*, now known to be a species-complex with the true *H. annosum* mainly associated with pines (Korhonen et al. 1998)] has been the subject of various studies involving antagonistic rhizosphere and soil organisms. Some of these have been mentioned above (Enikeyeva *et al*. 1972, Vasiliauskas & Kazhemekene 1977). Rhizosphere and mycorrhizosphere fungi antagonistic to *H. annosum* were also investigated by Kowalski (1974a), Bücking (1976), and Johansson & Marklund (1980). Kowalski (1974a) and Bücking (1976) found that *Cephalosporium* (probably = *Acremonium*, *Lecanicillium*, *Simplicillium* or *Pochonia*) spp. were very strong antagonists of *H. annosum*, and were commonly isolated from mycorrhizal roots. Other demonstrated antagonists of *H. annosum* included *Scopulariopsis* spp. (Bücking 1976), *Penicillium* and *Trichoderma* spp. (Kowalski 1974a, Johannson & Marklund 1980), *Paecilomyces* and *Verticillium* (ss. lato) spp. (Johansson & Marklund 1980), plus *Gliocladium fimbriata* J.C. Gilman & E.V. Abbott [= *Myrothecium verrucaria* (Albertini & Schw. : Fr.) Ditmar] and *Absidia orchidis* (Vuill.) Hagem (= *A. coerulea*) (Kowalski 1974a). Johansson & Marklund (1980) found that antagonists to *Heterobasidion* were generally more numerous in the rhizosphere of pine and alder than in control soils. They also found that trees growing in naturally regenerated forests on former pasture land had as many or more associated antagonists as trees in long-established forest soils. These results appear to contrast with those of Vasiliauskas & Kazhemekene (1977), but it is not clear

that the latter authors' formerly-agricultural land can be compared with the pastures examined by Johansson & Marklund (1980). If the pastures had previously been forest land, some elements of the forest microbiota are likely to have remained *in situ* (see Wilde 1954).

Johansson & Marklund (1980) isolated a very high number of actinomycetes antagonistic to *H. annosum* from rhizospheres. Alder rhizospheres were particularly rich in these organisms. The authors suggested that the well-known suppressive effect of alder on *H. annosum* inoculum in soils (Mikola 1956) might be due to this stimulation of actinomycetes. Mikola (1966) had previously found that many actinomycetes isolated from alder actinorrhizal nodules were antagonistic to *H. annosum*.

The inhibitory effect of alder on *H. annosum* and other root pathogens was further examined by Hutchins (1980). This author isolated a highly antagonistic *Bacillus* sp. from soil under *Alnus rubra* in Oregon, U.S.A. Besides inhibiting *H. annosum in vitro*, the bacterium also inhibited the pathogens *Phellinus weirii* (Murr.) Gilb., *Armillariella mellea* (*ss. lato*), and *Phytophthora cinnamomi*. The significance of this antagonism in nature was not determined.

The effect of soil, rhizosphere and mycorrhizosphere fungal populations on the facultative root pathogen *Cylindrocarpon destructans* was studied by Kowalski (1980d, 1982). This author observed that there was a strong correlation between antagonism shown *in vitro* by fungal populations isolated from disease-suppressive or -conducive sites and the actual degree of suppressiveness found within the sites. Particularly important antagonistic fungi included *Mortierella parvispora*, *Penicillium spinulosum*, *Trichoderma album* Preuss (= *T. polysporum*), and *T. lignorum* (probably = *T. viride* in this case). Even within an individual species, however, the degree of antagonism often varied from site to site.

Given the well-known shortcomings of testing antagonism in paired agar culture (Zogg 1951, Bowen 1980), a strong correlation between on-site suppressiveness and *in vitro* antagonism may seem purely fortuitous. However, the *in vitro* analytic method designed by Mańka (1968, 1974) appears to have been relatively dependable in terms of correspondence with field results, and gave useful results when employed with *H. annosum* (Kowalski 1974a), *C. destructans* (Kowalski 1980d, 1982), and *M. r. atrovirens* α (Mańka *et al*. 1968a, b). Other successful studies using this technique are recorded by Mańka (1974). The employment of various other *in vitro* assays of antagonism was defended by Johansson & Marklund (1980).

Apart from inhibiting mycelial growth, antagonists of a given pathogen may also act by inhibiting or otherwise disrupting spore germination. Johansson & Marklund (1980) showed that both fungi and actinomycetes antagonistic to *H. annosum in vitro* often caused an inhibition of *H. annosum* conidial germination on root surfaces. In fungi, the ability of individual strains to inhibit conidial germination appeared to be correlated with general antagonism towards *H. annosum*. In actinomycetes, no such correlation was found, and the existence of a separate germination-inhibiting mechanism was proposed. Strzelczyk *et al*. (1984) found that the culture metabolites of a small number of microorganisms isolated from silver-fir rhizospheres and mycorrhizospheres were capable of suppressing the germination of *C. destructans* conidia. In forest nurseries, Agnihotri & Vaartaja (1967b), Vaartaja & Agnihotri (1967) and Vaartaja (1974) found that toxins produced by unspecified soil organisms were capable of inhibiting germination of *Pythium* spp. sporangia.

Inhibition is not the only means by which spores of pathogens may be rendered inactive. Schisler & Linderman (1984) found that the near-absence of *Fusarium* spp. in many forest soils could be ascribed in part to an unusual stimulation of macroconidial germination in those soils. Macroconidia, which usually germinate sparingly and thus maintain a constant soil inoculum, germinated in relatively high numbers and formed a high proportion of abnormal chlamydospores under the influence of forest soils. Although a biotic factor appeared to be involved in the abnormal stimulation, the agents responsible were not detected.

Mycorrhizosphere organisms were also found to facilitate root diseases in some cases. These organisms were found, for example, to stimulate the production of oogonial resting stages in Peronosporalean pathogens (Vaartaja & Salisbury 1965, Brasier 1975). They were also found to stimulate production of sporangia in this group of oomycetes (Marx & Haasis 1965, Marx & Davey 1969a, b, Marx & Bryan 1970, Ayers & Zentmeyer 1971). According to Marx & Bryan (1970), bacterial metabolites in moist soils tend to inhibit mycelial growth and to induce zoosporogenesis in *Phytophthora cinnamomi*. Zoospores are less tolerant of antibiotics produced by mycorrhizal fungi than are hyphae, making zoospore-inducing soil conditions potentially relatively favourable for the loblolly pine roots. In somewhat drier conditions, mycelial growth of *P. cinnamomi* is favoured and relatively severe, mycelium-derived root infections occur. The mycelium-inhibiting, sporangium-inducing bacteria show a rhizosphere effect: that is, they are most common in the root zone of pine.

The genesis of root-invading rhizomorphs in members of the *Armillaria mellea* species complex appeared to be favoured by some members of *M. r. atrovirens* as broadly defined by Mańka (1960). This

effect, however, was shown by a minority of *M. r. atrovirens* strains, and an inhibition of *A. mellea* was shown by some others. The effects of other soil microorganisms on the formation of rhizomorphs by *A. mellea* were poorly known at the time this study was done.

Katznelson & Henderson (1962) showed that many soil fungi, including numerous taxa known from mycorrhizospheres, attracted the saprobic nematode *Rhabditis oxycerca* de Man. Of 56 fungal taxa tested by these authors, only "*Mortierella* sp." and "*Thielaviopsis* sp." actually repelled the nematodes. Twenty of the test fungi attracted them. It is likely that pathogenic nematodes (both plant pathogens and mycorrhiza pathogens) are also adapted to respond to the biochemical stimuli produced within the rhizosphere by indigenous microorganisms.

Finally, some studies found that the proliferation of pathogen-inhibiting microorganisms within the mycorrhizosphere might be forestalled by other elements of the microbiota. Beneficial organisms inhibitory to disease fungi may themselves be inhibited by rhizosphere fungi and bacteria. Johansson & Marklund (1980) tested some of these "mutual effects" of potentially-beneficial, disease-inhibiting organisms. They found, for example, that an *Aphanocladium* species (probably now a *Lecanicillium*, most likely *L. aphanocladii*) inhibitory to *H. annosum* also repressed conidium formation by *Paecilomyces* sp. The same *Paecilomyces* sp. was also an inhibitor of *H. annosum*.

The above results left little doubt that rhizosphere and mycorrhizosphere organisms were important in mediating the severity of pathogenic attacks on roots. It was clear that the microbial populations obtained from any given habitat must be understood in terms of the full range of their mutual antagonisms and synergies. It appeared that trees and their mycorrhizal partners had both evolved means of favouring pathogen-inhibiting organisms in the root zone. Also, since many virulent root pathogens were known to have little competitive saprobic ability (Garrett 1970), the very existence of a rhizosphere effect around roots itself suggested a curtailment of pathogenesis. Foster & Marks (1967) and Malajczuk (1979) both suggested that the extra stimulation of saprobes that sometimes occurs in the mycorrhizosphere may augment this disease-inhibiting effect.

Effect of mycorrhiza formation on populations of saprobes in the rhizosphere

Many of the pre-1985 studies that best attested to a regulatory effect of ectomycorrhizal fungi on the rhizosphere addressed the inhibition of pathogens by mycorrhizae or mycobionts. These studies, however, were thoroughly reviewed by Marx (1973) and Marx & Krupa (1978). Given that the studies in question don't involve mycorrhizosphere organisms except insofar as the pathogens themselves can be placed in this category, they will not be discussed here. Also, in many studies where the production of antibiotics by mycorrhizal fungi was assessed, some non-phytopathogenic organisms were used as testers. Most of these testers were non-rhizosphere saprobes, including such standard test organisms as *E. coli*.

It was clear in some studies, however, that the *in vitro* effect of ectomycorrhizal fungi on rhizosphere saprobes could be profound. Vaartaja & Salisbury (1965) rated their two ectomycorrhizal test organisms, *Suillus granulatus* and *Russula* sp., as among the species "usually exhibiting strong antagonism" towards other root-associated microorganisms. Marx (1969) found that the diatretyne-synthesizing mycorrhizal species *Leucopaxillus cerealis* var. *piceina* (Peck) H.E. Bigelow was strongly bacteriostatic *in vitro*, and acted against a wide range of bacterial types. Five other mycorrhizal test species were not bacteriostatic. *Leucopaxillus cerealis* var. *piceina* was also much more inhibitory towards pathogenic fungi than were the other mycorrhizal test species. A potent antibiotic produced by *Cenococcum geophilum* was shown to act against a wide range of saprobic bacteria (Krywolap & Casida 1964, Krywolap *et al*. 1964, Neal *et al*. 1968). This substance had little influence on the growth of fungi. On the other hand, a *Lactarius* species isolated by Park (1970) produced substances strongly inhibitory to many non-pathogenic soil fungi, including members of the genera *Mortierella* (*ss. lato*) and *Penicillium*.

The antibiotic effects registered with mycorrhizal fungi *in vitro* can generally be ascribed to the production of soluble metabolites. The production of inhibitory volatiles is also known (Krupa & Fries 1971). In addition, mycorrhizal infection may stimulate by as much as 40-fold the production of terpene and sesquiterpene volatiles by host roots (Krupa & Nylund 1972, Krupa *et al*. 1973). Some of these substances proved to be strongly inhibitory to fungal root pathogens (Krupa & Nylund 1972, Krupa *et al*. 1973). Their activity against rhizosphere saprobes was not examined, but a significant effect on root-associated populations would be expected.

A major means by which mycorrhizal infections were shown to regulate saprobic rhizosphere populations was by inducing the production of phenolics in host plants. Such a stimulation was shown to be instrumental in the repression by *Laccaria laccata* of *Fusarium oxysporum* root infections in Douglas-fir seedlings (Sylvia & Sinclair 1983). Electron microscopic studies of mycorrhizae often showed pronounced accumulations of tannins within the mantle (Foster & Marks 1967, Malajczuk 1979, see also plate II in Strullu & Gourret 1973). These compounds had been

found to inhibit many microbial enzymes (Williams 1963, Lewis & Starkey 1968) and thus to have a strong effect on microbial populations. Even mycorrhizal fungi were found to show some adverse reactions to the tannin-rich outer cortical cells of infected roots (Foster & Marks 1967), but they were apparently able to tolerate the compounds. The possession of extracellular oxidase enzymes by many of these fungi (Miller *et al*. 1983; Hutchison 1990a) appeared to be instrumental in maintaining this tolerance.

The effect of these tannins on mycorrhizosphere populations received little attention. Foster & Marks (1967), however, showed that no bacteria were detectable in the tannin layer of the mantle formed by a "type Ff mycorrhiza" of *Pinus radiata*. Just outside this layer, in a region of loosely-woven, "felt-like" hyphae, bacteria were abundant. Peklo (1909) showed that tannin-rich extracts of older mycorrhizae essentially served as a selective medium for *Penicillium* spp. In the experiments of Sylvia & Sinclair (1983), the number of *F. oxysporum* hyphae in root cortical sections of Douglas-fir was inversely proportional to the amount of osmiophilic (primarily polyphenolic) material detectable in the sections.

Additional circumstantial evidence for a partial inhibition of rhizosphere microorganisms by mycorrhiza-induced tannins could be seen in the experiments of Bokor (1958, 1959). This author found that the addition of powdered tannins to forest nursery soils increased the efficacy of artificial mycorrhizal inoculation of pines. He postulated that the tannins protected mycorrhizal inoculum from bacterial attack. It appeared possible that the tannins observed by Foster & Marks (1967) and Malajczuk (1979) in the inner mycorrhizal mantle protected the mantle hyphae against bacterial and fungal degradation. In electron microscopic studies, outer mantle hyphae were frequently found in a lysed condition (Foster & Marks 1967, Strullu & Gourret 1973); this lysis may have been carried out at least in part by specialized mycolytic bacteria and fungi.

The induction of root polyphenols was known in some cases to be stimulated by microorganisms other than mycorrhizal fungi (Sylvia & Sinclair 1983). Piché *et al*. (1981) suggested that phenolic compounds are also produced spontaneously by short roots of pine. As Sylvia & Sinclair (1983) pointed out, however, the growth pouch system these authors used was not sterile, and probably permitted induction of phenolics by saprobic microorganisms. In overview, it was seen that mycorrhizal fungi were not the only organisms able to induce polyphenol production in host plants, but they possessed the unique ability to cause an accumulation of polyphenolics near the root surface.

It has long been clear that the general stimulation of saprobic microbial growth often found adjacent to ectomycorrhizal roots (see the above section *Are fungal populations quantitatively stimulated by ectomycorrhizae or ectomycorrhizal root systems?*) must be brought about in part by the presence of mycobiont metabolites in the rhizosphere. By 1985, at least one mycorrhizosphere bacterium was known to be stimulated by mycobiont metabolites and not by plant root exudates (Rambelli 1970, Rambelli *et al*. 1972, Rambelli 1973). Various other means were known by which mycorrhiza formation might affect rhizosphere populations: briefly, they included the occlusion of the rhizoplane and absorption of root exudates by the mantle (Manteifel *et al*. 1950), and the production by mycobionts of various compounds, including plant hormones (Ulrich 1960, Slankis 1973, Pachlewski & Pachlewska 1974, Kampert & Strzelczyk 1978, Graham & Linderman 1979, Ng *et al*. 1982, Harley & Smith 1983, Strzelczyk & Pokojska-Burdziej 1984), oxalates (Graustein *et al*. 1977, Knutson *et al*. 1980), amino acids and common sugars such as glucose (Smith 1969, Agnihotri & Vaartaja 1967a, Bowen & Theodorou 1973, Malajczuk & McComb 1977), characteristic fungal sugars and sugar alcohols such as trehalose and mannitol (Lewis & Harley 1965, Wedding & Harley 1976), metal ion chelators (Szaniszlo *et al*. 1981), and various fungal phenolics such as variegatic acid (Tomaszewski & Wojceichowska 1973). Also, formation of ectomycorrhizae was known to profoundly affect the types and quantities of materials secreted by the plant (Lewis & Harley 1965, Harley & Smith 1983). However, the effect of these individual factors on mycorrhizosphere organisms and populations had generally received very little study.

Disseminated effect of mycorrhizal fungi on soil microbial populations

Some ectomycorrhizal fungi and related root-infecting Basidiomycetes were shown to be able to suppress microbial activity in an extended region of soil. As mentioned above, these fungi include *Tuber melanosporum* (Chalvignac *et al*. 1959) and *Tricholoma matsutake* (Ohara & Hamada 1967). In general, the fungi noted for their suppressive attributes are also renowned for their strong odours. The production of volatiles (e.g., see Ohta 1983) may contribute to a broad-ranging effect on the soil microbiota. An extensive production of hydrophobic compounds has also been implicated in the suppressive effect of *T. matsutake* (Ogawa 1976a).

More generally, however, there is evidence that all or most mycorrhizal fungi exert some suppressive effects on soil organisms. Romell (1939) was the first person to notice this phenomenon. At the time, he was attempting to determine if mycorrhizal fungi could fruit in forest soils when the roots they were associated with were severed from the host plant body.

Fruiting of these fungi was therefore monitored in test plots delimited by deep trenches. No mycobiont basidiomes were formed within the plots, but a strong stimulation of herbaceous plant growth was regularly observed. Romell attributed this stimulation to: 1) the "green-manuring" effect of the decomposing, severed roots, and 2) a release of the plots from mycorrhizal competition for mineral nutrients. He suggested that the continuous supply of carbon from host roots ordinarily gave mycorrhizal fungi a strong advantage as competitors for mineral nutrients in soil and litter. Since these fungi were unable to break down the components of litter themselves, and since they tended to remove the soluble minerals required by litter-decay organisms, they caused a general repression of litter decay. Trenching relieved this suppression.

Romell's observations were later confirmed by Gadgil & Gadgil (1971, 1975). These authors found that in *Pinus radiata* stands, trenching caused a reduction of litter accumulation, an increase in soil moisture, and a reduced development of mycelial mats in the litter. Nutrient content and pH of the soil did not appear to be altered. In a laboratory experiment Gadgil & Gadgil (1975) found that mycorrhizal *P. radiata* roots suppressed litter decomposition in unsterile soil. Non-mycorrhizal roots did not have a suppressive effect. Since soil moisture content and pH were not affected in the experiments, the authors concluded that mycorrhizal competition for nutrients might be involved in a suppression of litter-decay fungi. Unfortunately, the experiment was not well-controlled: litter-decay microbes in the mycorrhizal treatment were introduced in forest litter, while only pure cultures of selected litter-decay fungi were added to the non-mycorrhizal control. It is therefore possible that litter decomposition in the mycorrhizal treatment was actually suppressed by antagonistic saprobes, not by the mycorrhizal fungi themselves.

