MICROBIAL ANTAGONISM TO PHYTOPHTHORA

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INTRODUCTION

The genus Phytophthora is unique of all the pathogenic fungi known to man in that species within this genus have been recorded as colonizing and initiating disease on nearly all plant parts. It also constitutes a genera where species have either narrow or broad host ranges (Ribein, 1978). This fact alone undoubtly constitutes a problem in discussing microbial antagonism to Phytophtheras. However the knowledge to date relating to this topic has been solely restricted to the root-rotting Phytophthora, or to those species whose phase of the life cycle includes a period associated with the below ground plant components as in the case of Ph. infestans. It should be borne in mind that an exciting stage of work is now emerging concerning the antagonism of foliar plant pathogens on aerial plant surfaces such as the phyllosphere. A number of recent extensive reviews have been published (Fokkema, 1978; Skidmore, 1976) and it would appear that the principles are generally the same as those reported for the antagonism of root pathogens.

The Phytophthora species that are found in soil and involved in aspects of root and stem collar damage include Ph. boehmeriae, Ph. cactorum, Ph. carnbivora, Ph. cpasici, Ph. cinnamomi, Ph. erythroseptica, Ph. fragerial, Ph. heveae, Ph. infestans, Ph. lateralis, Ph. megasperma var megasperma and var sojae, Ph. parasitica var nicotianae and var parasitica, Ph. palmivora, Ph. primulae, Ph. quininea, Ph. richardiae, Ph. verrucosa and Ph. vignae. Their activity in most part is governed by the predisposition of host tissue as influences by soil parameters either physical, chemical or biological. The mode of penetration if now similar inovlving either mycelial or zoospore inoculum. To date must research including the authors, has been done on Ph. cinnamomi

primarily because it has the greatest impact to crops in both agriculture and forestry (Zentmyer, 1980). Aspects of microbial antagonism will therefore concentrate on this fungus.

PRINCIPLES ASSOCIATED WITH MICROBIAL INTERACTIONS

Interactions between microorganisms occur as a consequence of growth and development in the environment. These interactions can be either beneficial to the microorganism, in that it stimulates an increase in the inoculum potential or biomass to enable it to dominate the particular substrate; for detrimental, where the microorganism fails to establish and may or may not be eliminated from the environment. Ph. cinnamomi represents a good example in question. In natural soil it is dependent on metabolites from other bacterialfungi to stimulate production of sporangia and oospores respectively (Zantmyer, 1965; Ayers, 1971; Brozier, 1971) and can be severely antagonised by many biological agents (Malajczuk et al., 1977, 1979b).

Antagonism is a term that encompasses a number of mechanisms which result in the suppression of Phytophthoras. This may occur in the soil or in the infection court. Broadly, these are amensalism, parasitism and predation and competition which can operate together or independently resulting in the reduction of the Phytophthora inoculum. An understanding of these mechanisms is essential for the possible manipulat of antagonistic microorganisms for the biological control of these pathogens (Baker and Cook, 1974).

Amensalism.

The production of antibiotics or toxic metabolic by-products either volatile or non-volatile causing lysis. This has been the

subject of a number of reviews (Brian, 1957, 1960; Jackson, 1965; Katznelson, 1965; Baker, 1968; Garrett, 1970; Baker and Cook, 1974). The evidence that antibiosis is important in the ecology of soil microorganisms is largely circumstantial, primary because extraction of detection of antibiotics in soil or rhizosphere is difficult. This is probably due to their adsorption onto clay and humus particles or their unstable nature (Brian, 1951). Park (1967) agrees that there is inconclusive evidence that antibiotics are present in soil antibiotics probably do occur in microhabitats of adequate nutrient status such as in the rhizosphere/rhizoplane. Additions of nutrients as organic amendments so soil has attributed to the increased lysis and reduction of Phytophthora species (Zentmyer, 1963; Nesbitt et al. 1979). A range of soil microorganisms have been reported to produce antibiotics against pathogenic fungi in-vitro. These include bacteria actinomycetes and fungi (see reviews by baker and Synder, 1965; Baker, 1968; Baker and Cook, 1974). Often the reports mentioned simply assume that the correlation between disease suppression and antibiotic production on agar is adequate to indicate antibiosis in the soil or rhizosphore. However, care mus be taken in this assumption.

Predation and parasitism.

Predation and parasitism involves active contact between micro-organism resulting in either the hyphal degredation resultin in either the hyphal degredation of cells or the mycophagy of whole propagules (Barnett and Binder, 1973; Boosalis and Mankau, 1965; Boosalis, 1964; Alexander, 1971). Viruses, bacteria and other fungi have been recorded as colonizing both the vegetative and reproductive structures. The node of penetration and subsequent

lysis of the structures differs according to the active agent concerned. Extracellular secretion of toxins or degrading enzymes are typical of both fungal and bacterial hyperparasites. A number of fungi show typical coiling around the host hyphae e.g. Trichoderma spp. (Dennis and Webster, 1971a,b,c).

Mycaphageous animals have received little attention in literature but possibly play a major role in causing a decline of fungal propagules in soil and rhizosphere/rhizoplane. Amoebae in particular, are known to cause perforation in soils (Old, 1978). There is little information on the role of Collembolae and mites but they too might intervene in the decline of the fungal populations in soil. Their role as dispersing agents rather than fungal lytic agents has been suggested by a number of researchers (Shew and Beute, 1979).

A group of fungal parasites that deserve mention are viruses. Initial studies by Hollings (1962) reported the decline of fungal vigor of the cultivated mushroom Agaricus bisporus was initiated by a virus. Similarly, Lapierre et al. (1970) observed the presence of virus particles in a strain of Gaurnannomyces graminis var. tritici (=Ophiobolus graminis) showing reduced pathogenic vigor. Field decline of the fungal populations have subsequently been reported (Gerlogh, 1968).

Competition.

Competition may be used broadly to denote factors favouring on species over another, but in a narrower sense it can mean demand by two or more microorganisms for the same factor in excess of immediate supply. Clark (1968) defined competition as "the injurious effect of one organism on another because of the utilization or removal of some resources of the environment". This includes nutrients as well

as oxygen and space. It is likely that space and oxygen are important variables that can change in the rhizosphere/rhizoplane to the detriment of pathogen establishment (see later). Space and nutrient competition appear to go hand in hand as well, since occupation of a site by microorganisms must result in the diminution of the limited supply of nutrients either in soil or rhizosphere/rhizoplane. Carbon and nitrogen and vitamins are important growth factors in this respect determining the growth and infection of soil borne pathogens in competition with other microorganisms (Baker, 1968).

ANTAGONISM OF PHYTOPHTHORAS IN THE SOIL

Survival of propagules in soil.

Survival of plant pathogens in soil in the absence of host tissue has been discussed by Garrett (1970). These include survival (as mycelium) on organic substances and/or in soil as resting propagules. Survival is markedly influenced by a combination of environmental variables acting upon it and these include physical, chemical and biological parameters. The former two variables are subjects of review by Duniway and Schmitthenner in this book. Biological parameters are indicated below.

An examination of survival periods reported for a range of Phytophtheras is indicated in Table I. Undoubtly absolute values are meaningless in that all survival studies were performed under different environmental conditions however they do reflect the relative survival period of propagules. It is apparent that all propagules exhibit a natural decline in viability with time and presumably would eventually result in definite duration of survival in the absence of host tissue. Mycelia of all Phytophthoras repsesents

a stage least capable of long term survival followed by zoospores/ sporangia while chlamydospore and oospores are more resistant to environmental attrition forces. Studies on the influence of soil microorganism are few. Generally, their competitive saphrophytic ability is extremely low and rapid lysis of mycelium occurs in natural soil (Hine and Truijillo, 1966; Kuhlman, 1964; Lacy, 1962; Legge, 1953; Turner, 1965; Tsao, 1969; Vujicic and Park, 1964). These studies necessitate the use of steril soils with appropriate unsterile soil comparisons. Although the obvious dangers of sterilization need to be realized (Van Brogt et al., 1971) the studies to dprovide an insight of the influence of microbial antagonism to Phytophthoras.

Tsao and Bricker (1963) showed that diffusates prepared from natural soils were inhibitory to mycleial growth of Ph. parasitica while those propared from autocloved soils stimulated mycleial growth. Further, in natural soil amended with a supply of carbon and nitrogen rapid lysis occurred following a burst of initial mycleial growth (Fig. 1) (Tsao, 1969). Similar series of experiments have been performed with Ph. dreschleri (Mehrotra, 1972), Ph. infestans (Turner, 1965) and Ph. cinnamomi (Malajczuk and Theodorou, 1979). In all these examples lysis of mycelium was associated with intense bacterial colonization of hyphae and the breakdown of cytoplasmic content suggesting a general phenomenon of microbial antagonism.

Lysis of mycleium is invariably associated with the formation of zoosporangia and chlamydospores (Tsao, 1969). In fact we have found a direct relationship between lysis of mycelium of Ph. cinnamomi and the number of zoosporangia produced in a range of different soil types and incubation temperatures (Fig. 2). If one regards zoosporangia and chlamydospores as reproductive structures this phenomenon is

consistent with Kleb's principle (discussed in Kauffman, 1926) in that vegetative growth proceeds reproduction, and that reproduction does not occur as long as conditions favour growth. When severe antagonism of hyphae occurs, vegetative growth ceases and reproduction accelerates. In contrast, Broadbent and Baker (1974a) and Malajczuk and Parker (1981) have reported suppressive soils to Ph. cinnamomi where the pathogen failed to produce sporangia even though extensive hyphal lysis occurred. These soils may simply be examples where sporangia-stimulating bacteria are themselves suppressed.