The suppression of soil populations in pine forests was studied in plantations of different age by Vasiliauskas & Kazhemekene (1977). These authors showed that formerly-agricultural soils newly planted with pine possessed large populations of soil microbes. Plantations of increasing age harboured increasingly smaller microbial populations. The apparent suppression was much more evident in bacterial and actinomycetous populations than in fungal populations. One consequence of this suppression was that the number of soil microorganisms antagonistic to the root pathogen *Fomes annosus* (= *Heterobasidion annosum*) was drastically reduced, reaching a minimum in 12–36-yr-old plantations. Established forest soils, unlike formerly agricultural soils, tended to have a substantial humus layer containing microorganisms inhibitory to *H. annosum*. Even this layer, however, was not as microbially active as the humus layers of non-forest soils were. Vasiliauskas & Kazhemekene (1977) did not suggest a mechanism for the suppression of microbial populations in pine forests. Clearly, however, their results are congruous with those obtained by Romell (1939) and Gadgil & Gadgil (1971, 1975).

As mentioned previously, a repressive effect of ectomycorrhizal fungi on soil saprobic activity was also proposed by Bokor (1956). This author believed the effect to be due to unspecified "vital functions of mycorrhizal fungi." He showed that extracts of heavily mycorrhiza-colonized soils contained substances inhibiting tree seed germination, but that this inhibition was absent where the activity of mold fungi was high. This led him to conclude that a suppression of mould growth in forest soils was responsible for an accumulation of seed-germination inhibitors. Although Bokor believed that the seed toxins he observed were "antibiotics" produced by mycorrhizal fungi, it is possible that phenolic and flavonoid toxins deriving from the litter itself were active components of his extracts (e.g., see Olsen *et al*. 1971, Lindeberg *et al*. 1980). These compounds are indeed broken down by decomposers, but may accumulate in ectomycorrhizal forests if litter decomposition is repressed.

It may seem that there is a fundamental contradiction between the prevalent idea that mycorrhizal fungi repressed microbial communities in the litter layer, and the finding (see *Are fungal populations quantitatively stimulated by ectomycorrhizae or ectomycorrhizal root systems?*) that populations of microorganisms were generally stimulated in the mycorrhizosphere. However, this was clearly a matter of scale rather than discrepancy: the mycorrhizosphere is a relatively confined habitat distinguished by the immediate presence of the tree root and the mycorrhizal mantle. Hence, mycorrhizosphere conditions need not reflect more distant soil conditions in the symbiorhizosphere. The minority of studies showing a reduction of filamentous fungal growth in the mycorrhizosphere appeared to fit well in this context. It was clearly likely that this occasional suppression was highly influenced by individual mycobionts, as the studies of Neal *et al*. (1964) suggested. It appeared that some mycobionts might be unusually efficient at removing nutrients from soils, and might create a depauperate zone even around mycorrhizal root tips themselves. The production or stimulation of antifungal and antibacterial antibiotics might only serve to augment the effect of an existing nutritional deprivation.

Mycorrhizosphere microorganisms as stimulators of mycorrhiza formation

The effects of mycorrhizosphere saprobes and other saprobic soil organisms on mycorrhizal fungi fall into two categories: synergistic effects and competitive effects. Although competition might seem to be the

more elementary of the two situations – or at least, the easier situation to research – the bulk of pre-1985 research in this area concerned synergistic interactions. A portion of the research on both types of interactions was reviewed by Slankis (1974).

Perhaps the first person to reveal a synergistic interaction between rhizosphere organisms and mycorrhizal fungi was Fries (1941, 1943). Fries found that mycorrhizal basidiospores that normally did not germinate in artificial media could be induced to germinate by a number of soil fungi. By far the most effective germination-stimulator was the yeast *Torulopsis sanguinea* (Schimon) Will [= *Rhodotorula mucilaginosa* (Jörg.) Harr.]. In subsequent studies, Fries (1977, 1978) showed that the closely related *Rhodotorula glutinis* (Fres.) Harr. was equally effective. A few other root isolates were less effective generally, but did stimulate the germination of spores of some *Suillus* species. These fungi included *M. r. atrovirens* (?α), *Trichosporium heteromorphum* Nannf. [= *Exophiala heteromorpha* (Nannf.) de Hoog & Haase], *Pythium aphanidermatum* (Edson) Fitzpatrick, and the mycobiont *Cenococcum geophilum* (Fries 1943).

There was some indication that the stimulatory effect of microorganisms might be very important in the ecology of certain mycorrhizal species. According to Fries (1980), the germination of spores of *Cantharellus cibarius* Fr. and *Lactarius* spp. in pure culture was stimulated by *Rh. glutinis* but not by pine or birch seedling roots. The stimulation of the growth of microorganisms around tree roots in nature appeared to be instrumental in bringing about germination of some mycobiont spores.

Fries (1980) stated that "nothing is known" about the mechanism of the stimulation of basidiospore germination by *Rhodotorula* spp. Fries (1976) found that spore germination of *Suillus luteus* could be stimulated by certain amino acids in the absence of a *Rhodotorula* colony, but this was not true of most other mycobiont species (Fries 1978). It appeared that such organisms as *M. r. atrovirens*, which stimulated spore germination only in certain *Suillus* spp. (Fries 1943), acted by supplying amino acids to the spores. The stimulatory action of *Rhodotorula* spp. appeared to have a different basis.

Another sort of stimulation of mycorrhizal fungi by saprobes was reported by Rayner & Levisohn (1943) and Rayner & Neilson-Jones (1944). These authors found that mycorrhiza formation by *Boletus* (= *Suillus*) *bovinus* was inhibited in British heathland soils by toxic principles in the soil. This toxicosis could be relieved by applying composts that stimulated microbial growth. Rayner and colleagues suggested that the stimulated microbes not only decomposed the toxins, but also displaced the toxin-producing heath microorganisms. With these deleterious organisms suppressed, mycorrhiza formation could take place. This hypothesis was criticised by Bjorkman (1949), who felt that the English investigators were merely fertilizing an infertile soil. Later studies, however (Handley 1963, Robinson 1972), showed that the *Calluna* heathland vegetation is very toxic towards ectomycorrhizal fungi. One or more ericoid mycobionts of the *Calluna* plants was proposed as the source of the toxins (Handley 1963, Robinson 1972). It seems likely that the composts used by Rayner and colleagues did stimulate toxin breakdown by microbes, as originally suggested.

The stimulation of mycorrhiza formation in the field by the activity of an identified rhizosphere organism was first reported by Malyshkin (1951) and Mishustin (1951). The organism found to have this effect was *Trichoderma lignorum* (probably = *T. viride* or *T. harzianum*). Malyshkin (1951) in particular was inspired to inoculate young oaks with *T. lignorum* because of the fungus's reputation as a stimulator of the growth of agricultural crops (see Fedorinchik & Vanderflaas 1954). Examination of the roots of young oaks "bacterized" with *T. lignorum* revealed unusually intense mycorrhiza formation. In subsequent experiments, Malyshkin (1952, 1955) used a "biological fertilizer" preparation consisting of *Azotobacter chroococcum*, *T. lignorum*, and *Pseudomonas* sp. This mixture improved spontaneous mycorrhiza formation (i.e., infection from inoculum indigenous to the soil of the planting site) in oak seedlings by approximately 100 % in the first growing season. This stimulation of mycorrhiza formation was significantly greater than that observed in seedlings inoculated with pure mycorrhizal cultures or mycorrhiza-containing forest soils. Malyshkin concluded that the *Trichoderma*-bacterial mixture "improved the conditions for mycorrhiza formation with seedlings in dark-chestnut soil."

Unfortunately, Malyshkin does not appear to have tested the components of his combined saprobe inoculum individually. (N. B., however, that I have not been able to access all his publications.) That this presents problems is shown by the results of Vedenyapina (1955). This researcher found that surface inoculation of acorns with *Azotobacter chroococcum* alone could increase spontaneous mycorrhiza formation by over 400 % under favourable soil conditions. Vedenyapina was, however, working in a different edaphic zone than Malyshkin was, and her results may not be fully comparable to his.

The separate components of Malyshkin's mixture were ultimately tested on pine seedlings by Mishustin & Pushkinskaya (1961) and Shemakhanova (1962). Shemakhanova (1962) found that in the field, *T. viride* alone gave the greatest stimulation of spontaneous mycorrhiza formation, followed by *A. chroococcum*

and a fluorescent *Pseudomonas* strain. Some other microorganisms substantially inhibited mycorrhizal infection. In comparison trials with oak seedlings, the *Trichoderma-Azotobacter-Pseudomonas* mixture gave better results than any of the individual components alone. Mishustin & Pushkinskaya (1961) obtained a clear stimulation of mycorrhiza formation in seedlings treated with *A. chroococcum*, with a mycolytic strain of *Pseudomonas fluorescens*, and with an organic-phosphate-liberating strain of *Bacillus megaterium* de Bary. Seedlings treated with *T. viride* showed mixed results. On the one hand, the number of mycorrhizal seedlings in the *T. viride* treatment was lower by 18 % than that found in the control. On the other hand, the overall intensity of mycorrhiza formation in the treatment was judged to be somewhat greater than in the control. The *T. viride* treatment, in the final analysis, was much less effective in stimulating mycorrhiza formation than were the bacterial treatments.

The variability found between the field studies of Shemakhanova (1962) and Mishustin & Pushkinskaya (1961) may be partly due to site differences. However, as Bowen & Rovira (1961) have pointed out, such variation is often found in experiments with growth-stimulating non-symbiotic microorganisms.

Shemakhanova (1962) also conducted a complex series of laboratory pot experiments with microbial agents in various unsterile peaty soils. The growth of pine seedlings and the formation of mycorrhizae on their roots were measured. Besides varying the type of soil studied, Shemakhanova studied the effects of the microbial agents in combination with NPK, calcium, and combined NPK-calcium fertilizers, and in combination with pure culture inocula of mycorrhizal fungi. The soil types studied all contained indigenous mycorrhizal inoculum. In pots containing only this indigenous inoculum, amendment with *A. chroococcum* often had a stimulatory effect on mycorrhiza formation. The stimulation occurred only in near-neutral soils or in acidic soils to which calcium had been added (the acid-intolerance of *Azotobacter* has been mentioned earlier in this review). Inoculation with *T. viride* generally depressed spontaneous mycorrhiza formation considerably, although the fungus had a stimulatory effect in one calcium-amended soil.

In pots where *A. chroococcum* was co-inoculated with *Suillus bovinus* or *S. luteus*, the effect of the bacterium on mycorrhiza formation was inconclusive. In near-neutral soils amended with calcium, treatment with *A. chroococcum* alone induced more mycorrhiza formation than did treatment with *Azotobacter-Suillus* combinations. Apparently the bacterial inoculation was more stimulatory to indigenous soil mycobionts than it was to the *Suillus* spp. The effect of *T. viride* co-inoculation was generally insubstantial or distinctly inhibitory, depending on the treatment. However, in approximately 10 % of the treatments in which it was applied, either alone or in combination with *Suillus* spp., *T. viride* increased mycorrhiza formation.

Despite the variability introduced by the use of microbiologically-undefined pot soils, Shemakhanova's lab experiments showed that both *A. chroococcum* and *T. viride* were able to depress mycorrhiza formation as well as to stimulate it. Indeed, *T. viride* appeared to be relatively constant in its inhibition of both mycorrhiza formation and seedling growth. The contradiction of these results by various independently conducted field studies has not been explained. In all probability, both edaphic and microbiological factors are responsible for the discrepancy. An effect due to procedural variation is also possible. As mentioned above, numerous later studies (e.g., Galaaen & Venn 1977, Schönhar 1984) confirmed the harmful effect of *T. viride* on conifer seedlings under at least some circumstances.

Katayev & Koloshina (1955) recorded a stimulation of spontaneous mycorrhiza formation on steppe oak seedlings by known phytopathogenic isolates identified as *Rhizoctonia solani*. This discovery was incidental to an experiment meant to test the pathogenic potential of *R. solani* against planted oaks. Mycorrhizae on treated and control oaks were not quantified, but were rated as abundant on treated plants and as absent or nearly-absent on control plants. The stimulus of mycorrhiza formation was also reflected in a significant stimulus of seedling growth.

After the denouement in the early 1960's of Soviet experimentation on mycorrhiza-stimulation, little other field-oriented work was done in this area in the pre-1985 period. However, some interesting *in vitro* work was done. Rambelli (1973) and Rambelli *et al*. (1972) reported isolating an oligonitrophilous bacterium that produced metabolites stimulatory to *Suillus granulatus in vitro*. This bacterium was isolated from *S. granulatus* mantles on pine, and appeared to depend on fungal exudates for much of its nutrition.

A stimulation of root surface colonization by ectomycorrhizal fungi *in vitro* was shown with certain bacteria by Bowen & Theodorou (1979). These authors found one bacterium, a *Bacillus* sp., which increased colonization of *Pinus radiata* roots by *Corticium bicolor* Peck (= *Piloderma croceum*) by over 70 %. The same bacterium also stimulated the growth of several other mycobionts, but caused a slight depression in growth of *Thelephora terrestris* Ehrhart. The bacterium, like that obtained by Rambelli *et al*. (1972), was originally isolated from a mycorrhizal mantle. When this bacterium was paired with mycobionts in artificial media, results were obtained that were inconsistent with the results obtained in the presence of tree roots.

Bowen & Theodorou (1979) also found a number of bacteria markedly inhibitory to the growth of

mycorrhizal fungi. These bacteria, and their interactions with the growth-promoting *Bacillus*, will be mentioned in the next section of this review, below.

The stimulation of mycorrhiza formation and mycobiont growth by non-symbiotic microorganisms was the subject of a variety of explanatory hypotheses. Researchers generally recognized that nitrogen-fixing or phosphate-liberating bacteria should contribute mineral nutrients to their plant associates. That optimal fertilization improves ectomycorrhiza formation has long been well established (Bjorkman 1949, Mishustin & Pushkinskaya 1961, Meyer 1974). Vedenyapina (1955) pointed out that the stimulatory effect of *A. chroococcum* on oak seedlings was significant even before mycorrhiza formation took place. The high formation of mycorrhizae frequently seen on bacterized seedlings may at least in part have been due to their better or more developmentally advanced condition.

The effect of such organisms as *T. viride*, *P. fluorescens*, and *R. solani* might also be rationalized in terms of improved tree nutrition, since all these organisms are decomposers. However, it appeared difficult to see them as being more efficient in decomposition than the indigenous soil microbiota of most sites. Various authors (Moser 1959, Meyer 1962, 1967, 1974, Haselwandter 1973) therefore argued that certain saprobes could alter plant metabolism by secreting growth substances. These substances might induce the plant to translocate sugars to the roots (support from the literature for this idea was compiled by Meyer 1974), and this in turn might facilitate mycorrhiza formation. This hypothesis was quite plausible but remained largely unsubstantiated. No known mycorrhiza-stimulating strain was shown to produce significant amounts of plant hormones.

Voznyakovskaya & Ryzhkova (1955) suggested that cellulolytic and pectolytic saprobes might contribute enzymes allowing mycorrhizal fungi to penetrate roots. They assumed that pectolysis in particular would be essential in facilitating establishment of the Hartig net between root cortical cells. A variety of boletalean cultures (e.g., *Boletus edulis* Bull., *Suillus luteus*) possessed by these authors were shown to lack the ability to degrade pectins. Later, it became known that the production of pectolytic and cellulolytic enzymes by ectomycorrhizal fungi is usually minimal or absent (Harley & Smith 1983). Despite this, ectomycorrhizae form efficiently in axenic culture, something that by 1955 was already well known (e.g., Melin 1923). Voznyakovskaya & Ryzhkova (1955) appear to have been overly influenced by reports or personal experience of failed attempts to induce mycorrhizae in soil under axenic conditions, perhaps in experiments in which fungi were paired with inappropriate hosts (in terms of species or age class) or exposed to toxins formed during sterilization procedures. Though ectomycorrhizal fungi have no need of external assistance with establishment of symbiosis in axenic culture, some endomycorrhizal fungi, according to research done a few years later, penetrate roots significantly more effectively in the presence of pectolytic bacteria than in the absence of these bacteria (Mosse 1962). The bacteria themselves do not enter the roots.

Two other hypotheses regarding stimulation of mycorrhizal fungi by microorganisms were mentioned by various authors. One was that microorganisms might assist mycorrhizal fungi by supplying vitamins and other growth factors (see Meyer 1967). Many mycorrhizal fungi are heterotrophic for some such compounds, particularly thiamin. However, Davey (1970) pointed out that it was likely that host plants were able to satisfy the thiamin requirements of these fungi in the root zone. Another hypothesis was that microorganisms might break down toxins that ordinarily inhibit mycorrhizal fungi. Many types of tree litter contain such compounds (Olsen *et al*. 1971, Schoenberger & Perry 1982). Humus may also be inhibitory to some mycobionts (Möller 1902, Alvarez *et al*. 1979). Removal of unknown toxins from artificial media by means of an activated charcoal treatment was shown to be an essential step in achieving *in vitro* germination of most mycorrhizal basidiospores (Fries 1978). No pre-1985 study directly investigated the extent to which saprobic microorganisms assist mycorrhizal fungi by breaking down toxins.

Some other possible synergisms considered by ectomycorrhizosphere researchers will be mentioned in the next section, in conjunction with relevant information about mycorrhiza-inhibiting organisms.

Mycorrhizosphere and other soil organisms as inhibitors of mycorrhiza formation

That soil microorganisms could substantially inhibit the formation of mycorrhizae was well established before 1980 (Bowen 1980). In forestry practice, these inhibitory interactions were often compensated for by fumigating soils into which mycorrhizal inoculum was to be introduced (Theodorou 1967). Very little was known about the actual agents or mechanisms of the inhibition.

Brian *et al*. (1945) attempted to determine the source of the toxicity to mycorrhizal fungi in English heathland soils (see Rayner & Neilson-Jones 1944). They found that a *Penicillium* species [identified at first as *P. jensenii* Zal. and later (Brian 1946) as *P. terlikowskii* Zal.] was abundant in the inhibitory soils and could be demonstrated to produce significant quantities of gliotoxin. (A representative gliotoxin-producing isolate deposited by P.W. Brian as CBS 379.48 is currently identified as *P. glabrum*.) This fungus and its metabolites inhibited four ectomycorrhizal species

in vitro. A native heathland ericoid mycobiont, *Phoma radicis-callunae* Rayner, was inhibited to a much lesser degree.