Sporangia formation and survival in soils is poorly understood. This lack of information possible due to the fact that sporangia for most Phytophtheras represent a transient stage prior to zoospore formation or direct germination. Sneh and McIntoch (1974) found that Ph. cactorum sporangia survived for up to 35 days in soil under optimal soil temperatures although rapid lysis occurred within 15 days.

Phytophthora zoospores and cyst are effective inocula once they are brought into immediate contact with host tissue (Hickman, 1970). However, their biology in soil has received little attention. Survival periods reported range from a matter of days to a few weeks (Hickman and Ho, 1966; Zan, 1962). An exception to this general situation was found by Turner (1965) for Ph. palmivora which remained viable for up to six months. The role of microorganism influencing the survival of Ph. cinnamomi mobile zoospores and cysts has recently been demonstrated (Figs. 3 and 3). Zoospores introduced as cysts into soil leachates showed little difference in survival in either the sterile or non-sterile treatments, however when introduced as zoospores, there was a significant reduction in viability during the initial sampling period in the non-sterile treatment when compared

to the sterile soil leachate. The vunerability of these zoospore to antagonism by soil microorganisms may well be expected considering the thin walled nature and the gaps for microbial penetration during loss of flogellae prior to encystinent (Plate.....).

Chlamydospores and oospores are thickwalled structures and can survive for considerable periods of time in soil (Table 1). It is these that initiate disease in host plants when conditions became favourable for their germination and growth. The enforced dormancy in soils is markedly affected by a phenomena termed fungistatis (Lockwood, 1977). Although microorganisms have been implicated the exact mechanism is still questionable. It appears however, that the lack of required nutrients for the germination and for the presence of inhibitory compounds produced bh microorganisms and/or soil per se. Studies of Ph. cinnamomi [Mircetich et al. (1968), Tsao and Bricker (1968)] demonstrated the requirement of exogenous nutrients for germination and that soil sterilization suppressed soil fungistatis. The consequences of fungistatis are twofold, firstly the promotion of Phytophthora survival by avoiding germination which does not allow infection and secondly it may eventually result in the elimination of propagules due to microbial attrition following their prolonged incubation in soil.

Suppressive and conducive soils

In considering microbial antagonism of Phytophthoras in soil it is becoming increasingly obvious that soils vary in the ability to develop disease. Since natural soils differ in microbial composition as well as in nutrient content, and since Phytophthora growth is largely governed by nutrient availability and the intensity of inhibitory substances, differential growth may be expected. Soils which favour the expression of the disease have been termed conducive

whilst those where disease is minimal or where it diminishes even in the presence of susceptible host tissue with or without reduction of pathogen population are termed suppressive. Investigation of suppressiveness suggest that the principle soil component involved is microbial since sterilization by either autoclaving, irradiation or steam pasteurization renders soils to become conducive (Broadbent and Baker, 1974a; Halsell, 1978; Malajczuk et al., 1977). This natural biological control is particularly relevent in terms of explaining the establishment of Phytophthora diseases in both agriculture and forestry areas and may be the key in the understanding and development of potential control measure for the eradication of these diseases. Of particular relevance are studies of suppressive and conducive soils to Ph. cinnamomi in Australia. The pathogen is widely distributed (Newhook and Podger, 1972) and extremely destructive in many of the indigenous communities (Weste, 1974; Brown, 1976; Shea, 1975; Malajczuk and Glenn, 1981). Its spread and development suggest that the fungus has only recently been introduced (Newhook and Podger, 1972). However in a number of locations throughout Australia the impact of disease in these natural communities is minimal suggesting that these soils may be suppressive to the pathogen. Malajczuk and McComb (1979), Malajczuk (1979a,b) and Weste and Vithanage (1977,1978) have reported microbial populations of soil types of natural ecualypt communities in eastern and western Australia respectively. Invariably the populations differed qualitatively and quantitatively in both soil and the rhizosphers of plant species with increased numbers found in suppressive soils (Table 2). Broadbent and Baker (1974a), Malajczuk and Parker (1981) showed that there was a corresponding increase in the percentage of antagonistic bacteria and actinomycetes. This was correlated with reduced sporulation of

the fungus and increase in hyphal lysis. Specific isolates of Bacillus, Streptomyces, fluorescent Pseudomonas have been isolated that may be implicated in the suppression however it is more probable that a range of microbial components work in concert to produce a suppression of the pathogen.

In these preliminary investigations of soil types influencing diseas development many of the suppressive soils tested were kraznozems originaating from basaltic rock. These being typically high in clay content, exchangeable cation, organic content and microbial activity. Subsequent investigations by Broadbent, Baker and Malajczuk (unpublished), have found other suppressive soils not of basaltic origin. One particular soil occurred under a undisturbed rainforest vegetation stand where the original parent material was a silaceous beach sand. Invariable suppression of the pathogen was associated with the humus layer of the soil profile showing intense microbial activity. Nesbitt et al. (1979) has subsequently demonstrated that additions of decomposing litter in increasing amounts to be conducive soil resulted in an increase in the suppression of Ph. cinnamomi as indicated by hyphae lysis and formation of abortive sporangia. Thus presumably in natural ecosystems which are either undisturbed or where there is a high and rapid accumulation and incorporation of litter into the soil profile by intense microbial activity, pathogens like Ph. cinnamomi would find difficulty of establishing and initiating disease.

Microbial agents associates with antagonism of Phytophthoras

Bacteria and actinomycetes.

Bacteria, by virtue of their large population in soil, constitute a significant microbial component which influences the behaviour of

soil borne Phytophthora propagules (Baker and Cook, 1974). This is also due to the fact that both groups of microorganisms are dependent on adequate soil moisture for their growth and spread in soil (Cook and Papendick, 1970; Duniway, 1979). Observations by a number of workers of Phytophthora hyphae in soil (see Table I) have indicated intense colonization of Phytophthora hyphae by bacteria. More recently Malajczuk et al. (1977) carried out light and electron microscopic study of Ph. cinnamomi hyphae - soil interface showing the relationship of bacterial on hyphae in non-sterile soil or soil leachates. Bacteria accumulated on, or in the immediate vicinity of fungal hyphae (Plate.....). These included a range of morphological distinct types occurring as individuals or in microcolonies of 5-40 cells. The attachment of bacteria was either with their long axes directly against the hyphae or adsorbed onto the hyphae by their polar tips (Plate.....). Invariably accumulation of bacteria was associated with slime development as single strands or intertwinded within sheets enveloping groups of hyphae (Plate.....). Samples of hyphae colonized by bacteria prepared for transmission electron microscopy and stained with ruthenium red demonstrated the presence of acid mucopolysacchorides which is obviously involved in the attachment process binding bacteria to surfaces (Marshall and Cruickshank, 1972).

The attraction of bacteria to hyphae appear to be a chemotaxis response since inert glass fibres failed to show attraction and growth typical on hyphae (Nesbitt et al., 1981a). This observation raises the possibility that materials are exuded from the hyphae of Phytophthora species stimulating a hyphasphere population much the same as plant roots exudates attract a rhizosphere population (Bowen and Rovira, 1976). Recently Nesbitt et al. (1981b) demonstrated the

translocation and exudation of metabolites of phenylalanine and glucose from hyphae of P. cinnamomi which possibly serve as chemotatic attractants and/or metabolic substrate for bacteria. More work is needed, especially the chemical analysis of exudates, to determine the mechanism of attraction as this may help to elucidate the significance of hyphasphere populations. In the case of Ph. cinnamomi it may be postulated that attraction of a sporangial stimulating population would be advantageous to the pathogen for survival in soils.

In most experiments we have oberved a positive correlation between hyphal lysis and soil bacterial populations. This was demonstrated in an experiment where we added increasing amounts of soil organic matter = soil bacteria (Gray et al., 1968) to a microbialogical depauperate lateritic soil and determined hyphal lysis of Ph. cinnamomi incubated as mats on cellophane (Fig. 5). Hyphal lysis occurred within 24 hrs in soils containing greater than 50% organic matter and was maximal within 3-5 days while in lateritic soil little lysis (<2%) was observed over this period. In control (sterile soil) treatments little or no hyphal lysis occurred after 6 days. The number of bacteria firmly adheing to hyphae also increased with time. Examination of bacterial numbers on lysed and aline hyphae compared with dead (autoclaved) hyphae and inert fibre controls showed increased numbers on lysed hyphae (Fig. 6). Although it is tempting to suggest that this increased bacterial population initiated lysis it can be argued that the adhering bacteria are simply utilizing the products of hyphal lysis. Tu (1978) reported a large increase in the number of bacteria initially growing on active hyphal tips of Ph. megasperma resulting in hyphal lysis. He interpreted this as evidence for suppression of the pathogen. Nesbitt et al. (1978)

noted that hyphal tips (terminal 50 μm of hyphae) of Ph. cinnamomi lysed more rapidly than the rest of the hyphae (Plate.....). It is therefore possibly that colonizers of hyphae represent hyphalytic bacteria. There is need for further experimentation to confirm this suggestion.

Antibiotic production in vitro by bacteria involved in the antagonism to Phytophthora species is well established (Table 3). Species include Bacillus, Rhizobium, Flavobacterium and Pseudomenas isolates. Since many of these species have been isolated form the hyphasphere of Phytophthora species suggest that these microorganisms may be prime candidates involved in secreting extracellulare metabolites initiating lysis. This interpretation is consistent with the lack of direct penetration of hyphal wall during the ealry stages of hyphal lysis. At a later stage of lysis bacteria have been observed within the hyphae presumably entered via breaks in the walls initiated by other microbial agents (Plate.....).

Antagonism of sexual and asexual reproductive structures of Phytophthoras have also been observed. In suppressive soil, Broadbent and Baker (1974a,b) and Malajczuk et al. (1977) demonstrated inhibition of zoospore differentiation by Ph. cinnamomi sporangia in the presence of soil bacteria. The cytoplasm underwent one of two possible fates, it was either expelled in an undifferentiated state (Plate.....) or the aperculum failed to open and lysed within the sporangia. Transmission electron micrographs of these abortive sporangia showed bacteria on the outer surface immediately above the area of collapsing cytoplasm (Plate.....). This observation lends further support that some bacteria are actively involved in the production of extracellular compounds capable of initiating lysis. It may be profitable to pursue further research in the identification of these compounds for use as potential specific(?) fungicidal compounds.

Chlamydospores and oospores, being thick walled, are more resistant to antagonism by bacteria presumable because they do not exude compounds to attract soil bacteria while in a dormant state. Chlamydospores of Ph. cinnamomi incubated in soil showed little or no colonization by bacteria after 10 weeks even though most of the mycelium was lysed and buried in slime. Laboratory experiments (Malajczuk, unpublished) using selected antibiotic producing bacteria at 10^6 cells per gram soil showed some colonization of chalmydospores of Ph. cinnamomi however the viability was unaffected. To date no predatore bacterium capable of secreting extracellular enzymes to breakdown fungal cell walls have been isolated from Phytophthora propagules. Both Wynn and Epton (1979) and Sneh et al. (1977) found bacteria associated with lysed oospores however it may be assumed that in these instances they were not the primary parasites since parasitic chytrids and actinomycetes were also found attached to the spores.

Actinomycetes are also readily isolated from Phytophthora propagules and have been shown to be active parasitic agents of Ph. megasperma var. sojal and Ph. cactorum oospores (Sneh et al., 1977). They are a major group of microorganism that produce antibiotic in vitro against many of Phytophthora species found in agricultural and forest soils in Australia (Broadbent et al., 1971; Malajczuk and Parker, 1981) and are a dominant microorganism in Phytophthora suppressive soils (Weste and Wilhange, 1977, 1978; Malajczuk and McComb, 1979). Since actinomycetes are more prevalent in dry soils (Kouyeas, 1964; Chen and Griffin, 1966) and produce more antibiotics at low water potential (Wong and Griffin, 1974) their activity on Phytophthoras may be restricted to resting structures that are formed under adverse soil conditions where

zoospore movement and hyphal growth is minimal. Such conditions would prevail in well drained soils typical of these suppressive to the pathogen.

Fungi.

Although there are numerous studies reporting antagonism among fungi of great diversity (Barnett and Bender, 1973; Boosalis, 1964 and Bossalis and Mankau, 1965), the extent of these interaction between Phytophthora and other groups under in vitro and in vivo conditions and their possible importance in the mechanism of fungal propagle reduction remains largely unexplored (Table 4). There have been a limited number of observations of antibiotic production by soil fungi e.g. Penicillium and Trichoderma spp. with the main emphasis on Basidiomycetes because of their importance as possible biological detterents against Phytophthoras when in symbiotic association with plant roots (see later). Special interest has also been shown in species of Trichoderma because of their ability to induce development of sex organs in some normally sterile isolates of Phytophthoras (Brazier, 1967, 1971, 1972a,b; Pratt et al., 1972; Reeves and Jackson, 1972). Invariably this effect in the morphological change is associated with the antagonism of vegetative growth bt either volatile or soluble metabolites (Brazier, 1975a). In this in vitro study it was observed that Trichoderma volatiles initiated a reduction of growth role of Phytophthoras followed by vacuolation of cell contents which eventually resulted in lysis of hyphal tips. A similar reaction occurred when both species were grown on agar, however the Trichoderma eventually overgrew of Phytophthora culture and parasitized the hyphae. Antibiotics have subsequently been described by Dennis and Webster (1971a,b) which possibly accounts for much of the antagonistic activity of Trichodermas.

Studies in the behaviour of Ph. cinnamomi in soil reaffirmed the role of Trichodermas as common antagonists involved in the stimulation of oospore formation, lysis of hyphae (Reeves, 1975; Malajczuk and Theodorou, 1979) and chlamydospore production (Kelley, 1977). Clearly, the formation of resting structures in the presence of potential fungal antagonists parallels the role of antagonistic bacteria and is an important mechanism involved in the survival of Phytophtheras. The fact that Trichodermas are commonly associates of decaying plant tissue in soil (Jensen, 1963; Malajczuk and McComb, 1979) highlights how Phytophthora have developed survival mechanisms for their persistance in soils. It remains to be determined whether the metabolites are directly involved in the stimulation of the resting structures or whether it is a secondary response to breakdown of cytoplasm within Phytophthora hyphae. Some evidence favouring the latter suggestion is provided in the report by Mukerjie and Roy (1962) who showed the induction of Ph. parasitica oospores by a soil bacterium, Xanthomonas. In this context, it would be interesting to determine the range of soil fungi that may also initiate this reaction considering the range of species involved in the decomposition of plant tissue (Swift, 1979).

Hyphal lysis of Phytophthora initiated by soil fungi is rapid and as observed with Trichoderma species involves the contact and coiling as parasite around the hyphae prior to penetration (Plate....). Presumably, the attraction of these antagonistic fungi to Phytophthora hyphae is mediated by exudation of hyphal metabolites although this is an area where information is lacking and warrants research.

Mycoparasitism of Phycomycetes resting structures has been reported as a natural phenomenon occurring in soil (Drechsler, 1939) hwoever the significance of this antagonism in reducing the population

levels of Phytophthoras is less understood. To date a number of parasitic fungi have been identified capable of penetrating thick walls of both chlamydospores and oospores (Table 4). Sneh et al. (1977) and Wynn and Epton (1979) identified oomycetes, hyphomycetes and chytridiomycetes as parasitic agents of oospores of Ph. megasperma var sojae, Ph. cactorum and Ph. erythroseptica. Soil water moisture governs the succession of fungi invading oospores; in moist soils oomycetes genera and chyrids predominate while in relatively dry soils hyphomycete genera have been isolated. In this context we have observed chytrids parasitising Ph. cinnamomi sporangia (Plate.....) in soil leachates but rarely round in soil per se.

There is some suggestion that there may exist a degree of host specificity of fungal parasites to oospores of the different Phytophthoras which may suggest the selected fungi may be exploited for possible manipulation as biological controlling agents against the pathogesn.

Soil microfauna.

A large component of soil microbiota that has largely been ignored by pathologists is the microfauna. Only recently Old and Darbyshire (1978) and Old and Patrick (1979) demonstrated the mycophageous habit of vampyrellid and testate amoeba of a range of morphologically different fungal species. This involved the elaborate physical/chemical(?) hole production in the fungal walls and the digestion of the cellular contents (Old, 1977). Old and Darbyshire (1978) and Old and Oros (1980) showed lysis of oospores of Ph. fraganiae and hyphae and chlamydospores of Ph. cinnamomi respectively. In the latter study large holes were observed which were typical of spare destruction initiated by the vampyrellid amoebae Arachnula impatiens Cunk. (Old, 1978). Malajczuk (1979b) observed similar holes in

Ph. cinnamomi hyphae when incubated in soils suppressive to the pathogen (Plate.....). These soils were characterized as being totally "aline" with a wide range of morphological different types of testate and naked amoebae (Plate.....). Aliated protozoa were invariably associated with discharging sporangia (Plate.....). Similar groups belonging to the Hartmannellidae group have been reported injesting and lysing Ph. cinnamomi zoospores (Polzer, 1976 Thesis). Conducive soil also contained many of these amoebae but their numbers were much lower. It would appear that the occurrence of mycophagous amoebae is widespread and their action non-specific. They probably exert a general antagonism of most fungal propagules in both forest and agricultural soils such that their manipulation for biological contro of Phytophthoras may be limited. However studies need to be initiated to examine for their specific role (many) in diseas suppression before such conclusions are reached.

Predaceous nematodes and mites are groups of soil fauna that has not received any attention with regards to investigations of antagonism of Phytophthora propagules. As with amoebae, it is envisaged that their food preference may be non specific. Reports to date investigating soil nematodes and mite role in root disease development is somewhat discouraging Meagher et al. (1978) reported that nematodes enhance root disease severity as did soil mites (Shew and Beute, 1979).

ANTAGONISM OF PHYTOPHTHORAS IN THE RHIZOSPHERE

Root exudates and rhizosphere phenomenon.

As a plant root grows through soil the abrasive action of soil particles together with the expansion of root cells results in the

loss and leakage of organic compounds termed root exudates (Rovira, 1969; Hale and Moore, 1979; Hale et al., 1978). Among the constituents exuded are sugars, amino acids, organic acids, vitamins, nucleotides, flavones and enzymes. The root exudates differ qualitatively and quantitatively from different varieties as a resuls. Microorganisms are stimulated in the region around the plant roots (rhizosphere) or on the root surface (rhizoplane). Selectively stimulate different groups of microorganisms and/or influence the growth of certain pathogens have been reported (Bowen and Rovira, 1976).