A competing theory to explain the heath soil toxicity was put forward by Handley (1963). This author suggested that ericoid mycorrhizal fungi themselves might produce chemicals allelopathic towards ectomycorrhizal fungi. Robinson (1972) found that toxins leached from roots of heathland *Calluna* plants inhibited a variety of mycorrhizal fungi *in vitro*. "*Mycelium radicis callunae*," an ericoid mycobiont obtained from the plants, was not significantly affected by the leachates. Robinson did not determine whether the toxic principles in the leachates derived from the plants themselves, from the ericoid fungi, or from rhizosphere microorganisms.

Levisohn (1957) found that the soil fungus *Alternaria tenuis* Nees [= *A. alternata* (Fr.) Keissler], a common species in agricultural soils, was strongly inhibitory towards three *Suillus* species and *Rhizopogon luteolus* Fr. & Nordholm *in vitro*. She suggested (with due caution) that this interaction might be the reason the same ectomycorrhizal species were difficult to introduce into forest nurseries on agricultural land. *Leccinum scabrum*, an ectomycorrhizal species that was only mildly affected by *A. alternata in vitro*, proved to be substantially more successful than other ectomycorrhizal species in the affected nurseries. Also, *M. r. atrovirens* (α) and other pseudomycorrhiza-forming species grew readily in the agricultural soils and were unaffected by *A. alternata in vitro*.

As mentioned previously, Shemakhanova (1962) determined that *Trichoderma lignorum* (probably = *T. viride*) was inhibitory towards *Suillus bovinus* and *S. luteus* under a variety of conditions in pot studies. It was also frequently inhibitory to mycorrhiza formation by unknown mycobionts contained in forest litter. This inhibitory ability in pots contrasted with the stimulatory ability often reported for *T. viride* in field studies.

Since *T. viride* was long known as a virulent facultative mycoparasite strongly pathogenic to a wide range of Basidiomycetes and other fungi (Cook & Baker 1983, Komatsu 1976), an inhibition of mycorrhizal fungi was not implausible. However, research results on the interaction between *Trichoderma* spp. and ectomycorrhizal fungi presented a complex picture. Besides the studies on mycorrhiza-stimulation mentioned in the previous section, there were other studies that illustrated this complexity. The fumigation of soils with allyl alcohol was often found to lead to an abundant development of *Trichoderma* spp. in the soil and a vigorous spontaneous formation of ectomycorrhizae on planted seedlings (Yatazawa *et al*. 1960, Laiho & Mikola 1964). Apparently, some mycorrhizal fungi were able to thrive in the presence of *Trichoderma* populations that would be lethal to many other soil fungi. In methyl bromide-fumigated soils, Danielson & Davey (1969) found that mycorrhiza formation was delayed by the fumigant but that it resumed during a period in which *Trichoderma* species were the predominant fungi in the soil. There were strong indications that the mycobiont in the fumigated soil treatment was different from that commonly found in an unfumigated treatment. Whether this selection was due to the fumigant itself or to the soil microbiota was not determined. However, Laiho & Mikola (1964) suggested that ectomycorrhizal inoculum generally grows into fumigated soil from soil layers beneath the range of penetration of the fumigant. Especially when quickly-dissipating fumigants are used, it seems likely that the recolonization of soils by mycorrhizal fungi will be determined primarily by growth rate and by compatibility with the distinctive microbiota of fumigated soils.

Moser (1963), for unstated reasons, referred to *T. viride* as an "undesirable" species in fumigated forest nursery soils. He recommended that these soils be inoculated with mycorrhizal fungi after fumigation, in order to circumvent the "danger" posed by *T. viride* and another soil mold, *Botrytis cinerea*. He also noted that mycorrhizal inocula should be cultivated under sterile conditions, since *T. viride* and other "aggressive species" were able to suppress completely the growth of such inocula. On the other hand, Moser routinely used fast-growing Penicillia, Aspergilli, and Mucorales as co-inoculants when inoculating trees with ectomycorrhizal fungi.

In an *in vitro* experiment on artificial media, Vaartaja & Salisbury (1965) showed that *T. viride* stopped the growth of *Suillus granulatus* and *Russula* sp. on contact. The species did not, however, form a zone of (antibiotic) inhibition against the mycorrhizal fungi. Such zones were strongly formed by an antagonistic bacterium, and were also elaborated by *Pythium periplocum* Drechsler, two *Penicillium* spp., a *Streptomyces* sp., and *Armillaria mellea ss. lat*. Apart from looking for lysis of hyphae, Vaartaja & Salisbury did not attempt to detect mycoparasitic interactions. Mycoparasitism by *Trichoderma* spp. often proceeds with little or no cell lysis (Komatsu 1976, Chet *et al*. 1981).

Ridge & Theodorou (1972) fumigated two forest nursery soils with methyl bromide, and observed that *Trichoderma* spp. recolonized only one of the two soils. In the same soil, an inoculation with the mycorrhizal fungus *Rhizopogon luteolus* was unsuccessful. In the *Trichoderma*-free soil, *R. luteolus* was successfully introduced. A likely confounding factor, however, is that mycelial inoculum was used in the former soil, while basidiospores were used in the latter.

Finally, Sinclair *et al*. (1982) conducted a pot study in which the ectomycorrhizal fungus *Laccaria*

laccata was inoculated into unsterile soil with and without a *Trichoderma* sp. co-inoculant. Although Douglas-fir seedlings in both treatments had formed mycorrhizae with *L. laccata* by the end of the study, the *Trichoderma*-coinoculated trees were slightly suppressed. This caused Sinclair *et al*. (1982) to speculate that *Trichoderma* sp. "retarded the growth" of *L. laccata*.

The bulk of the disparate evidence obtained in early mycorrhizosphere research indicated that *Trichoderma* spp. could be antagonistic to mycorrhizal fungi. This was strongly confirmed by the present author's own later results with *T. viride* and *Laccaria bicolor* (Maire) P.D. Orton (Summerbell 1987). It was already evident in 1985, however, that not all mycorrhizal fungi were equally affected by this interaction – at least, not in nature. Also, in unsterile soils, interactions of *Trichoderma* and mycorrhizal fungi with other microbes further complicate an already complex situation.

The other microbes in question may also have inhibitory effects on mycorrhiza formation. The inhibition of mycorrhizal symbiosis by bacteria was first noted by Sideri & Zolotun (1951). These authors, however, did not give details of their observations. Likewise Bokor (1958) did not elaborate on his observation that mycorrhizal inoculum in forest nurseries was subject to the "attack of indigenous bacteria". This author added tannin along with mycorrhizal inoculum on the theory that this substance would inhibit bacterial competitors and antagonists. The tannin did improve mycorrhiza formation to some extent (Bokor 1959), but no evidence was given that saprobic fungal competitors were not inhibited along with the bacteria. Pseudomycorrhiza-inducing fungi, at least, did not appear to be adversely affected by the treatment.

Shemakhanova (1962) attempted to determine the effect of various bacteria on mycorrhiza formation in pine seedlings in unsterile soil. Inoculations of *Azotobacter* and a fluorescent bacterium had a salutary effect, while mycorrhiza formation was much less successful in seedlings inoculated with pigmented bacteria or mycobacteria. A yeast, identified under the now completely ambiguous name *Torulopsis* sp., also did not favour mycorrhiza formation. In addition, Shemakhanova noted an antagonism *in vitro* when soil actinomycetes were grown with mycorrhizal symbionts in the genera *Suillus* and *Tricholoma*. Some actinomycete-derived antibiotics were found to depress growth of mycorrhizal fungi in pure culture and in unsterile pot soils with seedlings.

The study of mycorrhiza-inhibiting bacteria under well-controlled conditions was initiated by Bowen & Theodorou (1973). These authors found that fluorescent *Pseudomonas* spp., the most common bacterial recolonizers of fumigated Australian nursery soils (Ridge & Theodorou 1972), greatly impeded surface colonization of pine roots by *Rhizopogon luteolus in vitro*. A spore-forming bacterium used for comparison had an insignificant effect on growth of the fungus.

A second, more thorough study by the same authors (Bowen & Theodorou 1979) indicated that many *Pseudomonas* spp. were strongly inhibitory to a broad taxonomic range of ectomycorrhizal fungi. *Pseudomonas* spp. often reduced colonization of *Pinus radiata* roots by mycorrhizal fungi to less than 20 % of control levels. Some *Bacillus* spp. were equally inhibitory, including one that completely eliminated growth of *Rhizopogon vinicolor* A.H. Smith. On the other hand, one test *Bacillus* had relatively little effect on root colonization. As mentioned previously, Bowen & Theodorou also found a *Bacillus* species that significantly stimulated growth of several mycorrhizal fungi.

When an inhibitory fluorescent pseudomonad and non-inhibitory bacteria were co-inoculated with *R. luteolus*, the deleterious effect of the pseudomonad was largely eliminated. Pseudomonad populations in the test growth tubes were undiminished, however, whereas populations of non-inhibitory bacteria tended to be reduced by the pseudomonad. Bowen & Theodorou interpreted this as evidence the non-inhibitory bacteria were decomposing inhibitors elaborated by the pseudomonad. The results they observed could not be explained in terms of exploitation competition. In a supplementary study, the authors added glucose to soil in tubes containing a pine seedling, *R. luteolus*, and the fluorescent pseudomonad. This additional bacterial substrate did not result in an increase in bacterial population over control levels, but increased the suppression of *R. luteolus*. It is likely that the glucose stimulated production of inhibitory metabolites by the bacterium.

It is appropriate to note here that fluorescent pseudomonads are recognized as important natural antagonists of root-colonizing fungi (Cook & Baker 1983). They are especially noted for causing soil suppressiveness to the fungal pathogen *Gaeumannomyces graminis* (Sacc.) Arx & D.L. Olivier, cause of take-all disease of wheat (Smiley 1979).

Keast & Tonkin (1983) tested the antagonistic effect of 2 367 strains of Australian soil actinomycetes against several pathogenic *Oomycetes* and *Laccaria laccata*. Many of the strains tested were antagonistic to *L. laccata* on agar media *in vitro*. A higher percentage of strains, however, was antagonistic to *Phytophthora cinnamomi*, one of the pathogens under examination. actinomycetes isolated from the rhizosphere of *Pinus radiata* were especially likely to inhibit *P. cinnamomi* but to leave *L. laccata* unaffected. Oomycetes other than *P. cinnamomi* tended to be inhibited by numbers

of actinomycetes similar to or greater than the numbers inhibiting *L. laccata*. None were inhibited as greatly as *P. cinnamomi*. This wide gradient of inhibition caused Keast & Tonkin to conclude that the specificity of actinomycete antifungal activity was minimal for most fungi (conceived of as including *Oomycetes* in this time period). Only *P. cinnamomi* seemed to be subject to specific inhibition, and this specificity was much more evident in the pine rhizosphere than in non-rhizosphere soil. These results were readily interpretable in light of what was already known about mycorrhizosphere biology. The production of broad-spectrum antifungal antibiotics was clearly less advantageous for a mycorrhiza-associated actinomycete strain than it was for a soil actinomycete strain.

It should be noted, though, that the generation of artefactual results is difficult to exclude in *in vitro* inhibition studies. When Bowen & Theodorou (1979) tested two *Streptomyces* strains known to inhibit *P. cinnamomi* for antagonism against *Rhizopogon luteolus* and *Suillus granulatus*, the antagonistic effect of the actinomycetes was highly dependent on the constitution of the medium used. Antagonism was found only on a minority of media. Keast & Tonkin (1983) used only a single medium. However, one factor linking all pre-1985 studies on actinomycetes vs. ectomycorrhizal fungi (Shemakhanova 1962, Vaartaja & Salisbury 1965, Bowen & Theodorou 1979, Brown & Sinclair 1981, Keast & Tonkin 1983) was that some degree of antagonism was found.

Only a small amount of work was done in the pre-1985 period on effects of whole soil microbial communities against mycorrhiza formation. Theodorou (1967) compared the formation of mycorrhizae by mycelial inoculum of *Rhizopogon luteolus* in fumigated, steam-treated, and untreated soils. *Pinus radiata* seedlings formed far more mycorrhizae in the treated soils than in the untreated soil. When treated soil was reinoculated with unsterile soil prior to introducing the mycorrhizal inoculum, mycorrhiza formation was substantially curtailed. This reinoculation procedure evidently re-introduced the inhibitory agents that were present in the untreated soil.

The favourable effect of soil fumigation on mycorrhiza formation in the nursery was confirmed by Ridge & Theodorou (1972), Lamb & Richards (1978) and others. Bowen & Theodorou (1973) reported that introduction of a "general soil microflora" into sterilized soil reduced mycorrhiza formation by 20-50 %. They blamed this reduction in part on inhibitory pseudomonads.

Somewhat later, Brown & Sinclair (1981) showed that *Laccaria laccata* was highly tolerant of the prokaryotic microbiota of forest nursery soils. These authors examined colonization of Douglas-fir roots by *L. laccata* in sterile soil and in soil reinoculated with a mixture of actinomycetes, fluorescent pseudomonads, and other bacteria. These organisms were isolated from rhizospheres of Douglas-fir seedlings grown in nursery soils. Four fluorescent pseudomonads and one actinomycete were shown to inhibit *L. laccata* in agar media. The microorganisms noticeably diminished root colonization by *L. laccata* in microscopic examinations. Nonetheless, they only delayed penetration of roots by *L. laccata* for three days at the most. Mycorrhiza formation was not substantially altered. This tolerance of *L. laccata* to many soil microorganisms appeared to partially explain its high degree of usefulness as a mycorrhizal inoculant of unsterile container-grown nursery stock (Molina 1982).

Garbaye (1983) studied colonization of *Fagus silvatica* roots by *Hebeloma crustuliniforme* in two edaphically different soils in France. Fumigated and unfumigated soil treatments were prepared in pots in the laboratory. The two soils gave strikingly different results when mycorrhiza formation was examined. In one, fumigation strongly increased mycorrhiza formation by *H. crustuliniforme*. Apparently, the microbiota of the unfumigated soil was strongly inhibitory to the mycorrhizal fungus. In the second soil, on the other hand, fumigation increased mycorrhiza formation to a much lesser degree. Indeed, during the first weeks of the study, mycorrhiza formation was actually stronger in the unfumigated pots. It would seem, then, the indigenous microbiota of the second soil was favourable or only slightly inhibitory towards *H. crustuliniforme*. The author concluded that "the soil microflora is not always the main obstacle to mycorrhizal infection."

Several pre-1985 reports documented increased mycorrhiza formation by a variety of mycorrhizal fungi in the presence of fungicides (Powell *et al*. 1968, Hong 1976, Pawuk *et al*. 1980, Marx & Rowan 1981). The now-discontinued fungicide benomyl, which at appropriate concentrations was well known as a a selective inhibitor of most ascomycetous fungi (Bollen & Fuchs 1970, Edgington *et al*. 1971), was reported to have this effect. Pawuk *et al*. (1980) found that this fungicide increased mycorrhiza formation by both *Pisolithus tinctorius* and *Thelephora terrestris* on *Pinus palustris* Mill. seedlings in the nursery. Marx & Rowan (1981) obtained similar results with *P. tinctorius* on *Pinus taeda*. Since the harmful effect of benomyl on bacteria was known to be minimal (Kao & Ko 1983), it appeared likely that the fungicide acted mainly against soil Ascomycetes. It did not stimulate mycorrhizal fungi in axenic culture; in fact, some mycorrhizal fungi such as members of the *Russulales* were later shown to be inhibited at concentrations over 3 ppm (Hutchison 1990b). At least some mycorrhizal species were also known, early on in the period in which benomyl was used, to be inhibited by it in the field

(Bakshi & Dobriyal 1970, Hong 1976). Nonetheless, the beneficial effect of benomyl on mycorrhiza formation by *P. tinctorius* and *T. terrestris* was clear and was probably due to a relief of competition from Ascomycetous soil organisms. Later *in vitro* studies by De la Bastide & Kendrick (1990) showed that benomyl significantly improved mycorrhiza formation by *Laccaria bicolor* in growth pouches, while inhibiting growth of concurrently inoculated *Mycelium radicis atrovirens* (α).

Later, Danielson *et al*. (1984) showed that a number of fungi that formed mycorrhizae with *Pinus contorta in vitro* were unable to colonize unsterile container-grown *P. contorta* seedlings. Some mycorrhizal fungi had long been known not to associate with seedlings except under axenic conditions, and the age-dependent physiological status of the tree was thought to have some bearing on this (Mason *et al*. 1983). Clearly a fungus adapted to mature trees would be at a strong disadvantage in a microbially complex situation where only young seedlings were available as partners. It is likely that the microbiota can out-compete many mycobionts, especially those specialized for mature tree root systems, for the limited nutrient resources made available by seedlings.

Such information on microbial communities vs. mycorrhizae made it possible to evaluate the question of why inhibitory organisms such as *Trichoderma* spp. should sometimes cause a stimulation of mycorrhiza formation *in vivo*. Clearly, such organisms could simply be more inhibitory to mycorrhiza-antagonists than they were to mycorrhizal fungi themselves. *Trichoderma* spp. are not only facultatively mycoparasitic (Dennis & Webster 1971c), but also produce both soluble (Bilai 1963, Dennis & Webster 1971a) and volatile (Bilai 1956, Dennis & Webster 1971b) antifungal antibiotics. Bacteria were shown to be inhibited by both soluble (Khasanov 1962) and volatile (Bilai 1956, 1963) *Trichoderma* metabolites. Pseudomonads, including fluorescent types, were very sensitive to *Trichoderma* volatiles (Dimovich 1960). On the other hand, as mentioned earlier, at least some mycorrhizal fungi seemed able to tolerate high levels of *Trichoderma* inoculum in soil (Yatazawa *et al*. 1960, Laiho & Mikola 1964). It was suggested that fungi in the genus *Trichoderma* might inhibit the pseudomonads and other soil organisms that generally repress mycorrhiza formation in unsterile soils. Their ability to induce a net stimulation of mycorrhiza formation was thought probably contingent upon: 1) the presence of soil conditions optimizing the production of antibiotics and deployment of mycoparasitic abilities, and 2) the presence of a *Trichoderma*-resistant mycorrhizal inoculum. Here it is interesting to note that the favourable effect of *Trichoderma* on mycorrhiza formation has generally been observed in forest-steppe soils, which tend to be near neutral in pH (Manteifel *et al*. 1950). The mycoparasitic capabilities of *Trichoderma* spp. are often accentuated in acidic soils (Aytoun 1953).