Considerable evidence has been provided to show that root exudates are of major importance in stimulating the germination of Phytophthora chlamydospores, growth of mycelium and the attraction of zoospore in the rhizosphere (Hickman, 1970; Zentmeyer, 1980) and this response appears to be non-specific, occurring alike to susceptible and resistant host roots (Malajczuk and McComb, 1977; Ho and Zentmyer, 1977; Chi and Sabo, 1978). The indirect effect of root exudates, in stimulating an antagonistic micorflora for suppressing growth and inhibition of spore germination and attraction, has been neglected and may have direct relationship to susceptibility and resistance of plant species to infection by Phytophthera. Garrett (1970) described the rhizosphere as the outmost defense of a plant against root attack since reports in the ature indicate that root exudates selectively stimulate microbial populations antagonistic to number of pathogens (Bowen and Rovira, 1976; Schroth and Hildebrand, 1964). This specificity is known to be partially determined by host (Neal et al., 1970) and is clearly exhibited in symbiotic associations between the root nodule bacterium (Rhizobium) and its legume host (Nutman, 1965; Vincent, 1965) and between mycorrhizal fungi and tree roots (Bowen and Theodorou, 1973; Harley, 1969).

Role of rhizosphere microorganisms in limiting Phytophthera

There are a number of reports which indicate that rhizosphere populations per se can limit Phytophthera disease. Palzer (1976) carried out a number of precise inoculation experiments of lupin (Lupinus angustifolia L.) roots, with and without established rhizospheres, with zoospores of Ph. cinnamomi. Clearly the evidence indicated that rhizosphere microorganisms significantly reduced the infection of lupins by zoospores (Table 5) however the mechanism for this suppression was not determined. Malajczuk et al. (1977) provided a more detailed study of this nature when examining the differential susceptibility of eucalypts to infection of Ph. cinnamomi. In conducive, lateritic soil E. marginata was susceptible while E. calophylla showed resistance to the pathogen. When grown aseptically on sterile sand both eucalypt seedlings succumbed readily to infection. The addition of small quantities of lateritic soil to the sterile sand resulted in the differential susceptibility to become apparent. Since the quantities of natural soil added were insignificant to alter the physical or natural soil added were insignificant to alter the physical or chemical nature of the sterile sand the basis of resistance of E. calophylla was ascribed to the differential selection of rhizosphere populations (Malajczuk et al. 1977). ubsequent studies indicated that E. calophylla seedlings harboured a more intense rhizosphere population which was significantly more antagonistic to Ph. cinnamomi than that found in the E. marginata rhizosphere (Table 2). Although E. marginata seedlings succumbed to infection by the pathogen the amount of diseased root was invariably less in natural soil than in sterile sand. Examination of eucalypt roots under light and scanning electron microscopy revealed microcolonies of bacterial and actinomycete cells in cell junctions where infection

of Ph. cinnamomi normally takes place (Malajczuk & McComb). Encysted zoospores on root surfaces have also been shown to be intensely colonized by both bacterial and actinomycete cells (Plate.....) suggesting active antagonism of the fungus. Although the rhizosphere bacteria and actinomycetes can significantly affect Phytophthora propagules when attracted to the root surface, their low surface occupancy (between 1-20% - Bowen and Rovira, 1976) may not offer a total protection against Phytophthoras which are rapid in their movement to and infection of root tissue. In this respect symbiotic systems of plant roots may be of more significance.

Role of root symbiotic microorganisms in limiting Phytophthora

Symbiotic microorganism associated with plant roots have the advantage over the other rhizosphere colonizers in that the association is specific allowing for a rapid build-up of these microorganisms in the rhizosphere in preference to other rhizosphere inhabitants. As well as colonization of the rhizosphere, symbiotic microorganisms invade the host tissue electing both monphological and biochemical changes in host tissue which possible incite additional resistance mechanisms to infection by Phytophthera species.

Rhizobial associations.

The legumes form symbiotic associations with members of the genus Rhizobium leading to the formation of nodules and participate in the aquisition of nitrogen (Vincent, 1965). The population of rhizobia in soil can be as high as 10^8 cells per g in soil (Nutman and Ross, 1969) and rhizosphere (Tuzimura and Watanabe, 1962; Chatel and Parker, 1973a,b). Undoubtly such high population levels must reflect their importance in influencing the establishment of alien microorganisms such as plant pathogens in the rhizosphere.

Trinick (1970) demonstrated the various types of interactions that exist between rhizobia and other microorganisms in the root of subclover (Trifolium subterraneum) which included antibiosis and competiton. More specifically rhizobia have been shown to produce antibiotics on agar against a range of root rot pathogens including Ph. cactorum (Drapeau et al., 1973) and colenize hyphae of Ph. megasperma initiating lysis (Tu, 1978, 1979). The evideor plant protection by rhizobia against Phytophtheras is somewhat contradictory. Chow and Schmitthenner (1974) found that Rhizobium inoculated soybean roots had no effect on reducing infection by Ph. megasperma var sojae while Tu (1978) observed in glasshouse trials root rot caused by this pathogen to be substantially reduced when the concentration of rhizobia in soil was increase (Table 6). Ina more recent study Tu (1980) confirmed these findings showing reduced root rot severity of alfalfa (Medicago sativa L.) to Ph. megasperma with increase concentration of rhizobia application. In both Tu's studies complete protection of plants did not occur. The failure to obtain disease free plants may be a reflection of the speed at which the Phytophthera zoospores colonized and infected roots preventing any interaction occurring with rhizobia. Obviously there is a need to understand the ecology of rhizobia in soil and rhizosphere in natural soils before conclusions of success or failure of Rhizobium inoculation are reached.

Mycorrhizal associations.

Mycorrhizae are widely distributed amont the high plant forms being recognized in 1000 genera of vascular plants (Gerdemann, 1968). The majority of agricultural crop species possess endo-mycorrhizae of the vesicular arbuscular type while the forest species

form ecto-mycorrhizae (Malajczuk and Lamont, 1980). These associations with plant roots have evolved with the exploitation of different habitats and function principally in nutrient uptake (Bowen, 1973). Their role as biological detterents to limit root infection by pathogenic fungi has only recently been recognized (Zak, 1964; Marx, 1972; Schönbeck, 1979). This latter function does seem a logical development since mycorrhizal associations and root rot initiated by Phytophthoras are similar in that both are intimately associated with the fine, unsuberized root system of plant species. The possession of this ecological niché by these microorganism would result in whether plant growth is stimulated (=mycorrhizae) or depressed (= Phytophtheras).

An examination of the anatomy of both type of mycorrhizal roots reveal a basic difference which possibly may reflect in different mechanisms for resistance to Phytophtheras. Ectomycorrhizas are characterized by having the fungus producing an intricate mesh of hyphae on the root surface as tightly woven tissue termed the mantle (Plate.....). The sheath varies in thickness from a few microns to greater than 100 µm. In transverse section the fungus can be seen to penetrate intercellularly to form a network pattern termed the Hartig net. Associated with this penetration marked changes have been noted in host tissue (Chilvers and Pryor, 1965; Marks and Foster, 1973). These include, 1. thickening of the intertangential and raidal walls of the cortex, 2. elongation of epidermal cells, 3. developmentof tanniferous cells containing phenol compounds. Compared with non-mycorrhizal roots, typically the mycorrhizae are thicker, more branched and lacking root hairs. The fungal symbionts involved are mainly basidiomycetes and ascomycetes (Trappe, 1962, 1971). The vesicular arbuscular mycorrhizae on the other hand lack a fungal

mantle and Hartig net formation. The fungus penetrates root epidermal cells and proliferates between and within cortical cells (Plate.....). Intracellularly it usually branches to form the characteristic multi-branched hyphae termed arbuscules. The fungal symbionts in this instance are members in the zygomycete family Endogonaceae.

The role of ectomycorrhizae in limiting infection by Phytophthora, and mainly Ph. cinnamomi, has been reported for a wide range of tree hosts and fungal symbionts (Marx, 1973; Marais and and Kotze, 1976; Malajczuk, 1981; Ross and Marx, 1972), however, vesicular arbuscular mycorrhizae appear to have little or no effect on disease development (Table 7). The one positive response of reduce disease severity was reported by Davis and Menge (1980). Tolerance of citrus seedlings to Ph. parasitica was attributed tothe fact that mycorrhizal seedlings had the ability to compensate loss of potential growth nutrients (mainly phosphorus) in decaying roots by absorbing more nutrients via healthy roots. Although this may not appear to be an active mechanism for antagonism of the pathogen it may be the most important means by which all mycorrhizal plants survive in diseased soil. Active mechanisms agains Phytophthora invasion contribute to reducing the Phytophthora inoculum. These have been attributed to one or a combination of the following factors; 1. Reducing altering the root exudation pattern so as to reduce the root chemotaxis response of Phytophthora zoospores and stimulus for germinating chlamydospores and oospores. Marx and Davey (1969b) observed this phenomenon when examining the chemotactic behaviour of Ph. cinnamomi zoospores towards ectomycorrhizae and non-mycorrhizal roots of shortleaf and loblolly pine seedlings. Invaraibly zoospores germinated faster and more vigorously at the growing tip of non-mycorrhizal roots while enscysted zoospores on the ectomycorrhizae, germinated slowly and

grew poorly. Marx (1972) speculated that mycorrhizal roots may exude somewhat different compounts from non-mycorrhizal roots which accounted for these differences. No work of this nature has been carried out for vesicular arbuscular mycorrhizae although it is supected that increased root exudation may result from points of penetration, and due to the fact that there exist little mycorrhizal biomass to absorb this increased leachage; Phytophthora growth may be stimulated in the rhizosphere. 2. Secretion of actibiotics. As with other soil microorganisms selected ectomycorrhizal fungi have been shown to produce antibiotics in agar culture against mycleium Phytophthora species (Table 8) Marx (1969a,b) was also able to show a diatretyne nitrite compound produce by the ectomycorrhizal fungus Leucopaxillus cerealis var. piceina (Pick) to inhibited germination of zoospores of Ph. cinnamomi at 50-70 parts per billion and killed zoospores at 2 parts per million. This a related compounts were extracted from ectomycorrhizal roots formed by the fungal symbiont and in the adjacent substrate of axenically growing seedlings and were functional in the resistance of feeder root infection by the pathogen. The fungal symbionts of vesicular-arbuscular mycorrhizae have not been cultures to date such that conclusions of antibiotics production cannot be ascertained. 3. Provision of a mechanical barrier to pathogen in the form of a fungal mantle. Considering the elaborate structure of ectomycorrhizal mantle (Plate....) it may be expected that it would pose a formitable barrier to Phytophthora zoospore and mycelium penetration. Histological evidence is presented for ectomycorrhizae of pines (Marx and Davey, 1969a,b; Marx, 1970) and ecualypts (Malajczuk, 1981) formed by different fungal symbionts, including non-antibiotic producing fungi, showing lack of entry by the pathogn. Ph. cinnamomi zoospores could be ssen germinating and

hyphae growing randomly over the mantle surface (Plate.....). Obviously this is atypical of Phytophthora zoospores which normally rapidly encysted and germinate directly into plant tissue (Plate....). In caaes where the mantle was incomplete or damaged by nematodes (Barham et al., 1974) invasion of the cortical cells occurred. The lack of a similar mantle invesicular-arbuscular mycorrhizae is possibly the main single factor that significantly reduces their role as potential detterents to invasion by Phytophthoras. 4. Antagonistic mycorrhizosphere microorganisms. The microbial population in the vicinity of mycorrhizae roots, as distinct fhe rhizosphere, can act as yet another barrier to infection by Phytophthoras propagules. This microbial population is not only unique (Rawlings, 1958; Rambelli, 1973) but is also more intensely colonized the rhizosphere (Katznelson, 1962; Malajczuk, 1979a). The only data reporting on mycorrhizosphere populations antagonistic to Phytophthoras is that of Malajczuk (1981). approximately 5 percent of the total bacteria and actinomycetes in the mycorhizosphere of E. calophylla and E. marginata were antagonistic to Ph. cinnamomi on agar. Inoculation of eucalypt mycorrhizae with the pathogen's zoospores or mycelium showed that within hours hyphae were colonized by bacteria and lysis was evident. Presumably, the failure to rapidly penetrate the mantle allowed for antagonism of Ph. cinnamomi by the mycorrhizosphere microorganisms.

MICROBIAL ANTAGONISM WITHIN PLANT TISSUE

The nature of antagonism has so far been considered external to the root tissue. Phytophthora species adapted to this environment and not being totally inhibited by antagonism by rhizosphere micro-organisms usually penetrate tissue of both resistant and susce½ton;e

species and varieties (Hohl and Stösse, 1976; Hohl and Suter, 1976; Klisiewriz and Johnson, 1968; Malajczuk et al., 1977; Tippett et al., 1976). Further development of the diseas depends on the pathogen overcoming resistant mechanisms within the root tissue. Host resistance to Phytophthora species have included mechanical barriers such as thickness of wall, suberization, lignification and physiological/ biochemical barriers such as phytalexin production, hypersensitive reactions or presence of phytotoxic phenols (Hol and Suter, 1976; Keen et al., 1971, Shimony and Friend, 1975; Tippett and Malajczuk, 1979; Tomiyama, 1971). The fungus in response to these mechanisms is either lysed or produces resting structures. An aspect that has been totally neglected is the role of secondary invaders, either sapraphytic or mildly parasitic, and their interaction with Phytophthora propagules in the infection court and the various resistant mechanisms. Obviously the penetration of root tissue by Phytophthora mycelium and zoospores result in the plant leaking an increased amount of root exudates which in turn would stimulate a greater microbial population in the rhizosphere and within plant tissue. Old and Nicolson (1975) demonstrated the presence of a wide range of morphological distinct bacteria and fungi in the epidermal and cortical cells and it is evident that bacteria are stimulated on the root surface Ph. cinnamomi infecting susceptible eucalypt root tissue (Plate.....). In a separate experiment we have shown that disease eucalypt root caused by Ph. cinnamomi of both susceptible and resistant eucalypt species had a preponderance of antibiotic producing Penicillium, Aspergillus and Trichoderma species. Since it is extremely difficult to isolate the pathogen from diseased feeder roots it was presumed that microbial antagonism resulted in an elimination of the fungus. This conclusion is supported by the observation of root regeneration

occurring immediately ahead of where the root was damaged in both susceptible and resistant species. It may appear that in this case it is again a question of growth rate of the Phytophthora mycelium in relation to the multiplication and growth of the secondary invaders which determines the success or failure of the pathogen. There is obviously a need for more precise investigations into this aspect of interaction within plant tissue of both susceptible and resistant species or varieties to determine the contribution (if any) of the antagonists in the host resistance.

A variation on this theme, which may have some practical importance, is the use of similar strains or aavirulent fungi for cross protecting against a pathogen. Much of the early work conducted in this area was in the field of plant virology. Matthews (1980) postulated that if two isolates of virus are identical, they will react similiarly, if they are related but distinct some degree of cross reaction between them will be observed. Further, the infection of a plant by one strain of a virus causing only mild disease symptoms, may protect it from a more severe strain by either inciting a host reaction or affecting the pathogenic strain directly. Evidence of cross-protection by Phytophthora species is limited. However, studies by Klarman and Gerdemann (1963a,b) and Klarman (1968) showed that phytoalexin production was stimulated in soybean tissue of both susceptible and resistant varieties following infection by both pathogenic and non-pathogenic strains of Ph. megasperma var sojae. Subsequent work by Paxton and Chamberlain (1967) demonstrated a marked degree of local cross protection of a susceptible soybean variety to the pathogen when plants were initially inoculated with a non-pathogenic fungus, Ph. cactorum. In a recent study Bonstel (1979) demonstrated in pot culture the cross-protection of two forest species in Western

Australia, Banksia grandis Willd. and Casuarina fraseriana Mig. to infection by the pathogen Ph. cinnamomi if the tree seedlings were preinoculated with Pythium irregulare Buism. The mechanism for pathogen suppression was not determined although indications were that there occurred an hypersensitive reaction in roots following P. irregulare inoculation which reduced tha ttractiveness of roots to Ph. cinnamomi. Further, many Pythium species are readily isolated from diseased roots in field samples in forest areas where Ph. cinnamomi occurs but cannot be isolated (Malajczuk, unpublished) suggest that the phenomenon of fross protection may be widespread with many other Pythium species involved.

Examples of host resistance incited by these mildly parasitic pathogen with a wide host range such as P. irregulare (Robertson, 1973) may offer a potential antagonist for manipulation against many of the pathogenic Phytophthoras. Obviously the benefits of reduced crop yield from Pythium damage need be weighed against more severe losses from the Phytophthoras.

MANIPULATION OF ANTAGONISTIC MICROORGANISMS AGAINST PHYTOPHTHORAS

Organic matter.

The augmentation of soil with organic matter for hardwood promoting biological control of soil borne pathogens has gained considerable interest in the last few years because of some spectacular results obtained by a number of researchers in both glasshouse and field experimentation (Baker and Cook, 1974). The role of these amendments appears to be related to the suppression of the pathogen in both soil and rhizosphere although little experimentation as to precise mechanisms involved has been determined (Cook, 1977). The

quality of the organic amendments has a strong influence on whether or not pathogens are suppressed and this has led to investigations of a range of different organic substrates for disease control. In this respect, control of Phytophthorus by this means has had an interesting history which has resulted in cases of effective control of the pathogen, in particular Ph. cinnamomi.

Early investivation sby Zentmyer (1963) showed that soils amended with alfalfa meal reduced the severity of root rot of avocado seedlings cause by Ph. cinnamomi. Increased microbial activity and presumably microbial antagonism of the pathogen was considered as the main factor associated with disease suppression. Subsequent research by Gilpatrick (1969a,b) indicated that ammonia production associated with the microbial decomposition of alfalfa meal as well as microbial antagonism were the main factors affecting pathogen survival. Although glasshouse trials and in vitro studies of the pathogen showed this marked response, field experimentation failed to give total control of the pathogen. In fact, alfalfa meal proved to be phytotoxic to root growth (Gilpatrick, 1969b). Differences in pot and field results are often difficult to explain but possible in this instance rate of alfalfa meal application as well as the rate at which it decomposes and build up the number of microbial antagonists may be possible explanations. In this context, composting of hardwood bark prior to the preparation of soil mixes for nursery grown plants has been successful in the control of Ph. cinnamomi and other pathogens in the ornamental plant industry (Haitink et al., 1975, 1976). The composting process involveds the natural, aerobic, thermophilic breakdown of bark with nitrogen amendments. This allows for rapid build up of various phageous and antagonistic microorganisms including actinomycetes, fluorescent pseudomonads and Trichoderma sp. (Hoitink,

1980) which contribute to lysis of Ph. cinnamomi hyphae, zoospores and germinating cysts (Hoitink et al., 1977).