Making a complex situation even more complex was the fact that *Pseudomonas* spp. with known antifungal properties could sometimes be more stimulatory to mycorrhiza formation *in vivo* than were *Trichoderma* spp. (Mishustin & Pushkinskaya 1961). Once again, these organisms might have been more effective against competing mycorrhiza-inhibitors than they were against the indigenous mycorrhizal inoculum of certain soils. The antagonistic activity of *Pseudomonas* spp. against various fungi in the root zone was already well known (e.g., Smiley 1979). *Pseudomonas* spp. also appear to inhibit the growth of some other bacteria in contact with pine roots (Bowen & Theodorou 1979). Although some pseudomonads seemed to be generally inhibitory to mycorrhizal fungi, others exercised a more selective inhibition of these fungi (Bowen & Theodorou 1979).

In general, experience tended to show that most means of reducing the number of competitors with mycorrhizal fungi in soil also served to facilitate mycorrhiza formation. Both fumigants and fungicides were shown to be effective in this regard. It was clear that, given correct conditions, there is no reason why "biological control" agents should not be equally effective.

It should be remembered that the physiological responses of the host to various microorganisms also play a part in the complex interactions in the rhizosphere. Sylvia & Sinclair (1983) showed that *Laccaria laccata*, *Trichoderma harzianum*, and *Pseudomonas cepacia* all stimulated the production of phenolic compounds by *Pseudotsuga menziesii*. These substances permitted root invasion by *L. laccata*, but severely curtailed invasion by the parasite *Fusarium oxysporum*. The production of such compounds, which selectively favour compatible mycobionts, appeared to be a major mechanism by which host plants facilitated root colonization by their fungal partners. Bokor (1958, 1959) stated that even exogenous polyphenolic substances may aid in mycorrhiza formation. Aggressive soil organisms like *Trichoderma* spp. and pseudomonads might facilitate mycorrhiza formation simply by inducing the production of phenolics by roots.

Conclusions

The situations described above exemplify the complexity pre-1985 researchers were obliged to deal with as they attempted to make sense of the interactions of plants, ectomycorrhizal fungi, pathogenic microorganisms, and soil saprobes. As is typical of ecological systems, all components of the

association were seen to respond to the influence of other components and in turn to influence them. The soil also could be seen to mediate the interactions of plants and microbes, and in turn was altered through their activity. The high level of complexity entailed by all these interactions and potential interactions, not to mention the enormous number of potentially participating species worldwide, was naturally only fractionally discovered and documented by the efforts of the pre-1985 pioneers in the field of ectomycorrhizosphere biology. A great deal of work, even fundamental work, was left for later investigators armed with more powerful and convenient techniques. That is not to say that this field is expected to provide smooth scientific sailing from now on. It is likely, for example, that the genetic complexity of fungi as eukaryotes, with many enzymatic programs that can be turned on and off and thus many ecological roles that can potentially be assumed, entails that even energetic genomic studies will not immediately lead to understanding of the diversity of interactions in which species and individual isolates can become involved. Putting this organismal complexity together with environmental complexity, it becomes clear that only when sophisticated bioinformatic systems for information handling are added to biological and chemical data will truly predictive patterns, at least as reliable as those generated by the weather service, start to emerge. It is because this area of study is so complex, however, that it remains very important to let as little as possible of the first 82 years' worth of work slip unnecessarily into obscurity. Inattention to what has already been done will surely lead to redundant study, and there is quite enough work that needs to be done without repeating the past, except for purposes of needed scientific verification and technical updating. (And speaking of verification, don't forget to deposit vouchers! Far too many organism identifications from pre-1985 papers are unnecessarily unverifiable or, in cases of taxonomic ambiguity or possible error, effectively lost to science.)

It is to be hoped that advances in techniques and information handling will lead to tremendous progress in ectomycorrhizosphere research, with the pre-1985 work serving as a solid basis for further study. Ultimately, it is expected that this field of study will yield techniques that will benefit silviculture, forest conservation, urban afforestation and the harvesting and other enjoyment of ectomycorrhizal mushrooms and gasteromycetes.

REFERENCES

Abraamova OP, Gavrilitsa GB, Sveshnikova MA (1953). Various regularities in the distribution of antagonistic fungi inside and outside the rhizosphere of trees in the Moscow area and in Crimea. [Nekotorye zakonomernosti rasprostraneniya gribov antagonistov v rizosfere i vne rizosfery derev'yev Podmoskov'ya i Kryma.] *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* **58**: 83–88.

Agerer R (1987–1998). *Colour Atlas of Ectomycorrhizae*. 1st-11th installment. Einhorn-Verlag, Schwäbisch Gmünd, Germany.

Agnihotri VP, Vaartaja O (1967a). Root exudates from red pine seedlings and their effects on *Pythium ultimum*. *Canadian Journal of Botany* **45**: 1031–1040.

Agnihotri VP, Vaartaja O (1967b). Effects of amendments, soil moisture contents, and temperatures on germination of *Pythium* sporangia under the influence of soil mycostasis. *Phytopathology* **57**: 1116–1120.

Akhromeiko AI, Shestakhova VA (1958). A study on the role of microorganisms in the uptake and release of phosphorus and sulfur by the seedlings of oak, ash, and maple. [Izuchenie roli mikroorganiszmov v pogloshchenii i vydelenii fosfora i sery seyantsami duba, yasenya i klena]. *Mikrobiologiya* **27**: 67–74.

Aleksakhina TI (1972). Soil algae in the rhizosphere of the dominant plants of forest biogeocoenoses. *Soviet Journal of Ecology* **3**: 32–37.

Alvarez IF, Rowney DL, Cobb FW Jr (1979). Mycorrhizae and growth of white fir seedlings in mineral soil with and without organic layers in a California forest. *Canadian Journal of Forest Research* **9**: 311–315.

Andersen TF, Stalpers JA (1993). A check-list of *Rhizoctonia* epithets. *Mycotaxon* **51**: 437–457.

Ayers WA, Zentmeyer GA (1971). Effect of soil solution and two soil pseudomonads on sporangium production by *Phytophthora cinnamomi*. *Phytopathology* **61**: 1188–1193.

Aytoun RSC (1953). The genus *Trichoderma*: its relationship with *Armillaria mellea* (Vahl. ex Fr.) Quel. and *Polyporus schweinitzii* Fr., together with preliminary observations on its ecology in woodland soils. *Transactions and Proceedings of the Botanical Society of Edinburgh* **36**: 99–114.

Azcón R, Barea JM, Hayman DS (1976) Utilisation of rock phosphate in alkaline soils by plants inoculated with mycorrhizal fungi and phosphate solubilizing bacteria. *Soil Biology and Biochemistry* **8**: 135–138

Bakshi BK, Dobriyal ND (1970). Effect of fungicides to control damping-off on development of mycorrhizae. *Indian Forestry* **96**: 701–703.

Balandreau J, Knowles R (1978). The rhizosphere. In: *Interactions between non-pathogenic soil micro-organisms and plants.* (Dommergues YR Krupa SV, eds). Elsevier Press, Amsterdam, the Netherlands: 243–268.

Barea JM, Azcón-Aguilar C (1983). Mycorrhizas and their significance in nodulating nitrogen-fixing plants. *Advances in Agronomy* **36**:1–54.

Bartholdy BA, Berreck M, Haselwandter K (2001). Hydroxamate siderophore synthesis by *Phialocephala*

fortinii, a typical dark septate fungal root endophyte. *Biometals* **14**: 33–42 .

Baxter DV, Middleton JT (1961). Geofungi in forest successions following retreat of the Alaskan glaciers. In: *Recent Advances in Botany. Vol. 2*. (Bailey DL, ed.). University of Toronto Press, Toronto, Canada: 1514–1517.

Bedr Chan TA (1923). About the mycorrhizae of beech [Über die Mycorhiza der Buche.] *Allgemeine Forst- und Jagd-Zeitung* **99**: 25–31.

Berestetskii OA, Borovkov AB (1977). Phytotoxic metabolites of soil penicillia. [Fitotoksicheskie metabolity pochvennykh penitsilliev.] *Mikrobiologicheskii Zhurnal (Kiev)* **41**: 291–302.

Bhatt GC (1970). Soil microfungi of white cedar forests in Ontario. *Canadian Journal of Botany* **48**: 333–339.

Bilai VI (1955). Symbiotrophic properties of *Fusarium* species and other soil fungi. In: *Mycotrophy in plants*. (Imshenetskii AA, ed.). Israel Program for Scientific Translations, Jerusalem, 1967: 129–141.

Bilai VI (1956). Volatile antibiotics in fungi of the genus *Trichoderma* Pers. [Letuchie antibiotiki u gribov roda *Trichoderma* Pers.] *Mikrobiologiya* **25**: 458–465.

Bilai VI (1963). *Antibiotic-producing microscopic fungi*. Elsevier Publ. Co., Amsterdam, the Netherlands.

Birraux D, Fries N (1981). Germination of *Thelephora terrestris* basidiospores. *Canadian Journal of Botany* **59**: 2062–2064.

Bjorkman E (1949). The ecological significance of the ectotrophic mycorrhizal association in forest trees. *Svensk Botanisk Tidskrift* **43**: 223–262.

Blaschke H (1980). Studies on fine roots and on biotic activities in the rhizosphere of *Abies alba* stands affected by fir dieback. [Feinwurzeluntersuchungen und biotische Aktivitäten in der Rhizosphäre vom Tannensterben befallener *Abies alba*-Bestände.] *European Journal of Forest Pathology* **10**: 181–185.

Blaschke H (1981). Symptoms and etiology of silver fir dieback. II. Mycorrhizal status and pathogenic processes in the rhizospheres of fine roots in relation to fir dieback symptoms. [Schadbild und Ätiologie des Tannensterbens. II. Mykorrhizastatus und pathogene Vorgänge im Feinwurzelbereich als Symptome des Tannensterbens.] *European Journal of Forest Pathology* **11**: 375–379.

Blaschke H (1982). Symptoms and etiology of silver fir dieback. III. Occurrence of a *Phytophthora* infection in fine roots of silver fir (*Abies alba* Mill.) [Schadbild und Ätiologie des Tannensterbens. III. Das Vorkommen einer *Phytophthora*-Fäule an Feinwurzeln der Weißtanne (*Abies alba* Mill.)]. *European Journal of Forest Pathology* **12**: 232–238.

Bloomberg WJ (1966). The occurrence of endophytic fungi in Douglas-fir seedlings and seed. *Canadian Journal of Botany* **44**: 413–420.

Bloomberg WJ, Sutherland JR (1971). Phenology and fungus-nematode relations of corky root disease of Douglas-fir. *Annals of Applied Biology* **69**: 265–276.

Bokor R (1956). Influence of antibiotics produced by mycorrhizal fungi on the germination of seeds. [A mykorrhiza-gombák által termelt antibiotikumok hatása egyes fenyőfelek magjának csírázására]. *Erdészeti Kutatások* **1956**: 67–79.

Bokor R (1958). Investigations on the determination of true mycorrhizal fungi of oaks and on the possibility of associating them artificially with mycorrhizae. [Vizsgálatok a tölgyek valódi mykorrhiza-gombáinak meghatározása és az ezekkel való társulásuknak mesterséges letrehozása terén]. *Erdészettudományi Közlemények* **1958**: 93–118.

Bokor R (1959). Artificial transplantation of mycorrhizae to the roots of Scots and Austrian pine in pure (complex) cultures containing several species of fungi. [Csemeték mesterséges mykorrhizálása terén többgombás (komplex) tiszta tenyészetekkel]. *Erdészeti Kutatások* **1959**: 355–388.

Bollen GJ, Fuchs A (1970). On the specificity of the *in vitro* and *in vivo* antifungal activity of benomyl. *Netherlands Journal of Plant Pathology* **76**: 299–312.

Bowen GD (1980). Misconceptions, concepts and approaches in rhizosphere biology. In: *Contemporary microbial ecology*. (Ellwood DC, Hedger JN, Latham MJ, Lynch JM, Slater JH, eds) Academic Press, New York, U.S.A: 283–304.

Bowen GD, Rovira AD (1961). The effects of microorganisms on plant growth. I. Development of roots and root hairs in sand and agar. *Plant and Soil* **15**: 166–188.

Bowen GD, Theodorou C (1967). Studies on phosphate uptake by mycorrhizae. XIV IUFRO-Kongress. München, Section **24**: 116–138.

Bowen GD, Theodorou C (1973). Growth of ectomycorrhizal fungi around seeds and roots. In: *Ectomycorrhizae. Their ecology and physiology*. (Marks GC, Kozlowski TT, eds). Academic Press, New York. U.S.A.: 107–150.

Bowen GD, Theodorou C (1979). Interactions between bacteria and ectomycorrhizal fungi. *Soil Biology and Biochemistry* **11**: 119–126.

Brasier CM (1975). Stimulation of sex organ formation in *Phytophthora* by antagonistic species of *Trichoderma*. I. The effect *in vitro*. *New Phytologist* **74**: 183–194.

Brian PW (1946). Production of gliotoxin by *Penicillium terlikowskii* Zal. *Transactions of the British Mycological Society* **29**: 211–218.

Brian PW, Hemming HG, McGowan JC (1945). Origin of a toxicity to mycorrhizae in Wareham Heath soil. *Nature* **155**: 637–638.

Broadbent P, Baker KF, Franks N, Holland J (1977). Effect of *Bacillus* spp. on increased growth of seedlings in steamed and in nontreated soil. *Phytopathology* **67**: 1027–1034.

Brown AC, Sinclair WA (1981). Colonization and infection of primary roots of Douglas-fir seedlings by the ectomycorrhizal fungus *Laccaria laccata*. *Forest Science* **27**: 111–124.

Bücking E (1976). Antagonists of *Fomes annosus*, the agent of butt rot, in the root zone of spruce (*Picea abies*). [Antagonisten gegen den Rotfäule-Erreger *Fomes annosus* aus dem Wurzelbereich der Fichte (*Picea abies*)]. *Mitteilungen des Vereins für Forstliche Standortskunde und Forstpflanzenzüchtung* **25**: 69–72.

Chalvignac MA, Tysset C, Pochon J (1959). Effect of the truffle (*Tuber melanosporum*) on the soil microflora [Action de la truffe (*Tuber melanosporum*) sur la microflore tellurique.] *Annales de l'Institut Pasteur* **96**: 355–358.

Chastukhin VYa, Nikolayevskaya MA (1962). Microflora of decomposing root residues and of the rhizosphere of oak [Mikroflora razlagayushchikhsya kornevykh ostatkov i rizosfery duba]. *Vestnik Leningradskogo Universiteta. Seriya 3. Biologiya* **1962 (2)**: 43–53.

Chet I, Harman GE, Baker R (1981). *Trichoderma hamatum*: its hyphal interactions with *Rhizoctonia solani* and *Pythium* spp. *Microbial Ecology* **7**: 29–38.

Cook RJ, Baker KF (1983). *The nature and practice of biological control of plant pathogens*. American Phytopathological Society, St. Paul, Minnesota, U.S.A.

Crafts CB, Miller CO (1974). Detection and identification of cytokinins produced by mycorrhizal fungi. *Plant Physiology* **54**: 586–588.

Currah RS, Tsuneda A (1993). Vegetative and reproductive morphology of *Phialocephala fortinii* (Hyphomycetes, *Mycelium radicis atrovirens*) in culture. *Transactions of Mycological Society of Japan* **34**: 345– 356.

Dangerfield JA, Westlake DW, Cook FD (1978). Characterization of the bacterial flora associated with root systems of *Pinus contorta* var. *latifolia*. *Canadian Journal of Microbiology* **24**: 1520–1525.

Danielson RM (1966). *The effect of soil fumigation on seedling growth, mycorrhizae, and the associated microflora of loblolly pine (Pinus taeda L.) roots*. M. S. Thesis, North Carolina State Univ., Raleigh, U.S.A. Original not seen. Cited by Davey (1970).

Danielson RM, Davey CB (1969). Microbial recolonization of a fumigated nursery soil. *Forest Science* **15**: 368–380.

Danielson RM, Visser S, Parkinson D (1984). The effectiveness of mycelial slurries of mycorrhizal fungi for the inoculation of container-grown jack pine seedlings. *Canadian Journal of Forest Research* **14**: 140–142.

Davey CB (1970). Nonpathogenic organisms associated with mycorrhizae. In: *Mycorrhizae*. (Hacskaylo E, ed.) US Dept. of Agriculture, Forest Service, Washington, DC, U.S.A.: 114– 121.

De la Bastide PY, Kendrick B (1990). The *in vitro* effects of benomyl on disease tolerance, ectomycorrhiza formation, and growth of white pine (*Pinus strobus*) seedlings. *Canadian Journal of Botany* **68**: 444–448.

De Laval J, Remacle J (1969). A microbiological study of the rhizosphere of poplar. *Plant and Soil* **31**: 31–47.

Dennis C, Webster J (1971a). Antagonistic properties of species-groups of *Trichoderma*. I. The production of non-volatile antibiotics. *Transactions of the British Mycological Society* **57**: 25–39.

Dennis C, Webster J (1971b). Antagonistic properties of species-groups of *Trichoderma*. II. Production of volatile antibiotics. *Transactions of the British Mycological Society* **57**: 41–48.

Dennis C, Webster J (1971c). Antagonistic properties of species-groups of *Trichoderma*. III. Hyphal interaction. *Transactions of the British Mycological Society* **57**: 363–369.

Dighton J (1983). Phosphatase production by mycorrhizal fungi. *Plant and Soil* **71**: 455–462.

Dimovich VO (1960). Effect of volatile antibiotics from various cultures of *Trichoderma* species on phytopathogenic fungi and bacteria. [Diya letkykh antibiotikiv riznykh kul'tur vydiv *Trichoderma* na fitopatogenni bakterii i gryby]. *Mikrobiologicheskii Zhurnal (Kiev)* **22**: 32–38.

Doak KD (1934). Cortical parasitism of conifer seedling roots in pure culture by mycorrhizal and non-mycorrhizal fungi. *Phytopathology* **24**: 6 (Abstract).

Doak KD (1955). Pine root reaction in sterile culture to mycorrhizal and other fungi. *American Midland Naturalist* **54**: 443–451.

Dominik T (1956). Proposal for a new classification of ectotrophic mycorrhizae based on morphological and anatomical characters. [Projekt nowego podziału mikoryz ektotrofycznych oparty na cechach morfologiczno-anatomicznych]. *Roczniki Nauk Leśnych* **14**: 223–246.