Perhaps the best example of field control of Phytophthora with organic amendments exist in Australia where a number of avoccado growers have addopted "organic farming: to maintain high levels of organic matter in soil. This is achieved by green cropping beneath the trees with legumes and forage crops and incorporating it into soil with minimal disturbance. Additional organic matter is added as mulches using straw. Fowl manure and dolimate is also added to the surface to encourage rapid breakdown of this organic matter (Pegg, 1977). Apart from the build-up in the nutrient status of soils, the microbial activity is enhanced which favours an antagonistic soil microflora and a disease free orchard; whereas orchards which have little build up of organic matter have a much reduced microflora and severe root rot (Broadbent and Baker, 1974a). Studies by Tsao (1977) showed promising in vitro control of Ph. cinnamomi and Ph. parasitica in avocado and citrus soils using nitrogenous organic amendments. Chicken mature, alfalfa meal and processed dewage sludge rendered the soil suppressive (increased hyphal lysis and sporangial abortion) as a result of increased microbial activity associated with the decomposing amendments in soil.

Logically if follows that depletion of the organic status of soils may be the all encompassing factor that has led to serve out breaks of disease caused by Ph. cinnamomi in Australia and perhaps Phytophthera diseases in general throughout agricultural and forestry soils. It is interesting to note that in Australian forest areas regular removal of litter is accomplished by a fire programme carried out on a cycling basis. The overall aim of this programme is to reduce the fire hazard of forests created during the dry summer

months. However, inadvertantly this produce may be reducing the microbial buffering capacity of soils to withstand invasion by Ph. cinnamomi thus contributing to severe outbreaks of damage in the indigenous eucalypt forests. Reduced mircobial activity (Weste and Vithanage, 1977; Malajczuk et al., 1977) and development of fewer mycorrhizal roots (Malajczuk and Hingston, 1981) have been shown to occur in Australian soils low in organic matter.

In Western Australia, the regular burning of the valuable E. marginata (jarrah) forest is being questioned in light of observations and experimentation that these regular low intensity fires are creating favourable conditions for the development of Ph. cinnamomi in these soils by reducing the organic matter status of soils and favouring development of a susceptive proteaceous understorey (Shea, 1975; Shea and Malajczuk, 1977). Field experiments have commenced to burn the forest with moderate to high intensity fires during the summer period at longer intervals between burns (Shea et al., 1979). This would allow for litter to accumulate and decompose over a longer period of time encouraging the development of antagonistic microorganisms (Nesbitt et al., 1979) and ectomycorrhizae (Malajczuk and Hingston, 1981). In addition high intensity fires favour the development of leguminous understorey in preference to the susceptible proteaceous one. The common legume, Acacia pulchella R.Br. has been shown to be totally resistant to infection by the pathogen (Tippett and Malajczuk, 1979) and appears to be to reduce the infection of susceptible jarrah seedlings when grown together in pots (Shea and Malajczuk, 1977). There is evidence of hyphal lysis and sporangial abortion indicated by microorganisms that develop in the rhizosphere and soil under legumes which reduce the inoculum of Ph. cinnamomi (Shea and Malajczuk, 1977).

Fertilizers.

The application of fertilizers to the environment to improve the nutrient supply for plant growth canals increase the resistance of plants by influencing an array of changes to both soil and rhizosphere microflora. These changes may be mediated via host physiology e.g., root exudates or soil chemical status e.g. pH (Baker and Cook, 1974; Cook, 1977; Hanis and Kotan, 1975).

Nitrogen fertilizers have been shown to have a wide range of effects on Phytophthora disease severity as well as on propagules. Invitro studies report NO_3^- and NH_4^+ fertilizers to be highly toxic to Phytophthoras (McIntosh, 1972; Tsao et al., 1975; Zentmyer and Bingham, 1956) on one hand while stimulating sporulation (Halsell, 1978) and increasing disease severity (Apple, 1961) on the other. In fact Tsao and Zentmyer (1979) showed that NH_4^+ and No_3^- applied to soil was toxic to Ph. cinnamomi sporangia but a little to non-toxic to Ph. parasitica. This differential tolerance may explain some of the difference in the results however it is more probable that metabolic byproducts produced by the utilization of these nitrogen compounds and their effect on Phytophtheras is the key to these discrepencies in literature. In a recent study by Tsao and Zentmyer suppression of Ph. cinnamomi and Ph. parasitica was obtained in pots when the soil was mended with urea. Aqueous extracts of amended soil inhibited germination and formation of Phytophthora sporangia where as the filter sterilized urea was non toxic to the pathogens. This type of suppression is an example of broadly defined biological control (Baker and Cook, 1974).

Phosphorus is a nutrient element that is second only to nitrogen in importance in plant and microbial growth. This element has been shown to be important for the development of mycorrhizae at levels

suboptimal for maximal plant growth (Bowen, 1973). It should follow therefore that increased mycorrhizal root development would influence the development of Phytophthora diseases. According to Newhook (1970) the outbreaks of Ph. cinnamomi in stands of Pinus radiata in New Zealand is simply a phosphorus deficiency problem since application of phosphorus fertilizers to some of these stands not only improved tree vigor directly but increased the development of ectomycorrhizal root growth.

A similar effect was also observed by Boughton et al. (1978) where suppression of Ph. cinnamomi infection of E. marginata roots occurred with the application of calcium carbonate. The decrease in frequency of Ph. cinnamomi isolated from burned seedlings was correlated with an increase in the development of ectomycorrhizal roots.

Sulphur application to pineapple cropps infested with P. cinnamomi was found by Pegg (1977) to control the pathogen. The nature of suppression appeared to be related to the explosion in the population of Trichoderma viride in sulphured soils. T. veride is known to be a potential antagonist of Ph. cinnamomi (Table 4).

Pesticides

As with fertilizers, pesticides can act directly in controlling plant pathogens via stimulating microbial antagonists (Rodriguez-Kabana and Curl, 1980). Exmaples of this intergrated approach to controlling Phytophthoras are few possibly because of the researchers pre-occupation with the firect action of pesticides. Recently Boughton and Malajczuk (unpublished) found that there exists a marked interaction between soil microorganisms and the fungicide Ridomil® (CGA48988 - Cieber-Giegy) (Fig. 7). Hyphal lysis of Ph. cinnamomi was accelerated non-sterile leachates plus Ridomil® to a rule of 10 mg/l as compared with sterial treatments.

Obviously it is necessary to carry out similar types of studies to determine the mechanisms of action of other potential pesticides to develop prudent application rates to minimize possible side-effects associated with an overkill situation.

Introduced Antagonists.

The introduction of specific antagonists into soil for biological control of plant pathogens represents an aspect of research which aims to emulate that of chemical control without the possible side effects. However the poor success to date is a reflection of the lack of appreciation of the complex interactions that exist in natural by pathologist. Often there is a tendency to ignore preliminary work of findout out how the antagonist survives, grows and functions in soil and immediately embark on investigations into the success or failure of these antagonists in limiting disease. Successful examples of biological control of Phytophthora are limited to situations where the antagonists are introduced into pretreated soil e.g., sterilized fumigated or steamed consisting of a much simpler microflora-fauna of reduced interactive complexity. Malajczuk (1980) introduced a range of bacterial and actinomycete isolates into sterile soil and examined their effect on limiting root rot of two eucalypts caused by Ph. cinnamomi. The presence of these selected isolates of microorganisms had varying effects on disease development in both eucalypts and this varied with time of sampling (Table 9). Streptomycete isolates were most effective in limiting disease of both eucalypts while bacterial isolate #8 only with E. marginata seedlings. No single microorganism total eliminated disease development even though all isolates showed antibiotic production to Ph. cinnamomi on agar. Failure of protection of eucalypt seedlings with these micro

organisms may have been due to either the failure of the isolates to colonize the soil substrate or the inability to grow and function in the rhizosphere. Biological control of Ph. megasperma var sojae was reported by Sarbini and Kmmendahl (1977) by inoculation of soybean seed pellets with an antagonistic Pseudomonas isolate. In this instance, the antagonists colonized and persisted in the rhizosphere for considerable lengths of time.

The few fungi tested for Phytophthora disease suppression have also given some mixed results. El-Goorangi et al. (1976) found that Ph. cryptogea was prevented by Pencillium patulum from attacking summer squash seedlings in autoclaved soil whil Vaatoya et al. (1979) reported that the antagonist GlioElodium urens gave not significant protection to soybean plants from Ph. megasperma var sojae in either greenhouse of field experiments even though G. virens was readily isolated from the soil.

CONCLUSION

Microbial antagonism of Phytophthoras may be expected in all situations involving a wide range of microflora and fauna. The pathogens in turn have evolved the ability to counter these interactions by producing propagules which enable it to survive under these adverse conditions. The challenge for pathologist is to anticipate possible changes in the Phytophthoras life stage to bring about control. The control by using antagonistic microorganism is considered to be the ultimate goal that we face however to date the state of art is severely deficient in the number of positive examples. There is the need to develop an understanding of not only the behaviour of the pathogen in soil, rhizosphere or within plant tissue but the

antagonist as well. The approach by Bowen (1980) of developing theoretical models to understand the changes of the pathogen in relationship to the antagonist under different environmental parameters will help lay down principles for predicting epidermics or control of the pathogen. Obviously, using guides provided to us in situations where the Phytophthoras are naturally suppressed wil help along the way. The use of selective stains, fluorescent brightners (Tsao, 1970) and immuno-fluorescent techniques (Malajczuk et al., 1975, 1978) would be powerful tools to help visualize the activity of both Phytophthora and antagonist(s) in situ while scanning and transmission electron microscopy may indicate the type and nature of interaction. Only with this information the realization of biocontrol of Phytophthoras will be brought about.

SUMMARY

Behaviour of Phytophthora species is markedly affected by soil micro-organisms resulting in either the stimulation or antagonism of fungal propagules. Forms of antagonism include predation, parasitism, amensalism and competition and occurs in both soil and rhizosphere of plant species. The degree to which suppression of the Phytophthora disease occurs varies with soil type and cultural practive.

Hyphal lysis is rapid and is invariably associated with spore formation. Sporangia and zoospores are themselves subjected to rapid breakdown following their invitation and release in soil. Chlamydospores and oospores can survive for considerably longer periods in soil prior to their microbial degradation.

Stimulation of microbial activity in the hyphasphere is due to exudation of organic compounds from growing hyphae and the autolysis of older portions of hyphae. Bacteria are common associates of

hyphae and include Pseudomonas, Bacillus and Streptomycete species. Many of these species isolated from lysed hyphae have been shown to be antagonistic in vitro however it is still uncertain as to the precise role of these specific bacteria in hyphal and sporangial lysis. Chyrids and Trichoderma species have been observed to be active in parasitism of Phytophthora hyphae leading to its breakdown and decay in soil. Protozoa and fungal mites are commonly mycophagous biota attacking hyphae and chlamydospores. Small naked amoebae have also been seen to ingest and lyse zoospores.

The rhizosphere poses a more formidable microbial barrier and is attributed to the resistance of some plant species to root disease. Symbiotic microorganisms (mycorrhizal fungi and rhizobia) have been implicated in antagonism of Phytophthora species.

The fact that microorganisms are involved in the suppression of Phytophthora disease indicates that the manipulation of these microorganisms by various land management techniques may realize the goal of biological control of Phytophthora in both agriculture and forestry. Obviously more work is needed to develop a better understanding of the interaction of soil and rhizosphere microorganisms and Phytophthoras.

REFERENCES

ALEXANDER, M. 1971. Microbial Ecology. John Wiley, New York. 511pp.

AYERS, W.A. 1971. Induction of sporangia in Phytophthora cinnamomi by a substance from bacteria and soil. Can. J. Microbiol. 17:1517-1523.

BAKER, K.F., and R.J. COOK. 1974. Biological Control of Plant Pathogens. San Francisco, Freeman. 433pp.

BAKER, R. 1968. Mechanisms of biological control of soil-borne pathogens. Annu. Rev. Phytopathol. 6:263-294.

BAKER, K.F., and W.C. SNYDER. 1965. Ecology of Soil-borne Plant Pathogens. Prelude to Biological Control. Univ. Calif. Press, Berkeley. 571 pp.

BALD, J.G. 1937. The use of number of infections for comparing the concentration of plant virus suspensions. I. Dilution experiments with pure suspensions. Ann. Appl. Biol. 24:33-55.

BARHAM, R.O., D.H. MARX, AND J.L. RUELHE. 1974. Infection of ectomycorrhizal and nonmycorrhizal roots of short leaf pine by enmatodes and Phytophthora cinnamomi. Phytopathology 64:1260-1264.

BARNETT, H.L., and F.L. BENDER. 1973. The fungal host-parasite relationship. Annu. Rev. Phytopathol. 11:273-292.

BASU, P.K. 1980). Production of chlamydospores of Phytophthora megasperma and their possible role in primary infection and survival in soil. Can. J. Pl. Pathol. 2:70-75.

BOOSALIS, M.G. 1964. Hyperparasitism. Annu. Rev. Phytopathol. 2:363-76.

BOOSALIS, M.G., and R.H. MANKAU. 1965. Parasitism and predation of soil microorganisms. Pages 374-391 in: K.F. Baker and W.C. Snyder, eds, Ecology of Soil-Borne Plant Pathogens. Univ. California Press.

BORSTEL, P.J. 1979. Cross protecting several West Australian native plants against Phytophthora cinnamomi Rands. unsing Pythium irregulare Buism. Honours Dissertation. University of Western Australia. 130 pp.

BOUGHTON, T., N. MALAJCZUK., and A.D. ROBSON. 1978. Suppression of the infection of jarrah roots by Phytophthora cinnamomi with application of calcium carbonate. Aust. J. Bot. 26:611-615.

BOWEN, G.D. 1973. Mineral nutrition of ectomycorrhizae. Pages 151-205 in: G.C. Marks and T.T. Kozlowski, eds. Ectomycorrhizae: Their Ecology and Physiology. Academic Press, New York.

BOWEN, G.D. 1980. Misconceptions, concepts and approaches in rhizosphere biology. Pages 283-304 in: D.C. Ellwood, J.N. Hedger, M.L. Latham, J.M. Lynch and J.H. Slater, eds. Contemporary Microbial Ecology. Academic Press, London.

BOWEN, G.D., and A.D. ROVIRA. 1976. Microbial colonization of plant roots. Annu. Rev. Phytopathol. 14:121-144.

BOWEN, G.D., and C. THEODOROU. 1973. Growth of ectomycorrhizal fungi around seeds and roots. Pages 107-150 in: G.C. Marks and T.t. Kozlowski, eds. Ectomycorrhizae: Their Ecology and Physiology. Academic Press, New York.

BRASIER, C.M. 1971. Induction of sexual reproduction in single A^2 isolates of Phytophthora by Trichoderma viride. Nature New Biol. Lond. 231:283.

BRASIER, C.M. 1972. Observations on the sexual mechanism in Phytophthora palmivora and related species. Trans. Br. mycol. Soc. 58:237-251.

BRASIER, C.M. 1975a. Stimulation of sex organ formation of Phytophthora by antagonistic species of Trichoderma. I. The effect in vitro. New Phytol. 74:183-194.

BRASIER, C.M. 1975b. Stimulation of sex organ formation in Phytophthora by antagonistic species of Trichoderma. II. Ecological implications. New Phytol. 74:195-198.

BRIAN, P.W. 1957. The ecological significance of antibiotic production. Pages 156-188 in: R.E.O. Williams and C.C. Spicer, eds. Microbial Ecology. Cambridge Univ. Press, Cambridge.

BRIAN, P.W. 1960. Antagonistic and competative mechanisms limiting survival and activity of fungi in soil. Pages 115-129 in: D. Parkinson and J.S. Waid, eds. Liverpool Univ. Press, Liverpool.

BROADBENT, P., K.F. BAKER, Y. WATERWORTH. 1971. Bacteria and actinomycetes antagonistic to fungal root pathogens in Australian soils. Aust. J. Biol. Sci. 24:925-944.

BROADBENT, P., and K.F. BAKER. 1974a. Behaviour of Phytophthora cinnamomi in soils suppressive and conducive to root rot. Aust. J. Agric. Res. 25:121-37.

BROADBENT, P., and K.F. Baker. 1974b. Association of bacteria with sporangium formation and breakdown of sporangia in Phytophthora spp. Aust. J. Agric. Res. 25:139-45.

BROWN, B.N. 1976. Phytophthora cinnamomi associated with patch death in tropical rain forests in Queensland. A.P.P.S. Newsletter 5:1-4.

BUMBIERIS, M. 1979. Aspects of the biology of Phytophthora cryptogea. Aust. J. Bot. 27:11-16.

CHATEL, D.L., and C.A. PARKER. 1973a. Survival of field-grown rhizobia over the dry summer period in Western Australia. Soil Biol. Biochem. 5:415-423.

CHATEL, D.L., and C.A. PARKER. 1973b. The colonization of host-root and soil by rhizobia. I. Species and strain differences in the field. Soil Biol. Biochem. 5:425-432.

CHEN, A.W.C., and D.M. GRIFFIN. 1966. Soil physical factors and the ecology of fungi. V. Further studies in relatively dry soils. Trans. Br. mycol. Soc. 49:419-426.

CHI, C.C., and E. SABO. 1978. Chemataxis of zoospores of Phytophthora megasperma to primary roots of alfalfa seedlings. Can. J. Bot. 56:795-800.

CHILVERS, G.A., and L.D. PRYOR. 1965. The structure of eucalypt mycorrhizae. Aust. J. Bot. 13:245-259.

CHOU, L.G., and A.F. SCHMITTHENNER. 1974. Effect of Rhizobium japonicum and Endogone mosseae on soybean root rot caused by Phythium ultimum and Phytophthora megasperma var. sojae. Plant Dis. Rep. 58:221-225.

CLARK, F.E. 1968. The concept of competition in microbial ecology. Pages 339-345 in: K.F. Baker and W.C. Snyder, eds. Ecology of Soil-Borne Plant Pathogens. Univ. California Press.

COOK, R.J. 1977. Management of the associated microbiota. Pages 145-166 in: J.G. Horsfall and E.B. Cowling, eds. Plant Disease: An Advanced Treatise. Academic Press, New York.

COOK, R.J., and R.I. PAPENDICK. 1972. Influence of water potential of soils and plant on root diseases. Annu. Rev. Phytopathol. 10:349-374.

DANIELSON, R.M., and C.B. DAVEY. 1973. The abundance of Trichoderma propagules and distribution of species in forest soil. Soil Biol. Biochem. 5:485-494.