Domsch KH (1963). The influence of saprophytic soil fungi on the early development of higher plants. [Der Einfluss saprophytischer Bodenpilze auf die Jugendentwicklung höherer Pflanzen]. *Zeitschrift für Pflanzenkrankheiten Pflanzenpathologie und Pflanzenschutz* **70**: 470–475.

Domsch KH, Gams W, Anderson T-H (1980). *Compendium of soil fungi*. Academic Press, New York, U.S.A.

Durrell LW (1968). Hyphal invasion by *Trichoderma viride*. *Mycopathologia et Mycologia Applicata* **35**: 138–144.

Edgington LV, Khew KL, Barron GL (1971). Fungitoxic spectrum of benzimidazole compounds. *Phytopathology* **61**: 42–44.

Elad Y, Chet I, Katan J (1980). *Trichoderma harzianum*: A biocontrol agent effective against *Sclerotium rolfsii* and *Rhizoctonia solani*. *Phytopathology* **70**:119–121.

Enikeyeva MG, Rudneva VL, Sizova TP (1970). On the mycoflora of different types of pine forests. Species composition and prevalence of species. [O mikoflore sosnyakov raznykh tipov. 1.Vidovoi sostav i predstavlennost' vidov]. *Vestnik Moskovskogo Universiteta, Seriya 6, Biologiya, Pochvovodenie* **1970 (3)**: 100–103.

Enikeyeva MG, Rudneva VL, Sizova TP (1972). On the mycoflora of different types of pine forests. 3. Antibiotic properties of the fungi. [O mikoflore sosnyakov raznykh tipov. 3. Antibioticheskie svoistva gribov]. *Vestnik Moskovskogo Universiteta, Seriya 6, Biologiya, Pochvovodenie* **1972 (3)**: 39–44.

Fasolo Bonfante P, Fontana A, Montacchini F (1971). Studies on the ecology of *Tuber melanosporum*. I. Demonstration of a phytotoxic effect. [Studi sull'ecologia del *Tuber melanosporum*. I. Dimostrazione di un effeto fitotossico]. *Allionia* **17**: 47–54.

Fedorinchik NS, Vanderflaas LK (1954). Effect of the antibiotic activity of the soil fungus *Trichoderma lignorum* Harz. on increase in yield of agricultural crops. [Vliyanie antagonisticheskoi aktivnosti pochvennogo griba *Trichoderma lignorum* Harz. na povyshenie urozhaya sel'skokhozyaistvennykh kul'tur]. *Trudy Vsesoyuznogo Instituta Zashchity Rastenii* **5**: 17–37.

Fontana A, Luppi Mosca AM (1966). Saprophytic fungi isolated from ectomycorrhizae. [Funghi saprofiti isolati da ectomicorrize.] *Allionia* **12**: 38–46.

Foster RC, Marks GC (1967). Observations on the mycorrhizas of forest trees. II. The rhizosphere of *Pinus radiata* D. Don. *Australian Journal of Biological Sciences* **20**: 915–926.

Frank B (1885). On the root-symbiosis-based nutrition

of certain trees via underground fungi. [Über die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze]. *Berichte der Deutschen Botanischen Gesellschaft* **3**: 128–145.

Fries N (1941). On spore germination in some *Gasteromycetes* and mycorrhiza-forming *Hymenomycetes* [Über die Sporenkeimung bei einigen Gasteromyceten und mykorrhizabildenen Hymenomyceten]. *Archiv für Mikrobiologie* **12**: 266–284.

Fries N (1943). Studies on spore germination and mycelial development in soil-inhabiting *Hymenomycetes*. [Untersuchungen über Sporenkeimung und Mycelentwicklung bodenbewohnender Hymenomyceten]. *Symbolae Botanicae Upsalienses* **6 (4)**: 1–81.

Fries N (1976). Spore germination in *Boletus* induced by amino acids. *Proceedings Koningklijke Nederlandse Akademie van Wetenschappen, C* **79**: 142–146

Fries N (1977). Germination of *Laccaria laccata* spores *in vitro*. *Mycologia* **69**: 848–850.

Fries N (1978). Basidiospore germination in some mycorrhiza-forming *Hymenomycetes*. *Transactions of the British Mycological Society* **70**: 319–324.

Fries N (1980). Effects of plant roots and growing mycelia on basidiospore germination in mycorrhiza-forming fungi. In: *Arctic and alpine mycology* (Laursen GA, Ammirati JF, eds). University of Washington Press, Seattle, Washington, U.S.A.: 493–511.

Fuchs J (1911). On the connection of *Agaricaceae* and other humus-inhabiting fungi to mycorrhiza formation in forest trees. [Über die Beziehungen von Agariceen und anderen humusbewohnenden Pilzen zur Mycorhizenbildung der Waldbäume]. *Bibliotheca Botanica* **76**: 1–32.

Gadgil RL, Gadgil PD (1971). Mycorrhiza and litter decomposition. *Nature (London)* **233**: 133.

Gadgil RL, Gadgil PD (1975). Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *New Zealand Journal of Forest Science* **5**: 33–41.

Galaaen R, Venn K (1979). *Pythium sylvaticum* Campbell & Hendrix and other fungi associated with root dieback of 2-0 seedlings of *Picea abies* (L.) Karst. in Norway. *Meddelelser fra Norsk Institutt for Skogforskning* **34**: 265–280.

Gams W (1963). *Mycelium radicis atrovirens* in forest soils, isolation from soil microhabitats and identification. In: *Soil organisms* (Docksen J, van der Drift J, eds). North-Holland Publ., the Netherlands: 176–182.

Gams W (1971). *Cephalosporium-like filamentous fungi (Hyphomycetes).* [*Cephalosporium-artige Schimmelpilze (Hyphomycetes)*]. Gustav Fischer Verlag, Stuttgart, Germany.

Garbaye J (1983). Initial results of studies on the competitiveness of ectomycorrhizal fungi. [Premiers résultats de récherches sur la competitivité des champignons ectomycorhiziens]. *Plant and Soil* **71**: 303–308.

Garbaye J (1994). Helper bacteria – a new dimension to the mycorrhizal symbiosis. *New Phytologist* **128**: 197–210.

Garrett SD (1951). Ecological groups of soil fungi: a survey of substrate relationships. *New Phytologist* **50**: 149–166.

Garrett SD (1970). *Pathogenic root-infecting fungi*. Cambridge University Press, London U.K. and New York, U.S.A.

Graham JH, Linderman RG (1979). Ethylene production by mycorrhizal fungi and *Fusarium oxysporum* ssp. *pini in vitro* and by aseptically synthesized mycorrhizal and *Fusarium*-infected roots of Douglas-fir. Proc. 4th NACOM, Fort Collins, Colorado, U.S.A.: 61.

Graham JH, Linderman RG (1981). Effect of ethylene on root growth, ectomycorrhiza formation, and *Fusarium* infection of Douglas-fir. *Canadian Journal of Botany* **59**: 149–155.

Graustein WC, Cromack K Jr, Sollins P. (1977). Calcium oxalate: occurrence in soils and effect on nutrient and geochemical cycles. *Science* **198**: 1252–1254.

Greenwood AJ, Lewis DH (1977). Phosphatases and the utilisation of inositol hexaphosphate by soil yeasts of the genus *Cryptococcus*. *Soil Biology and Biochemistry* **9**: 161–166.

Grünig CR, Sieber TN, Holdenrieder O (2001). Characterization of dark septate endophytic fungi (DSE) using inter-simple-sequence-repeat-anchored polymerase chain reaction (ISSR-PCR) amplification. *Mycological Research* **105**: 24–32.

Grünig CR, Sieber TN, Rogers SO, Holdenrieder O (2002). Genetic variability among strains of *Phialocephala fortinii* and phylogenetic analysis of the genus *Phialocephala* based on rDNA ITS sequence comparisons. *Canadian Journal of Botany* **80**: 1239–1249.

Grünig CR, Sieber TN (2005). Molecular and phenotypic description of the widespread root symbiont *Acephala applanata* gen. et sp. nov., formerly known as dark-septate endophyte Type 1. *Mycologia* **97**: 628–640.

Grünig CR, McDonald BA, Sieber TN, Rogers SO, Holdenrieder O (2004). Evidence for subdivision of the root-endophyte *Phialocephala fortinii* into cryptic species and recombination within species. *Fungal Genetics and Biology* **41**: 676–687

Hagem O (1910). Studies on Norwegian *Mucorales*. II. [Untersuchungen über Norwegische Mucorineen. II.] *Videnskabs-Selskabets Skrifter, I. Matematisk-Naturvidenskabelig Klasse* **1910 (4)**: 1–152.

Hambleton S, Sigler L (2005). *Meliniomyces*, a new anamorph genus for root-associated fungi with phylogenetic affinities to *Rhizoscyphus ericae* (≡ *Hymenoscyphus ericae*), *Leotiomycetes*. *Studies in Mycology* **53**: 1-27.

Handley WRC (1963). Mycorrhizal associations and *Calluna* heathland afforestation. *Forestry Commission Bulletin (London)* **36**: 1–70.

Hanso M (1981). Review of forest pathology papers in the main USSR journals in 1978. *European Journal of Forest Pathology* **11**: 315–325.

Harley JL (1939). Beech mycorrhiza: re-isolation and the effect of root extracts upon *Mycelium radicis fagi* (Chan). *New Phytologist* **38**: 352–363.

Harley JL (1948). Mycorrhiza and soil ecology. *Biological Reviews* **23**: 127–158.

Harley JL, Smith SE (1983). *Mycorrhizal symbiosis*. Academic Press, New York, U.S.A.

Harley JL, Waid JS (1955a). A method of studying active mycelia on living roots and other surfaces in the soil. *Transactions of the British Mycological Society* **38**: 104–118.

Harley JL, Waid JS (1955b). The effect of light upon the

roots of beech and its surface population. *Plant and Soil* **7**: 96–111.

Haselwandter K (1973). Indole hormone relations between rhizosphere microorganisms and a mycorrhizal fungus from *Pinus cembra* L. [Indol-/wuchs-/stoffbeziehungen zwischen Mikroorganismen aus der Rhizosphäre und einem Mykorrhizapilz von *Pinus cembra* L.]. *Archiv für Mikrobiologie* **94**: 259.

Hatch AB (1934). A jet-black mycelium forming ectotrophic mycorrhizae. *Svensk Botanisk Tidskrift* **28**: 371–383.

Hong LT (1976). Mycorrhizal short root development on *Pinus caribaea* seedlings after fungicide treatment. *Malaysian Forestry* **39**: 147–156.

Horak E (1963). Studies on hormone synthesis by mycorrhizal fungi. [Untersuchungen zur Wuchsstoffsynthese der Mykorrhizapilze]. In: *Mykorrhiza*. (Rawald W, Lyr H, eds). Gustav Fischer Verlag, Jena, Germany: 147–163.

How JE (1942). The mycorrhizal relations of larch. II. Mycorrhiza formation in nature. *Annals of Botany (London)*, N. S. **6**: 103–129.

Hubbard JP, Hannan GE, Hadar Y (1983). Effect of soilborne *Pseudomonas* spp. on the biological control agent, *Trichoderma hamatum*, on pea seeds. *Phytopathology* **73**: 655–659.

Hutchins, AS (1980). *In vitro* inhibition of root-rot pathogens *Phellinus weirii*, *Armillariella mellea*, *Fomes annosus*, and *Phytophthora cinnamomi* by a newly isolated *Bacillus* sp. *Microbial Ecology* **6**: 253–259.

Hutchison LJ (1990a). Studies on the systematics of ectomycorrhizal fungi in axenic culture. 3. Patterns of phenol oxidase activity. *Mycologia* **82**: 424–435.

Hutchison LJ (1990b). Studies on the systematics of ectomycorrhizal basidiomycetes in axenic culture. 4. The effect of some selected fungitoxic compounds upon linear growth. *Canadian Journal of Botany* **68**: 2172–2178.

Ivarson KC, Katznelson H (1960). Studies on the rhizosphere microflora of yellow birch seedlings. *Plant and Soil* **12**: 30–40.

Jahn E (1934). The peritrophic mycorrhiza. [Die peritrophe Mykorrhiza]. *Berichte der Deutschen Botanischen Gesellschaft* **52**: 463–474.

Jahn E (1936). The peritrophic mycorrhiza. 2. On the physiology and biology of the accompanying fungi. [Die peritrophe Mykorrhiza. 2. Zur Physiologie und Biologie der Begleitpilze]. *Berichte der Deutschen Botanischen Gesellschaft* **53**: 847–856.

Johann F (1932). Studies on Mucorales of forest soils. [Untersuchungen über Mucorineen des Waldbodens]. *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten, II Abteilung* **85**: 305–338.

Johansson M, Marklund E (1980). Antagonists of *Fomes annosus* in the rhizosphere of grey alder (*Alnus incana*) and Norway spruce (*Picea abies*). *European Journal of Forest Pathology* **10**: 385–395.

Jumpponen A (2001). Dark septate endophytes – are they mycorrhizal? *Mycorrhiza* **11**: 207–211.

Jumpponen A, Trappe JM (1998). Dark septate endophytes: a review of facultative biotrophic root colonizing fungi. *New Phytologist* **140**: 295–310.

Kampert M, Strzelczyk E (1975a). Synthesis of auxins by fungi isolated from the roots of pine seedlings (*Pinus sylvestris* L.) and from soil. *Acta Microbiologica Polonica, Series B* **4**: 223–230.

Kampert M, Strzelczyk E (1975b). Influence of soil microorganisms on growth of pine seedlings (*Pinus sylvestris* L.) and microbial colonization of the roots of these seedlings. *Polish Journal of Soil Science* **8**: 59–66.

Kampert M, Strzelczyk E (1978). Production of cytokinins by mycorrhizal fungi of pine (*Pinus sylvestris* L.). *Bulletin de l'Academie Polonaise de Sciences, Série des Sciences Biologiques* **26**: 499–503.

Kampert M, Strzelczyk E, Pokojska A (1975a). Production of auxins by bacteria isolated from the roots of pine seedlings (*Pinus sylvestris* L.). *Acta Microbiologica Polonica, Series B* **7**: 135–143.

Kampert M, Strzelczyk E, Pokojska A (1975b). Production of gibberellin-like substances by bacteria and fungi isolated from the roots of pine seedlings (*Pinus sylvestris* L.). *Acta Microbiologica Polonica, Series B* **7**: 157–166.

Kao CW, Ko WH (1983). Nature of suppression of *Pythium splendens* in a pasture soil in South Kohala, Hawaii, U.S.A. *Phytopathology* **73**: 1284 –1289.

Karimbayeva LYa, Sizova TP (1976). On the mycoflora of certain forest trees. [O mikoflore rizosfery nekotorykh drevesnykh porod] *Vestnik Moskovskogo Universiteta, Seriya 6, Biologiya, Pochvovedenie* **1976 (5)**: 24–29.

Karimbayeva LYa, Sizova TP (1977). Effects of root exudates of pine and spruce seedlings on developing mycoflora of the rhizospheres of these tree species. [Vliyanie kornevykh vydelenii prorostkov sosny i eli na formirovanie mikoflory rizosfery etikh porod]. *Mikologiya i Fitopatologiya* **11**: 191–199.

Karimbayeva LYa, Sizova TP (1978). Effects of some amino and organic acids on fungal growth in the rhizosphere of pines. II. [Vliyanie nekotorykh aminokislot i organicheskikh kislot na rost gribov iz rizosfery sosny. II.] *Mikologiya i Fitopatologiya* **12**: 120–123.

Katayev IA, Koloshina LM (1955). *Rhizoctonia solani* Kühn. as a stimulator of the growth of petiolate-oak seedlings and of the formation of mycorrhizae on their roots. [*Rhizoctonia solani* Kühn. kak stimulyator rosta seyantsev duba chereshchatogo i obrazovaniya mikorizy na ikh kornyakh]. *Mikrobiologiya* **24**: 700–704.

Kattner D (1992). Influence of drought stress on the colonization of fine roots of Norway spruce (*Picea abies* Karst.) by *Trichoderma viride* and other endogenous microfungi. *Forstwissenschaftliches Centralblatt* **111**: 383–389.

Katznelson H, Bose B (1959). Metabolic activity and phosphate-dissolving capability of bacterial isolates from wheat roots, rhizosphere and non-rhizosphere soil. *Canadian Journal of Microbiology* **5**: 79–85.

Katznelson H, Henderson VE (1962). Studies on the relationships between nematodes and other soil microorganisms. I. The influence of actinomycetes and fungi on *Rhabditis* (*Cephaloboides*) *oxycerca* de Man. *Canadian Journal of Microbiology* **8**: 875–882.

Katznelson H, Rouatt JW, Peterson EA. (1962). The rhizosphere effect of mycorrhizal and non-mycorrhizal roots of yellow birch seedlings. *Canadian Journal of Botany* **40**: 377–382.

Keast D, Tonkin C (1983). Antifungal activity of Western

Australian soil Actinomycetes against *Phytophthora* and *Pythium* species, and against a mycorrhizal fungus, *Laccaria laccata*. *Australian Journal of Biological Science* **36**: 191–203.

Khasanov OKh (1962). The antibiotic properties of fungi in the genus *Trichoderma* Pers. found in the swamp soil of Uzbekistan. [Antibioticheskie svoistva gribov roda *Trichoderma* Pers., vydelennykh iz lugovo-bolotnykh pochv Uzbekistana]. *Akademiya Nauk Uzbekskoi SSR, Uzbekskii Biologicheskii Zhurnal* **6**: 62–67.

Kilbertus G, Kiffer E, Proth J (1978). The influence of asymbiotic roots and of mycorrhizae of *Picea abies* (L.) Karst. on the soil microflora. [Influence des racines asymbiotiques et des mycorhizes de *Picea abies* (L.) Karst. sur la microflore tellurique]. *Revue d'Écologie et de Biologie du Sol* **15**: 297–310.

Kloepper JW, Leong J, Teintze M, Schroth MN (1980). Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. *Nature (London)* **286**: 885–886.

Knutson DM, Hutchins AS, Cromack K Jr (1980). The association of calcium oxalate-using *Streptomyces* with conifer mycorrhizae. *Antonie van Leeuwenhoek* **46**: 611–619.

Komatsu M 1976. Studies on *Hypocrea*, *Trichoderma*, and allied fungi antagonistic to shiitake, *Lentinus edodes* (Berk.) Sing. *Report of the Tottori Mycological Institute* **13**: 1–113. (In Japanese).

Korhonen K, Capretti P, Karjalainen R, Stenlid J (1998). Distribution of *Heterobasidion annosum* intersterility groups in Europe. In (Woodward S, Stenlid J, Karjalainen R, Hüttermann A, eds) Heterobasidion annosum: *Biology, ecology, impact and control*. CAB International, Egham, U.K.: 43–70.

Kowalski S (1970). Mycorrhizal synthesis of *Pinus sylvestris* L. and *Fomes annosus* (Fr.) Cke. *Bulletin de l'Academie Polonaise de Sciences, Série des Sciences Biologiques* **18**: 405–408.

Kowalski S (1973). Mycorrhiza forming properties of various strains of the fungus *Mycelium radicis atrovirens* Melin. *Bulletin de l'Academie Polonaise de Sciences, Série des Sciences Biologiques* **21**: 767–770.

Kowalski S (1974a). The problem of root rot *Fomes annosus* (Fr.) Cke. against a background of the fungal communities in the forest soil. *Zeszyty Problemowe Postępów Nauk Rolniczych* **160**: 25–45.

Kowalski S (1974b). Fungal communities of the forest environment in selected pine stands. [Zbiorowiska grzybów leśnego środowiska glebowego wybranych drzewostanów sosnowych]. *Poznańskie Towarzystwo Przyjaciół Nauk. Wydział Nauk Rolniczych i Leśnych. Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych* **38**: 123–165.

Kowalski S (1980a). Studies on the communities of soil in selected mountain stands in southern Poland. [Badania zbiorowisk grzybów glebowych w wybranych drzewostanach górskich południowej Polski]. *Acta Mycologica* **16**: 55–87.

Kowalski S (1980b). *Cylindrocarpon destructans* (Zins.) Scholt., causative agent of mortality in fir (*Abies alba* Mill.) natural regeneration in some mountain forests in Poland. [*Cylindrocarpon destructans* (Zins.) Scholt., sprawca zamierania samosiewu jodły (*Abies alba* Mill.) w niektórych drzewostanach górskich południowej Polski]. *Acta Agraria et Silvestria, Series Silvestris* **19**: 57–73.

Kowalski S (1980c). Studies on the mycorrhizae of fir (*Abies alba* Mill.) natural regeneration in selected forests of the Carpathian and Sudety Mountains. [Badanie mikoryz samosiewu jodły (*Abies alba* Mill.) w wybranych drzewostanach w Karpatach i Sudetach]. *Acta Agraria et Silvestria, Series Silvestris* **19**: 75–94.

Kowalski S (1980d). Influence of soil fungi community in selected mountain stands on the development of *Cylindrocarpon destructans* (Zins.) Scholt. *Acta Societatis Botanicorum Poloniae* **49**: 487–492.

Kowalski S (1982). Role of mycorrhiza and soil fungi in natural regeneration of fir (*Abies alba* Mill.) in Polish Carpathians and Sudetes. *European Journal of Forest Pathology* **12**: 107–112.

Kozlova EI (1958). Microbiological characteristics of the oak rhizosphere. [Mikrobiologicheskaya kharakteristika rizosfery duba]. *Vestnik Moskovskogo Universiteta* **1**: 81–87.

Krasil'nikov NA, Raznitsina EA (1946). A bacterial method of combating fusariosis of pine-tree seedlings. [Bakterial'nyi metod bor'by s fuzariozom seyantsev sosny.] *Agrobiologiya*, **1946 (5–6)**: 109–121.

Krupa S, Fries N (1971). Studies on ectomycorrhizae of pine. I. Production of volatile organic compounds. *Canadian Journal of Botany* **49**: 1425–1431.

Krupa S, Nylund JE (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. *European Journal of Forest Pathology* **2**: 88–94.

Krupa S, Andersson J, Marx DH. (1973). Studies on ectomycorrhizae of pine. IV. Volatile organic compounds in mycorrhizal and non-mycorrhizal root systems of *Pinus echinata* Mill. *European Journal of Forest Pathology* **3**: 194–200.

Krywolap GN, Casida LE Jr (1964). An antibiotic produced by the mycorrhizal fungus *Cenococcum graniforme*. *Canadian Journal of Microbiology* **10**: 365–370.

Krywolap GN, Grand LF, Casida LE Jr (1964). The natural occurrence of an antibiotic in the mycorrhizal fungus *Cenococcum graniforme*. *Canadian Journal of Microbiology* **10**: 323– 328.

Kubíková J (1965). Mycoflora synusias on the roots of woody plants. *Rozpravy Československé akademie Věd. Řada Matematických a Přírodních Věd* **75**: 1–53.

Kucey RMN (1983). Phosphate-solubilizing bacteria and fungi in various cultivated and virgin Alberta soils. *Canadian Journal of Soil Science* **63**: 671–678.

Kunze G (1906). On acid secretion from roots and fungal hyphae and its significance. (Über Säureausschieidung bei Wurzeln und Pilzhyphen und ihre Bedeutung). *Jahrbuch für Wissenschaftliche Botanik* **42**: 357–393.

Kürbis P (1936). Mycological studies on the root zone of the ash (*Fraxinus excelsior* L.). [Mykologische Untersuchungen über den Wurzelbereich der Esche (*Fraxinus excelsior* L.)]. *Flora (Jena)* **131**: 129–175.

Laiho O, Mikola P (1964). Studies on the effect of some eradicants on mycorrhizal development in forest

nurseries. *Acta Forestalia Fennica* **77** (2): 1–33.

Lamb RJ, Richards BN (1978). Inoculation of pines with mycorrhizal fungi in natural soils. III. Effect of soil fumigation on rate of infection and response to inoculum density. *Soil Biology and Biochemistry* **10**: 273–276.

Levisohn I (1954). Aberrant root infections of pine and spruce seedlings. *New Phytologist* **53**: 284–290.

Levisohn I (1957). Antagonistic effects of *Alternaria tenuis* on certain root-fungi of forest trees. *Nature (London)* **179**: 1143–1144.

Levisohn I (1960a). Effects of *Gibberella fujikoroi* on fungal root infections of *Pinus*. *Nature (London)* **186**: 987–988.

Levisohn I (1960b). Physiological and ecological factors influencing the effects of mycorrhizal inoculation. *New Phytologist* **59**: 42–47.

Levisohn I (1963). About mycorrhizas and pseudomycorrhizas. [Über Mykorrhizen und Pseudomykorrhizen]. In: *Mykorrhiza*. (Rawald W, Lyr H, eds). Gustav Fischer Verlag, Jena, Germany: 27–34.

Lewis DH, Harley JL (1965). Carbohydrate physiology of mycorrhizal roots of beech. I. Identity of endogenous sugars and utilization of exogenous sugars. *New Phytologist* **64**: 224–237.

Lewis JA, Starkey RL (1968). Vegetable tannins, their decomposition and effects on decomposition of some organic compounds. *Soil Science* **106**: 241–247.

Libbert E, Silhengst P (1970). Interactions between plants and epiphytic bacteria regarding their auxin metabolism. 8. Transfer of carbon-14 indoleacetic acid from epiphytic bacteria to corn coleoptiles. *Physiologia Plantarum* **23**: 480–487.

Lindeberg G, Lindeberg M, Lundgren L, Popoff T, Theander O (1980). Stimulation of litter-decomposing Basidiomycetes by flavonoids. *Transactions of the British Mycological Society* **75**: 455–459.

Lindquist B (1939). Spruce mycorrhizae in light of modern research on growth substances. [Die Fichtenmykorrhiza im Lichte der modernen Wuchsstofforschung.] *Botiska Notiser* **1939**: 315–356.

Linhell D (1939). Studies on the mycorrhizae and root fungi of *Juniperus communis*. [Untersuchungen über die Mykorrhizen und die Wurzelpilze von *Juniperus communis*.]. *Symbolae Botanicae Upsalienses* **3** (3): 1–141.

Livingston WH, Blaschke H (1984). Deterioration of mycorrhizal short roots and occurrence of *Mycelium radicis atrovirens* on declining Norway spruce in Bavaria. *European Journal of Forest Pathology* **14**: 340–348.

Lohmann P (1931). Comparative studies on the determination of quantities of plant nutrient substances in soil. [Vergleichende Untersuchungen über die Bestimmung des Gehaltes von Böden an Pflanzennährstoffen]. *Botanisches Archiv. Zeitschrift für die gesamte Botanik* **31**: 489–518.

Loll MJ, Bollag JM (1983). Protein transformation in soil. *Advances in Agronomy* **36**: 351–382.

Luppi Mosca AM, Gribaldi L, Jaretti Sodano G (1970). The mycoflora of the rhizosphere in truffle beds. III. Mycological analysis of Piedmontese truffle soils. [La micoflora della rizosfera nelle tartufaie. II. Analisi micologiche di terreni tartufiferi piemontesi]. *Allionia* **16**: 115–132.

Luppi Mosca AM (1972). The mycoflora of the rhizosphere in truffle beds. III. Mycological analysis of French truffle soils. [La micoflora della rizosfera nelle tartufaie. III. Analisi micologiche di terreni tartufiferi francesi]. *Allionia* **18**: 3–40.

Luppi Mosca AM (1973). The mycoflora of the rhizosphere in truffle beds. IV. Microfungi of poplar roots mycorrhizal with *Tuber magnatum*. [La micoflora della rizosfera nelle tartufaie. IV. Microfunghi da radici di pioppo micorrizate da *Tuber magnatum*]. *Allionia* **18**: 3–40.

Luppi Mosca AM, Fontana A (1982). Micromycetes from ectomycorrhizae of *Abies alba* Mill. [Micromiceti da ectomicorrize di *Abies alba* Mill.]. *Allionia* **25**: 27–30.

Lynch JM (1972). Identification of substrates and isolation of microorganisms responsible for ethylene production in the soil. *Nature (London)* **240**: 45–46.

Lynch JM, Harper SHT (1974). Fungal growth rate and the formation of ethylene in soil. *Journal of General Microbiology* **85**: 91–96.

Malajczuk N (1979). The microflora of unsuberized roots of *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn. ex Sm. seedlings grown in soils suppressive and conducive to *Phytophthora cinnamomi* Rands. II. Mycorrhizal roots and associated microflora. *Australian Journal of Botany* **27**: 255–272.

Malajczuk N, McComb AJ (1977). Root exudates from *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn ex Sm. seedlings and their effect on *Phytophthora cinnamomi* Rands. *Australian Journal of Botany* **25**: 501–514.

Malajczuk N, McComb AJ (1979). The microflora of unsuberized roots of *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn ex Sm. seedlings grown in soil suppressive and conducive to *Phytophthora cinnamomi* Rands. I. Rhizosphere bacteria, actinomycetes, and fungi. *Australian Journal of Botany* **27**: 235–254.

Maliszewska W, Moreau R (1959). On the rhizosphere of silver fir (*Abies alba* Mill.) [Sur la rhizosphère du sapin blanc (*Abies alba* Mill.)]. *Comptes Rendus de l' Académie des Sciences* **249**: 303–305.

Malyshkin PE (1951). Influence of soil microorganisms on the growth of oak [Vliyanie pochvennykh mikroorganizmov na rost duba]. *Pochvovedenie* **5**: 280–288.

Malyshkin PE (1952). Acceleration of growth of oak under the influence of soil microorganisms. [Uskorenie rosta duba pod vliyaniem pochvennykh mikroorganismov]. *Uchenye Zapiski Saratovskogo Gosudarstvennogo Universiteta, Vol. 29, Vypusk Biologiya-Pochvovedenie*: 55–74. Original not seen. Cited by Voznyakovskaya (1954) and Shemakhanova (1962).

Malyshkin PE (1955). Stimulation of tree growth by microorganisms. In: *Mycotrophy in plants*. (Imshenetskii AA, ed.). Israel Program for Scientific Translations, Jerusalem, 1967: 211–220.

Mandyam K, Jumpponen A (2005). Seeking the elusive function of the root-colonising dark septate endophytic fungi. *Studies in Mycology* **53**: 173–189.

Mangenot F, Diem HG (1979). Fundamentals of biological

control. In: *Ecology of root pathogens* (Krupa SV, Dommergues YR, eds) Elsevier, Amsterdam, the Netherlands: 207–265.

Mańka K (1953). *Field and laboratory experiments on the honey mushroom* Armillaria mellea. [*Badanie terenowe i laboratoyjne nad opieńką miodową* Armillaria mellea]. Państwowe Wydawnictwo Rolnicze i Leśne, Pracach Instytutu Badawczego Leśnictwa, publication nr. 94, Warszaw, Poland.

Mańka K (1960). On the root fungus *Mycelium radicis atrovirens* Melin. [O grzybie korzeniowym *Mycelium radicis atrovirens* Melin]. *Monographiae Botanicae* **10**: 147–158.

Mańka K (1968). Some investigations of *Fomes annosus* carried out in Poland. In: *Proceedings of the Third International Conference on Fomes annosus* (Hodges CS, Rishbeth J, eds). US Department of Agriculture, Forest Service, Washington DC, USA: 82–90.

Mańka K (1974). Fungal communities as a criterion for estimating the influence of the environment on plant disease. [Zbiorowiska grzybów jako kryterium oceny wpływu środowiska na choroby roślin]. *Zeszyty Problemowe Postępów Nauk Rolniczych* **160**: 9–23.

Mańka K, Gierczak M (1961). Studies on the root mycoflora of common pine (*Pinus sylvestris* L.). [Badania nad florą grzybową korzeni sosny zwyczajnej (*Pinus sylvestris* L.)]. *Poznańskie Towarzystwo Przyjaciół Nauk. Wydział Nauk Rolniczych i Leśnych. Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych* **9**: 3–47.

Mańka K, Gierczak M, Prusinkiewicz Z (1968a). The damping-off of yew (*Taxus baccata* L.) seedlings in Wierzchlas and the saprotrophic fungi in the soil environment. [Zamieranie siewek cisa (*Taxus baccata* L.) w Wierzchlesie na tle zespołów saprofitycznych grzybów środowiska glebowego]. *Poznańskie Towarzystwo Przyjaciół Nauk, Wydział Nauk Rolniczych i Leśnych, Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych* **25**: 177–195.

Mańka K, Gierczak M, Strzelczyk A, Szajer C (1968b). Further investigations on the damping-off of yew tree seedlings in the Wierzchlas forest. [Dalsze badania nad zamieraniem siewek cisa (Taxus baccata L.) w Wierzchlesie]. *Poznańskie Towarzystwo Przyjaciół Nauk, Wydział Nauk Rolniczych i Leśnych, Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych* **25**: 163–175.

Mańka K, Rząsa S (1961). Studies on the mycoflora of the roots of forest trees. [Badania nad mikoflorą korzienową drzew leśnych]. *Folia Forestalia Polonica* **6**: 27–48.

Mańka K, Truszkowska W (1958). An exploratory mycological analysis of the roots of spruce (*Picea excelsa* Lk.). [Próba mikologicznej analizy korzeni świerka (*Picea excelsa* Lk.)]. *Acta Societatis Botanicorum Poloniae* **27**: 45–73.

Manteifel AYa, Zhukova AI, Dem'yanova EK (1950). Studies on the rhizosphere microflora of oak. [Izuchenie mikroflory rizosfery duba]. *Mikrobiologiya* **19**: 547–556.

Manturovskaya NV, Sizova TP (1967). Interactions between spruce seedlings and soil-borne fungi. I. [Vzaimodeistviya prorostkov eli i pochvennykh gribov. I.]. *Mikologiya i Fitopatologiya* **1**: 500–503.

Marks GC, Foster RC (1967). Succession of mycorrhizal associates on individual roots of radiata pine. *Australian Forestry* **31**: 194–201.

Marletto F (1969). Rhizosphere microflora in truffle beds. I. Blastomycetes from truffles and from the rhizosphere in the truffle beds. [La micoflora della rizosfera nelle tartufaie. I. Blastomiceti dei tartufi e della rizosfera nelle tartufaie]. *Allionia* **15**: 155–171.

Marx DH (1969). The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. *Phytopathology* **59**: 153–163.

Marx DH (1973). Mycorrhizae and feeder root disease. In: *Ectomycorrhizae. Their ecology and physiology*. (Marks GC, Kozlowski TT, eds). Academic Press, New York. U.S.A.: 351–382.

Marx DH, Bryan WC (1970). The influence of soil bacteria on the mode of infection of pine roots by *Phytophthora cinnamomi*. In: *Root diseases and soil-borne plant pathogens*. (Toussoun TA, Bega RV, Nelson PE, eds). University of California Press, Berkeley, CA, U.S.A.: 171–172.

Marx DH, Davey CB (1969a). The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. III. Resistance of aseptically formed mycorrhizae to infection by *Phytophthora cinnamomi*. *Phytopathology* **59**: 549–558.

Marx DH, Davey CB (1969b). The influence of ectotrophic mycorrhizae on the resistance of pine roots to pathogenic infections. IV. Resistance of naturally-occurring mycorrhizae to infections by *Phytophthora cinnamomi*. *Phytopathology* **59**: 559–565.

Marx DH, Haasis FA (1965). Induction of aseptic sporangial formation in *Phytophthora cinnamomi* by metabolic diffusates of soil microorganisms. *Nature (London)* **206**: 673–674.

Marx DH, Jarl K, Ruehle JJ, Bell W (1984). Development of *Pisolithus tinctorius* ectomycorrhizae on pine seedlings using basidiospore-encapsulated seeds. *Forest Science* **30**: 897–907.

Marx DH, Krupa SV (1978). Ectomycorrhizae. In: *Interactions between non-pathogenic soil microorganisms and plants*. (Dommergues YR, Krupa SV, eds). Elsevier Scientific Publishing Co., Amsterdam, the Netherlands: 373–400.

Marx DH, Rowan SJ (1981). Fungicides influence growth and development of specific ectomycorrhizae on loblolly pine seedlings. *Forest Science* **27**: 167–176.

Mason PA, Wilson J, Last FT, Walker C (1983). The concept of succession in relation to the spread of sheathing mycorrhizal fungi on inoculated tree seedlings growing in unsterile soils. *Plant and Soil* **71**: 247–256.

Matturi ST, Stenton H. (1964). Distribution and status in the soil of *Cylindrocarpon* species. *Transactions of the British Mycological Society* **47**: 577–587.

Medvedev ZA (1971). *The Rise and Fall of T.D. Lysenko*. Columbia University Press, New York, U.S.A.

Melin E (1921). The mycorrhizal fungi of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. [Über die Mykorrhizenpilze von *Pinus sylvestris* L. und *Picea abies* (L.) Karst.]. *Svensk Botanisk Tidskrift* **15**: 192–203.

Melin E (1923). Experimental studies on the constitution and ecology of mycorrhizae of *Pinus sylvestris* L. and *Picea abies* [L.] Karst. [Experimentelle Untersuchungen über die Konstitution und Ökologie der Mykorrhizen von *Pinus sylvestris* L. und *Picea abies* (L.) Karst.]. In: *Mycological studies and reports*. [*Mykologische Untersuchungen und Berichte*]. 2nd vol. (Falck R, ed.). Druck und Verlag G. Gottheilt, Kassel, Germany: 73–334.

Melin E (1963). Some effects of forest tree roots on mycorrhizal Basidiomycetes. In: *Symbiotic Associations*. (Mosse B, Nutman PS, eds). Cambridge University Press, Cambridge, U.K.: 124–145.

Meyer FH (1962). Beech and spruce mycorrhizae in various soil types, as influenced by mineral nutrients as well as by factors important in mycorrhizal development. [Die Buchen- und Fichtenmykorrhiza in verschiedenen Bodentypen, ihre Beeinflussing durch Mineraldünger sowie für die Mykorrhizabildung wichtige Faktoren]. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* **54**: 1–73.

Meyer FH (1967). Influence of soil and soil microflora on the development of ectotrophic mycorrhizae. [Einfluss von Boden und Bodenmikroflora auf die Bildung ektotropher Mykorrhizen]. In: *Progress in soil biology* (Graff O, Satchell JE, eds). North-Holland Press, Amsterdam, the Netherlands: 49–56.

Meyer FH (1974). Physiology of mycorrhiza. *Annual Review of Plant Physiology* **25**: 567–586.

Mikola P (1956). Studies on the decomposition of forest litter by Basidiomycetes. *Communicationes Instituti Forestalis Fenniae* **48**: 1–22.

Mikola P (1966). *The value of alder in adding nitrogen in forest soils. Final report of research conducted under grant authorized by US Public Law 480*. University of Helsinki, Department of Silviculture, Helsinki, Finland.

Miller CO (1969). Control of deoxyisoflavone synthesis in soybean tissue. *Planta* **87**: 26–35.

Miller CO (1971) Cytokinin production by mycorrhizal fungi. In: *Mycorrhizae*. (Hacskaylo E, ed.) US Dept. of Agriculture, Forest Service, Washington, DC, U.S.A.: 168–174.

Miller OK Jr, Miller SL, Palmer JG (1983). Description and identification of selected mycorrhizal fungi in pure culture. *Mycotaxon* **18**: 457–481.

Mishra RR, Kanaujia RS (1973). Investigations into rhizosphere microflora. XII. Seasonal variation in the mycoflora of certain gymnosperms. *Sydowia* **27**: 302–311.

Mishustin EN (1951). Microflora of soil and the formation of mycorrhizae on oak. [Mikroflora pochvy i obrazovanie mikorizy u duba]. *Agrobiologiya* **2**: 27–39.

Mishustin EN, Pushkinskaya OI (1961). Means of facilitating growth and mycorrhiza formation with pines and oaks in the conditions of the forest-steppe zone of the USSR. [Priemi, blagopriyatstvuyushchie rostu i mikorizoobrazovaniyu u sosny i duba v usloviyakh lesostepnoi zony SSSR]. *Izvestiya Akademii Nauk SSSR, Seriya Biologicheskaya* **1961**: 764–775.

Mishustin EN, Mirzoeva VA, Enikeyeva MG (1966). Microflora of podzolic and sod-podzolic soils. In: *Microflora of soils in the northern and central USSR*. (Mishustin EN, ed.). Israel Program for Scientific Translation, Jerusalem 1972: 64–115.

Möbius, Karl (1877). *The oyster and the oysterbed*. [*Die Auster und die Austernwirtschaft*]. Wiegumdt, Hempel and Parey, Berlin. English translation: U.S. Commission Fish and Fisheries Report, 1880: 683–751.

Molina R (1982). Use of the ectomycorrhizal fungus *Laccaria laccata* in forestry. I. Consistency between isolates in effective colonization of containerized conifer seedlings. *Canadian Journal of Forest Research* **12**: 469–473.

Möller A (1902). On root development in one- and two-year-old pines in sandy soils of the Brandenburg region. [Über die Wurzelbildung der ein- und zweijährigen Kiefer im märkischen Sandboden]. *Zeitschrift für Forst- und Jagdwesen* **34**: 197–215.

Möller A (1903). Studies on one- and two-year-old pines in sandy soils of the Brandenburg region. [Untersuchungen über ein- und zweijährige Kiefern im märkischen Sandboden]. *Zeitschrift für Forst- und Jagdwesen* **35**: 321–338.

Moser M (1956). The significance of mycorrhizae in afforestation of high altitude sites. [Die Bedeutung der Mykorrhiza für Aufforstungen in Hochlagen]. *Forstwissenschaftliches Centralblatt* **75**: 8–18.

Moser M (1959). A contribution to knowledge about hormonal relationships in ectotrophic mycorrhizae. [Beiträge zur Kenntnis der wuchstoffbeziehungen in ectotrophen Mykorrhizen]. *Archiv für Mikrobiologie* **34**: 251–264.

Moser M (1963). The significance of mycorrhizae in afforestation with particular regard to high elevation. [Die Bedeutung der Mykorrhiza bei Aufforstungen unter besonderer Berücksichtigung von Hochlagen]. In: *Mykorrhiza*. (Rawald W, Lyr H, eds). Gustav Fischer Verlag, Jena, Germany: 407–424.

Mosse B (1962). The establishment of vesicular-arbuscular mycorrhiza under aseptic conditions. *Journal of General Microbiology* **27**: 509–520.

Neal JL Jr, Bollen WB, Zak B (1964). Rhizosphere microflora associated with mycorrhizae of Douglas-fir. *Canadian Journal of Microbiology* **10**: 259 –265.

Neal JL Jr, Larsen RI, Atkinson TG (1973). Changes in rhizosphere populations of selected physiological groups of bacteria related to substitution of specific pairs of chromosomes in winter wheat. *Plant and Soil* **39**: 209–212.

Neal JL Jr, Lu KC, Bollen WB, Trappe JM (1968). A comparison of rhizosphere floras associated with mycorrhizae of red alder. In: *Biology of alder* (Trappe JM Franklin JF, Tarrant RF, Hansen GM, eds). Pacific Northwest Forest Service, U.S. Dept. of Agriculture, Portland, Oregon: 57–71.

Ng PP, Cole ALJ, Jameson PE, McWha JA (1982). Cytokinin production by ectomycorrhizal fungi. *New Phytologist* **91**: 57–62.

Nylund J-E, Unestam T (1982). Structure and physiology of ectomycorrhizae. I. The process of mycorrhiza formation in Norway spruce *in vitro*. *New Phytologist* **91**: 63–79.

Ogawa M (1976a). Microbial ecology of "shiro" in *Tricholoma matsutake* (S. Ito et Imai) Sing. and its allied species. II. *Tricholoma matsutake* in *Pinus pumila*

var. *yezoalpina* forest. *Transactions of the Mycological Society of Japan* **17**: 176–187.

Ogawa M (1976b). Microbial ecology of "shiro" in *Tricholoma matsutake* (S. Ito et Imai) Sing. and its allied species. III. *Tricholoma matsutake* in *Picea glehnii* and *Picea glehnii-Abies sachalinensis* forests. *Transactions of the Mycological Society of Japan* **17**: 188–198.

Ogawa M (1977a). Microbial ecology of mycorrhizal fungus *Tricholoma matsutake* (S. Ito et Imai) Sing. in pine forest. III. Fungal florae in shiro soil and on the mycorrhiza. *Bulletin of the Government Forest Experimental Station* **293**: 105–170.

Ogawa M (1977b). Microbial ecology of "shiro" in *Tricholoma matsutake* (S. Ito et Imai) Sing. and its allied species. IV. *Tricholoma matsutake* in *Tsuga diversifolia* forests. *Transactions of the Mycological Society of Japan* **18**: 20–33.

Ogawa M (1977c). Microbial ecology of "shiro" in *Tricholoma matsutake* (S. Ito et Imai) Sing. and its allied species. V. *Tricholoma matsutake* in *Tsuga sieboldii* forests. *Transactions of the Mycological Society of Japan* **18**: 34–46.

Ogawa M (1977d). Microbial ecology of "shiro" in *Tricholoma matsutake* (S. Ito et Imai) Sing. and its allied species. VI. *Tricholoma fulvocastaneum* in *Quercus serrata-Quercus acutissima* forest. *Transactions of the Mycological Society of Japan* **18**: 286–297.

Ogawa M (1978). Microbial ecology of "shiro" in *Tricholoma matsutake* and its allied species. VII. *Tricholoma fulvocastaneum* Hongo in *Castanopsis cuspidata* forest. *Transactions of the Mycological Society of Japan* **19**: 37–46.

Ogawa M and H. Ohara (1978). Microbial ecology of "shiro" in *Tricholoma matsutake* and its allied species. VIII. *Tricholoma bakamatsutake* Hongo in *Quercus mongolica* var. *grosseserrata* forest and *Q. serrata* forests. *Transactions of the Mycological Society of Japan* **19**: 391–405.

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

Ohara H, Ogawa M (1982). Microbial ecology of "shiro" in *Tricholoma matsutake* and its allied species. XI. *Tricholoma caligatum* in *Cedrus libanoticum* forest. *Transactions of the Mycological Society of Japan* **23**: 365–377.

Ohta A (1983). Quantitative analysis of odorous compounds in the fruit bodies of *Tricholoma matsutake*. *Transactions of the Mycological Society of Japan* **24**: 185–190.

Oliveira VL de, Garbaye J (1989). Microorganisms stimulating the establishment of mycorrhizal symbiosis (a review). [Les microorganisms auxiliaries de l'établissement des symbioses mycorhiziennes (Revue bibliographique)]. *European Journal of Forest Pathology* **19**: 54–64.

Olsen R, Odham G, Lindeberg G (1971). Aromatic substances in leaves of *Populus tremula* as inhibitors of mycorrhizal fungi. *Physiologia Plantarum* **25**: 122–129.

Orlos H, Dominik T (1960). On the biology of the root-rot fungus *Fomes annosus* (Fr.) Cooke. [Z biologii huby korzeniowej *Fomes annosu*s (Fr.) Cooke]. *Sylwan (Warszawa)* **104**: 1–13.

Otrosina WJ (1977). *Microbial and ectomycorrhizal aspects of kaolin spoil*. PhD Dissertation, University of Georgia, Athens, Georgia, U.S.A.

Ozino Marletto OI, Sartoris A (1978). Studies on the ecology of *Tuber melanosporum*. V. The blastoflora of "burnt areas" in central Italy. [Studi sull'ecologia del *Tuber melanosporum*. V. La blastoflora delle "aree bruciate" nell'Italia Centrale]. *Allionia* **23**: 91–94.

Pachlewski R, Pachlewska J (1974). *Studies on symbiotic properties of mycorrhizal fungi of pine* (*Pinus sylvestris L.*) *with the aid of mycorrhizal synthesis in pure cultures on agar*. Forest Research Institute, Warsaw, Poland.

Park JY (1970). Antifungal effect of an ectotrophic mycorrhizal fungus, *Lactarius* sp., associated with basswood seedlings. *Canadian Journal of Microbiology* **16**: 798–800.

Parkinson D, Crouch R (1969). Studies on fungi in a pinewood soil. V. Root mycofloras of seedlings of *Pinus nigra* var. *laricio*. *Revue d'Écologie et de Biologie du Sol* **6**: 263–275.

Pawuk WH, Ruehle JL, Marx DH (1980). Fungicide drenches affect ectomycorrhizal development of container-grown *Pinus palustris* seedlings. *Canadian Journal of Forest Research* **10**: 61–64.

Peklo J. (1909). A contribution towards solving the problems posed by mycorrhizae. [Beiträge zur Lösung des Mykorrhiza-problems]. *Berichte der Deutschen Botanischen Gesellschaft* **27**: 239–247.

Peña-Cabriales JJ, Valdes M (1975). Rhizosphere of fir (*Abies religiosa*). I. Microbiology and microbial activity. [Rhizosphère du sapin (*Abies religiosa*). I. Microbiologie et activité microbienne]. *Revista Latino-Americana de Microbiologia* **17**: 25–31.

Piché Y, Fortin JA, Lafontaine JG (1981). Cytoplasmic phenols and polysaccharides in ectomycorrhizal and nonmycorrhizal short roots of pine. *New Phytologist* **88**: 695–703.

Piercey MM, Graham SW, Currah RS (2004). Patterns of genetic variation in *Phialocephala fortinii* across a broad latitudinal transect in Canada. *Mycological Research* **108**: 955–964.

Ponomareva AV, Pron'ko VI. (1955). Application of *Azotobacter* in forest nurseries and silvicultural plots. [Primenenie azotobaktera v lesnykh pitomnikakh i na lesokul'turnykh ploshchadyakh] *Lesnoe Khozyaistvo* **2** : 36–39.

Powell WM, Hendrix FF, Marx DH (1968). Chemical control of feeder root necrosis of pecans caused by *Pythium* species and nematodes. *Plant Disease Reporter* **52**: 577–578.

Rambelli A (1962). Investigations on the rhizosphere of *Eucalyptus*. [Richerche sulla rizosfera dell'eucalitto.] *Pubblicazioni del Centro di Sperimentazione Agricola e Forestale* **6**: 83–93.

Rambelli A (1963). Investigations on the rhizosphere of *Pinus pinea*. [Richerche sulla rizosfera di *Pinus pinea*]. *Pubblicazioni del Centro di Sperimentazione Agricola e Forestale* **7**: 117–126.

Rambelli A (1965). Investigations on the rhizosphere of poplar. [Richerche sulla rizosfera del pioppo]. *Pubblicazioni del Centro di Sperimentazione Agricola e Forestale* **8**: 27–37.

Rambelli A (1966). *Pinus radiata* D. Don and its relations with the microbial environment of the soil. [Il P*inus radiata* D. Don nei suoi rapporti con l'ambiente microbico del terreno]. *Pubblicazioni del Centro di Sperimentazione Agricola e Forestale* **9**: 31–56.

Rambelli A (1970). Relations between mycorrhizae and the mycorrhizosphere in *Pinus radiata* D. Don. [Rapporti tra micorrizia e micorrizosfera in *Pinus radiata* D. Don.]. *Atti dell'Accademia di Scienze Forestali* **19**: 393–421.

Rambelli A (1973). The rhizosphere of mycorrhizae. In *Ectomycorrhizae. Their ecology and physiology* (Marks GC, Kozlowski TT, eds) Academic Press, New York, U.S.A. 299–349.

Rambelli A, Freccero V, Fanelli C (1972). Investigations on the mycorrhizosphere of *Pinus radiata* D. Don. [Indagini sulla micorrizosfera del *Pinus radiata* D. Don.]. *Pubblicazioni del Centro di Sperimentazione Agricola e Forestale* **11**: 271–287.

Raper K, Thom C (1949). *A manual of Penicillia*. The Williams and Wilkins Co., Baltimore, Maryland, U.S.A.

Rayner MC (1927). *Mycorrhiza: an account of non-pathogenic infection by fungi in vascular plants and bryophytes*. New Phytologist Reprint, no. 15. Wheldon & Wesley, London, U.K.

Rayner MC, Levisohn I (1943). The mycorrhizal habit in relation to forestry. IV. Studies on mycorrhizal response in *Pinus* and other conifers. *Forestry* **15**: 1–36.

Rayner MC, Neilson-Jones W (1944). *Problems in tree nutrition*. Faber & Faber Ltd., London., U.K.

Richard C (1969). About pseudomycorrhizae. [À propos des pseudomycorrhizes]. *Revue de la Société Savante de Haute-Normandie–Sciences* **56**: 79–86.

Richard C, Fortin J-A (1970). Mycorrhizae of *Picea mariana* (Mill.) BSP.: morphological, anatomical and systematic aspects. [Les mycorrhizes de *Picea mariana* (Mill.) BSP.: aspects morphologiques, anatomiques, et systématiques]. *Naturaliste Canadien* **97**: 163–173.

Richard C, Fortin J-A (1973). The identification of *Mycelium radicis atrovirens* (*Phialocephala dimorphospora*). *Canadian Journal of Botany* **51**: 2247–2248.

Richard C, Fortin J-A (1974). Geographic distribution, ecology, physiology and pathogenicity of *Mycelium radicis atrovirens*. [Distribution géographique, écologie, physiologie, pathogenicité et sporulation du *Mycelium radicis atrovirens*]. *Phytoprotection* **55**: 67–88.

Richard C, Fortin J-A (1975). Protective role of *Suillus granulatus* against *Mycelium radicis atrovirens* on seedlings of *Pinus resinosa*. [Rôle protecteur du *Suillus granulatus* contre le *Mycelium radicis atrovirens* sur les semis de *Pinus resinosa*]. *Canadian Journal of Forest Research* **5**: 452–456.

Richard C, Fortin J-A, Fortin A (1971). Protective effect of an ectomycorrhizal fungus against the root pathogen *Mycelium radicis atrovirens*. *Canadian Journal of Forest Research* **1**: 246–251.

Ridge EH, Theodorou C (1972). The effect of soil fumigation on microbial recolonization and mycorrhizal infection. *Soil Biology and Biochemistry* **4**: 295–305.

Robertson NF (1954). Studies on the mycorrhiza of *Pinus sylvestris*. I. The pattern of development of mycorrhizal roots and its significance for experimental studies. *New Phytologist* **53**: 253–283.

Robinson RK (1972). The production by roots of *Calluna vulgaris* of a factor inhibitory to growth of some mycorrhizal fungi. *Journal of Ecology* **60**: 219–224.

Romell L-G (1938). A trenching experiment in spruce forest and its bearing on problems of mycotrophy. *Svensk Botanisk Tidskrift* **32**: 89–99.

Rosendahl RO (1942). The effect of mycorrhizal and non-mycorrhizal fungi on the availability of difficultly soluble potash and phosphate minerals. *Soil Science Society of America Proceedings* **7**: 477–479.

Runov EV, Zhdannikova EN (1960). The rhizosphere microflora of birch and spruce on various soils of the central taiga in the Vologda region. *Akademiya Nauk SSSR, Soobshcheniya Laboratorii Lesovedeniya* **1960 (2)**: 69–79. Environment Canada Translation OOENV TR 128, Ottawa, Canada.

Salt GA (1965). *Pathology experiments on sitka spruce seedlings*. Report on Forest Research for 1964. Forestry Commission, London, U.K: 89–95.

Samson R, Frisvad JC (2004). *Penicillium* subgenus *Penicillium*: new taxonomic schemes, mycotoxins and other extrolites. *Studies in Mycology* **49**: 1–257.

Samtsevich SA (1955). Microflora of soil under mound-planted oaks in arid steppe. In: *Mycotrophy in plants*. (Imshenetskii AA, ed.). Israel Program for Scientific Translations, Jerusalem, 1967: 348–285.

Samtsevich SA (1956). The biodynamics of the rhizosphere of deciduous and coniferous tree-plantings in the forest-steppe. [Biodinamika rizosfery listvennykh i khvoinykh nasazhdenii v lesostepi]. *Mikrobiologiya* **25**: 49–56.

Samtsevich SA, Korets'ka ZM, Sosnyagova GA (1952). Microflora of the oak rhizosphere. [Mikroflora rizosferi duba]. *Pratsi Institutu Lisivnitstva Akademii Nauk URSR* **3**: 184–206.

Santoro T, Casida LE Jr (1962). Growth inhibition of mycorrhizal fungi by gibberellin. *Mycologia* **54**: 70–71.

Schisler DA, Linderman RG (1984). Evidence for the involvement of the soil microbiota in the exclusion of *Fusarium* from coniferous forest soils. *Canadian Journal of Microbiology* **30**: 142–150.

Schoenberger MM, Perry DA (1982). The effect of soil disturbance on growth and ectomycorrhizae of Douglas-fir and western hemlock seedlings: a greenhouse bioassay. *Canadian Journal of Forest Research* **12**: 343–353.

Schönhar S (1984). Infection tests on spruce and pine seedlings with fungi frequently isolated from deteriorated fine roots of conifers. [Infektionsversuche an Fichten- und Kiefernkeimlingen mit aus faulen Feinwurzeln von Nadelbäumen häufig isolierten Pilzen]. *Allgemeine Forst- und Jagd-Zeitung* **155**: 191–192.

Schönhar S (1991). Infection tests with root fungi on spruce seedlings in strongly acidic and neutral soil substrata. [Infektionsversuche an Fichtenkeimlingen mit Wurzelpilzen auf Bodensubstraten mit stark saurer und neutraler Reaktion]. *Allgemeine Forst- und Jagdzeitung* **162**: 134–136.

Sharma GD (1981). Influence of mycorrhizal developmental stages and plant age on rhizosphere mycoflora of *Pinus kesiya* Royle. *Acta Mycologica* **17**: 45–51.

Shemakhanova NM (1961). The significance of individual components of forest soil in the development of oak and

pine seedlings. [O znachenii otdel'nykh komponentov lesnoi pochvy dlya razvitiya seyantsev sosny i duba]. *Trudy Instituta Mikrobiologii, Akademiya Nauk SSSR* **11**: 139–149.

Shemakhanova NM (1962). *Mycotrophy of woody plants*. Translated by US Dept. of Agriculture and the National Science Foundation, Washington, D. C., Israel Program for Scientific Translations 1967. (orig. Mikotrofiya drevesnykh porod. Institut Mikrobiologii, Akademiya Nauk SSSR, Moscow).

Shipman RD (1957). Microbial population in the rhizosphere of yellow poplar seedlings. *American Midland Naturalist* **58**: 413–421.

Sideri DI, Zolotun VP (1952). Improvement of conditions for growth of oak on the eroded soils of Zaporozh'ye. [Ob uluchshenii uslovii rosta duba na smytykh pochvakh Zaporozh'ya]. *Les i Step'* **8**: 28–33.

Sieber TN (2002). Fungal root endophytes. In: *Plant roots: the hidden half*. (Waisel Y, Eshel A, Kafkafi U, eds) Marcel Dekker, New York, U.S.A: 887–917.

Sigler L, Gibas C (2005). Utility of a cultural method for identification of the ericoid mycobiont *Oidiodendron maius* confirmed by ITS sequence analysis. *Studies in Mycology* **53**: 63–74.

Sinclair WA, Cowles DP, Hee SM (1975). *Fusarium* root rot of Douglas-fir seedlings: suppression by soil fumigation, fertility management, and inoculation with spores of the fungal symbiont *Laccaria laccata*. *Forest Science* **21**: 390–399.

Sinclair WA, Sylvia DM, Larsen AO (1982). Disease suppression and growth promotion in Douglas-fir seedlings by the ectomycorrhizal fungus *Laccaria laccata*. *Forest Science* **28**: 191–201.

Sizova TP (1977). Some regularities in the distribution of soil fungi. [Nekotorye zakonomernosti rasprostraneniya pochvennykh gribov]. *Mikologiya i Fitopatologiya* **11**: 377–381.

Sizova TP, Itakayeva EA (1956). Dynamics of the mycoflora of the rhizosphere of birch. [K voprosu o dinamike mikoflory rizosfery berezy]. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* **61**: 83–93.

Sizova TP, Suprun TP (1962). Some data on the mycoflora of soils covered with birch, lime and spruce forests in the Zvenigorod Biostation of Moscow State University and of the rhizospheres of the corresponding tree species. [Nekotorye dannye po mikoflore pochv berezovogo, lipovogo i elovogo lesov Zvenigorodskoi Biostantsii MGU i rizosfer sootvetstvuyushchikh porod]. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* **67**: 112–119.

Sizova TP, Vasin VB (1961). Mycoflora of the oak rhizosphere. [Mikoflora rizosfery duba]. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody. Otdel Biologicheskii* **66**: 102–115.

Slankis V (1973). Hormonal relationships in mycorrhizal development. In: *Ectomycorrhizae. Their ecology and physiology*. (Marks GC, Kozlowski TT, eds). Academic Press, New York. U.S.A.: 231–298.

Slankis V (1974). Soil factors influencing formation of mycorrhizae. *Annual Review of Phytopathology* **12**: 437–457.

Smiley RW (1979). Wheat rhizosphere pH and the biological control of take-all. In: *The soil-root interface* (Harley JL, Russell RS, eds). Academic Press, New York, U.S.A.: 327–338.

Smith RS Jr (1967). Decline of *Fusarium oxysporum* in the roots of *Pinus lambertiana* seedlings transplanted into forest soils. *Phytopathology* **57**: 1265.

Smith WH (1969). Release of organic materials from the roots of tree seedlings. *Forest Science* **15**: 138–143.

Sobotka A (1956). Practical application of mycorrhiza in silviculture. [Vnužití mykorrhizy v praxi.] *Česká Mykologie* **10**: 162–168.

Söderström BE (1975). Vertical distribution of microfungi in a spruce forest soil in the south of Sweden. *Transactions of the British Mycological Society* **65**: 419–425.

Söderström BE, Bååth E (1978). Soil microfungi in three Swedish coniferous forests. *Holarctic Ecology* **1**: 62–72.

Stack RW, Sinclair WA (1975). Protection of Douglas-fir seedlings against *Fusarium* root rot by a mycorrhizal fungus in the absence of mycorrhiza formation. *Phytopathology* **65**: 468–472.

Stone EL Jr (1950). Some effects of mycorrhizae on the phosphorus nutrition of Monterey pine seedlings. *Soil Science Society of America Proceedings* **14**: 340–345.

Strullu D-G, Gourret J-P (1973). Study of the ectotrophic mycorrhizae of *Pinus brutia* Ten. with scanning and transmission electron microscopy. [Étude des mycorhizes ectotrophes de *Pinus brutia* Ten. en microscopie électronique à balayage et à transmission]. *Comptes Rendus de l'Académie des Sciences, Paris, Sér. D*. **277**: 1757–1760.

Strzelczyk E, Pokojska-Burdziej A (1982). Production of auxins and gibberellin-like substances by *Cylindrocarpon destructans* (Zins.) Scholt. isolates pathogenic and non-pathogenic to fir (*Abies alba* Mill.). *Phytopathogische Zeitschrift* **105**: 327–335.

Strzelczyk E, Pokojska-Burdziej A (1984). Production of auxins and gibberellin-like substances by mycorrhizal fungi, bacteria, and actinomycetes isolated from soil and the mycorrhizosphere of pine (*Pinus sylvestris* L.). *Plant and Soil* **81**: 185–194.

Strzelczyk E, Sitek JM, Kowalski S (1977). Synthesis of auxins from tryptophan and tryptophan precursors by fungi isolated from mycorrhizae of pine (*Pinus sylvestris* L.). *Acta Microbiologica Polonica* **26**: 255–264.

Summerbell RC (1987). The inhibitory effect of *Trichoderma* species and other soil microfungi on formation of mycorrhiza by *Laccaria bicolor in vitro*. *New Phytologist* **105**: 437–448.

Summerbell RC (1989). Microfungi associated with the mycorrhizal mantle and adjacent microhabitats within the rhizosphere of black spruce. *Canadian Journal of Botany* **67**: 1085–1095.

Summerbell RC (2005). Root endophyte and mycorrhizosphere fungi of black spruce, *Picea mariana*, in a boreal forest habitat: influence of site factors on fungal distributions. *Studies in Mycology* **53**: 121–145.

Sylvia DM, Sinclair WA (1983). Phenolic compounds and resistance to fungal pathogens induced in primary roots of Douglas-fir seedlings by the ectomycorrhizal fungus *Laccaria laccata*. *Phytopathology* **73**: 390–397.

Szaniszlo PJ, Powell PE, Reid CPP, Cline GR (1981). Production of hydroxamate siderophore iron chelators by ectomycorrhizal fungi. *Mycologia* **73**: 1158–1175.

Theodorou C (1967). Inoculation with pure cultures of mycorrhizal fungi of radiata pine growing in partially sterilized soil. *Australian Forestry* **31**: 303–309.

Theodorou C, Bowen GD (1969). The influence of pH and nitrate on mycorrhizal associations of *Pinus radiata*. *Australian Journal of Botany* **17**: 59–67.

Timonin MI (1941). The interaction of higher plants and soil microorganisms. III. Effect of by-products of plant growth on activity of fungi and actinomycetes. *Soil Science* **52**: 395– 413.

Timonin MI (1966). Rhizosphere effect of healthy and diseased lodgepole pine seedlings. *Canadian Journal of Microbiology* **12**: 531–537.

Tomaszewski M, Wojciechowska B (1973). The role of growth regulators released by fungi in pine mycorrhizae. In: *Plant Growth Substances. Proceedings of the 8th International Conference on Plant Growth Substances*. Hirokawa Publishing, Tokyo, Japan: 217–227.

Tominanga Y (1963). Studies on the life history of Japanese pine mushroom, *Armillaria matsutake* Ito et Imai. *Bulletin of the Hiroshima Agricultural College* **2**: 105–145. (In Japanese)

Tribunskaya AYa (1955). Investigations on the rhizosphere microflora of pine seedlings. [Izuchenie mikroflory rizosfery seyantsev sosny]. *Mikrobiologiya* **24**: 188–192.

Truszkowska W (1961). An orientational analysis of the mycoflora of the younger components of the root system of poplar (*Populus euramericana marilandica* Bosc.) from various localities in Turew. [Orientacyjne badania mikoflory najmłodszych części systemu korzienowego topól (*Populus euramericana marilandica* Bosc.) z różnych stanowisk w Turwi]. *Acta Societatis Botanicorum Poloniae* **30**: 395–421.

Tserling GI (1960). Mycorrhiza formation in larch under the conditions found in Transvolga chernozem soils and how to stimulate it. [Mikorizoobrazovanie u listvennitsy v usloviyakh chernozemnykh pochv Zavolzh'ya i priemy ego stimulirovaniya]. *Mikrobiologiya* **29**: 401–407.

Turner PD (1962). Morphological influence of exudates of mycorrhizal and non-mycorrhizal fungi on excised root cultures of *Pinus sylvestris* L. *Nature (London)* **194**: 551–552.

Ulrich JM (1960). Auxin production by mycorrhizal fungi. *Physiologia Plantarum* **13**: 429–443.

Vaartaja O (1974). Inhibition of *Pythium ultimum* in molecular fractions from gel filtration of soil extracts. *Canadian Journal of Microbiology* **20**: 1273–1280.

Vaartaja O, Salisbury PJ (1965). Mutual effects *in vitro* of micro-organisms isolated from tree seedlings, nursery soil, and forests. *Forest Science* **11**: 160–168.

Vaartaja O, Agnihotri VP (1970). A comparison of rhizosphere floras in conifer beds treated with fungitoxicants. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene. II Abteilung, Naturwissenschaftliche* **124**: 157–164.

Vaartaja O, Cram WH, Morgan GA (1961). Damping-off etiology, especially in forest nurseries. *Phytopathology* **51**: 35–42.

Vasiliauskas AP, Kazemekiene BYu (1977). Soil microflora of pines growing on former agricultural soils and its antagonistic activity against *Fomes* root rot. [Pochvennaya mikroflora sosnyakov, proizrastayustsikh na pochvakh byvshikh sel'khozugodiy i yeye antagonisticheskaya aktivnost' k kornevoy gubke]. *Trudy Litovskogo Nauchno-Issledatel'skogo Instituta Lesnogo Khozyaistva* **16**: 103–116.

Vavulo FP, Ponomareva AV (1955). Results obtained through bacterization of seeds and seedlings of tree species. In: *Mycotrophy in plants*. (Imshenetskii AA, ed.). Israel Program for Scientific Translations, Jerusalem, 1967: 238–245.

Vavulo FP, Yanushkevich KH (1953). Local strains of *Azotobacter* and *Trichoderma* and their effect on the yield of agricultural crops. [Mestnye shtammy azotobaktera i trikhodermy i ikh vliyanie na urozhai sel'skokhozyaistvennykh kul'tur.] *Izvestiya Akademii Nauk Belorusskoi SSR* **4**: 73–90.

Vedenyapina NS (1955). Effect of *Azotobacter* on the growth of seedlings. In: *Mycotrophy in plants*. (Imshenetskii AA, ed.). Israel Program for Scientific Translations, Jerusalem, 1967: 253–259.

Vörös J (1954). Antibiotics and antagonistic microorganisms as control agents against damping-off of pine seedlings. [Antibiotikumok és antagonista mikroorganizmusok felhasználása fenyőesemetedőlés ellen.] *Növénytermelés* **3**: 115–122.

Voznyakovskaya YuM (1954). Mycorrhiza and its practical value. [Problema mikorizy i ee prakticheskoye znachenie]. *Mikrobiologiya* **23**: 204 –220.

Voznyakovskaya YuM, Ryzhkova AS (1955). Microflora accompanying mycorrhizas. In: *Mycotrophy in plants*. (Imshenetskii AA, ed.). Israel Program for Scientific Translations, Jerusalem, 1967: 320–323.

Vozzo JA, Hacskaylo E (1971). Inoculation of *Pinus caribaea* with ectomycorrhizal fungi in Puerto Rico. *Forest Science* **17**: 239–245

Waid JS (1957). Distribution of fungi within the decomposing tissues of rye-grass roots. *Transactions of the British Mycological Society* **40**: 391–406.

Waid JS (1962). Influence of oxygen upon growth and respiratory behavior of fungi from decomposing rye-grass roots. *Transactions of the British Mycological Society* **45**: 479–487.

Wang CJK, Wilcox HE (1985). New species of ectendomycorrhizal and pseudomycorrhizal fungi – *Phialophora finlandica*, *Chloridium paucisporum*, and *Phialocephala fortinii*. *Mycologia* **77**: 951–958

Warcup TH (1952). Effect of partial sterilization by steam or formalin on damping-off of Sitka spruce. *Transactions of the British Mycological Society* **35**: 248–262.

Wedding RT, Harley JL (1976). Fungal polyol metabolites in the control of carbohydrate metabolism of mycorrhizal roots of beech. *New Phytologist* **77**: 675–688.

Weidling R (1932). *Trichoderma lignorum* as a parasite of other soil fungi. *Phytopathology* **22**: 837–845.

Weidling R (1934) Studies on a lethal principle effective in the parasitic action of *Trichoderma lignorum* on *Rhizoctonia solani* and other soil fungi. *Phytopathology* **24**: 1153–1179.

Went FW (1971) Mycorrhizae in a montane pine forest. In:

Mycorrhizae (Hacskaylo E, ed.) USDA Forest Service Miscellaneous Publication no. 1189, USDA Forest Service, Washington, D.C.: 230–232.

Werner A, Zadworny M, Idzikowska K (2002). Interaction between *Laccaria laccata* and *Trichoderma virens* in co-culture and in the rhizosphere of *Pinus sylvestris* grown *in vitro*. *Mycorrhiza* **12**: 139–145

Whitney R (1962). Studies in forest pathology. XXIV. *Polyporus tomentosus* Fr. as a major factor in stand-opening disease of white spruce. *Canadian Journal of Botany* **40**: 1631–1658.

Wicklow DT (1981). Interference competition and the organization of fungal communities. In: *The fungal community. Its organization and role in the ecosystem*. (Wicklow DT, Carroll GC, eds). Marcel Dekker, New York, U.S.A.: 351–375.

Wilcox HE, Wang CJK (1985). Ecto-, ectendo-, and pseudomycorrhizae of dematiaceous fungi with *Pinus resinosa*. In: *Proceedings of the 6th North American Conference on Mycorrhizae*. (Molina R, ed.) Forest Research Laboratory, Corvallis, Oregon, U.S.A.: 437.

Wilde SA (1946). *Forest Soils and Forest Growth*. Chronica Botanica, Waltham, MA, U.S.A.

Wilde SA (1954). Mycorrhizal fungi: their distribution and effect on tree growth. *Soil Science* **78**: 23–31.

Wilde SA, Rosendahl RO (1945). Value of potassium feldspar as a fertilizer in forest nurseries. *Journal of Forestry* **43**: 366–367.

Williams AH (1963). Enzyme inhibition by phenolic compounds. In: *Enzyme chemistry of phenolic compounds* (Pridham JB, ed.). Pergamon Press, Oxford, U.K.: 87–95.

Yatazawa M, Persidsky DJ, Wilde SA (1960). Effect of allyl alcohol on micropopulation of prairie soils and growth of tree seedlings. *Proceedings of the Soil Science Society of America* **24**: 313–316.

Zadworny M, Werner A, Idzikowska K (2004). Behaviour of the hyphae of *Laccaria laccata* in the presence of *Trichoderma harzianum in vitro*. *Mycorrhiza* **14**: 401–405.

Zaias N (1966). Superficial white onychomycosis. *Sabouraudia* **5**: 99–103.

Zaias N (1972). Onychomycosis. *Archives of Dermatology* **105**: 263–274.

Zogg H (1951). Studies on the pathogenicity of etiologic agent mixtures in stem rots of crop plants. [Studien über die Pathogenität von Erregergemischen bei Getreidefuss krankheiten]. *Phytopathologische Zeitschrift* **18**: 1–54.