DAVIS, R.M., J.A. MENGE, and G.A. ZENTMYER. 1978. Influence of vesicular-arbuscular mycorrhizae on Phytophthora root rot of three crop plants. Phytopathology 68:1614-1617.

DAVIS, R.M., and J.A. MENGE. 1980. Influence of Glomus fasciculatus and soil phosphorus on Phytophthora root rot of citrus. Phytopathology 70:447-452.

DENNIS, C., and J. WEBSTER. 1971a. Antagonistic properties of species-groups of Trichoderma. I. Production of non-volatile antibiotics. Trans. Br. mycol. Soc. 57:25-39.

DENNIS, C., and J. WEBSTER. 1971b. Antagonistic properties of species-groups of Trichoderma. II. Production of volatile antibiotics. Trans. Br. mycol. Soc. 57:41-49.

DENNIS, C., and J. WEBSTER. 1971c. Antagonistic properties of Species-groups of Trichoderma. III. Hyphal interaction. Trans. Br. mycol. Soc. 57:363-369.

DRAPEAU, R., J.A. FORTIN, and C. GAGON. 1973. Antifungal activity of Rhizobium. Can. J. Bot. 51: 681-682.

DRECHSLER, C. 1938. Two hypomycetes parasitic on oospores of root-rotting Oomycetes. Phytopathology 28:81-103.

DUNIWAY, J.M. 1975. Formation of sporangia by Phytophthora drechsleri in soil at high matric potentials. Can. J. Bot. 53:1270-1275.

DUNIWAY, J.M. 1979. Water relations of water molds. Annu. Rev. Phytopathol. 17:431-460.

DURRELL, L.W. 1966. Hyphal invasion by Trichoderma viride. Mycopath. Mycol. appl. 35:138-144.

EL-GOORANGI, MA., S.A. FARAG, and M.R.A. SHEHATA. 1976. The effect of Bacillus subtilis and Penicillium patulum on in vitro growth and pathogenicity of Rhizoctonia salani and Phytophthora crytogea. Phytopath. Z. 85:345-351.

ERWIN, D.C., and H. KATZNELSON. 1961. Suppression and stimulation of mycelial growth of Phytophthora cryptogea by certain thiamine-requiring and thiamine-synthesizing bacteria. Can. J. Microbiol. 7:945-950.

FOKKEMA, N.J. 1978. Fungal antagonists in the phyllosphere. Ann. Appl. Biol. 89:115-119.

GARRETT, S.D. 1970. Pathogenic Root-Infecting Fungi. Cambridge Univ. Press, Cambridge. 294 pp.

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

GERLAH, M. 1968. Introduction of Ophiobolus graminis into new polders and its decline. Neth. J. Plant Pathol. 74(Suppl. 2):1-97.

GILPATRICK, J.D. 1969a. Role of ammonia in the control of avocado root rot with alfalfa meal soil amendment. Phytopathology 59:973-978.

GILPATRICK, J.D. 1969b. Effect of soil amendments upon inoculum survival and function of Phytophthora root rot of avocado. Phytopathology 59:979-985.

GISI, U., and D. MEYER. 1973. Okologische Unter-suchungen an Phytophthora cactorum (Leb. et Cohn) Schroet. im Boden mit direkten Beobachtungs-methoden. Phytopathol. Z. 76:276-279.

GRAY, T.R.G., P. BAXBY, I.R. HILL, and M. GOODFELLOW. 1968. Direct observation of bacteria in soil. Pages 171-192 in: T.R.G. Gray and D. Parkinson, eds. The ecology of Soil Bacteria. Liverpool Univ. Press, Liverpool.

HALE, M.G., C.L. FOY, and F.J. SHAY. 1971. Factors affecting root exudation. Adv. Agron. 24:89-109.

HALE, M.G., L.D. MOORE, G.J. GRIFFIN. 1978. Root exudates and exudations. Pages 163-203 in: Y.R. Dommergues and S.V. Krupa, eds. Interactions Between Non-Pathogenic Soil Microorganisms and Plants. Elsevier Sci. Pub. Co., Amsterdam, Oxford, New York.

HALE, M.G., and L.D. MOORE. 1979. Factors affecting root exudation. II:1970-1978. Adv. Agron. 31:93-100.

HALSELL, D.M. 1978. Examination of a forest soil suppressive to Phytophthora cinnamomi. Pages 360-363 in: M.W. Loutit and J.A.R. Miles, eds. Microbial Ecology. Springer-Verlag, Berlin, Heidleberg.

HARLEY, J.L. 1969. The Biology of Mycorrhiza. London, Leonard Hill. 334 pp.

HENIS, Y., and J. KATAN. 1975. Effect of inorganic amendments and reaction of soil borne pathogens. Pages 100-106 in: G.W. Bruehl, ed. Biology and Control of Soil Borne Pathogens. The american Phytopathol. Soc. St. Paul, Minnosota.

HICKMAN, C.J. 1970. Biologi of Phytophthora zoospores. Phytopathology 60:128-1135.

HICKMAN, C.J., and H.H. Ho. 1966. Behaviour of zoospores in plant pathogenic phycomycetes. Annu. Rev. Phytopathol. 4:195-220.

HINE, R.B., and E.E. TRUIJILLO. 1966. Manometric studies on residue colonization in soil by Pythium aphanidermatum and Phytophthora parasitica. 56:344-336.

HO, H.H. 1969. Notes on the behavior of Phytophthora megasperma var. sojae in soil. Mycologia 61:835-838.

HO, H.H., and G.A. ZENTMYER. 1977. Infection of avocado and other species of Persea by Phytophthora cinnamomi. Phytopathology 67:1084-1089.

HOHL, H.R., and P. STÖSSELL. 1976. Host-parasite interfaces in a resistance and susceptible cultivar of Solanum tuberosum inoculated with Phytophthora infestans: Tuber tissue. Can. J. Bot. 54:900-912.

HOHL, H.R., and E. SUTER. 1976. Host-parasite interfaces in a resistant and a susceptible cultivar of Solanum tuberosium inoculated with Phytophthora infestans: Leaf tissue. Can. J. Bot. 54:1956-1970.

HOITINK, H.A.J., A.F. SCHMITTHENNER, and L.J. HERR. 1975. Composted bark for control of root rot of ornamentals. Ohio Report 60:25-26.

HOITINK, H.A.J., A.F. SCHMITTHENNER, and L.J. HERR. 1976. Survival of some plant pathogens during composting of hardwood tree bark. Phytopathology 66:1369-1372.

HOITINK, H.A.J., L.J. HERR, and A.F. SOHMITTHENNER. 1977. Suppression of Phytophthora cinnamomi in a composting hardwood bark potting medium. Phytopathology 67:561-565.

HOITINK, J.A.J. 1980. Composted bark, a lightweight growth medium. Plant Dis. 64:142-147.

HOLLINGS, M. 1962. Viruses associated with a dieback disease of cultivated mushroom. Nature 196:962-965.

HONOUR, R.C., and P.H. TSAO. 1973. Lysis of Phytophthora parasitica oospores in soil. Abstract No.36 in Abstracts of papers. 2nd Int. Congr. Plant Pathol., 5-12 September 1973, Minneapolis, Minnesota, (unpaged).

HWANG, S.C. and W.H. Ko. 1978. Biology of chlamydospores, sporangia and zoospores of Phytophthora cinnamomi in soil. Phytopathology 68:726-731.

JACKSON, R.M. 1965. Antibiosis and fungistasis of soil microorganisms. Pages 363-373 in: K.F. Baker and W.C. Snyder, eds. Ecology of Soil Borne Plant Pathogens. Univ. California Press.

KASSABY, F.Y., P.C. FAGG, and G.C. MARKS. 1977. Survival in and colonisation of mountain forest soil by Phytophthora cinnamomi Rands in eastern Victoria. Aust. For. Res. 7:173-183.

KATZNELSON, H., J.W. ROUTT, and E.A. PETERSON. 1962. The rhizosphere effect of mycorrhizal and non-mycorrhizal roots of yellow birch seedlings. Can. J. Bot. 40: 257-276.

KATZNELSON, H. 1965. Nature and importance of the rhizosphere. Pages 187-207 in: K.F. Baker and W.C. Snyder, eds. Ecology of Soil Borne Plant Pathogens. Univ. California Press.

KAUFFMAN, C.H. 1926. Klebs' theory of the control of developmental processes in organisms and its application to fungi. 4th Int. Bot. Congr. Proc. 2:1603-1611.

KEEN, M., J. SIMS, D. ERWIN, E. RICE, and J. PARTRIDGE. 1971. 6a-Hydroxyphaseollin: An antifungal chemical induced in soybean hypocotyls by Phytophthora megasperma var. sojae. Phytopathology 61:1084-1089.

KELLEY, W.D. 1976. Competition between Phytophthora cinnamomi and Trichoderma spp. in auto-claved soil. Can. J. Microbiol. 22:1120-1127.

KELLEY, W.D. 1977. Interactions of Phytophthora cinnamomi and Trichoderma spp. in relation to propagule production in soil cultures at 26°C. Can. J. Microbiol. 23:288-294.

KELLEY, W.D., and R. RODRIQUEZ-KABANA. 1976. Competition between Phytophthora cinnamomi and Trichoderma spp. in autoclaved soil. Can. J. Microbiol. 22:1120-1127.

KLARMAN, W.L., and J.W. GERDEMANN. 1963a. Induced susceptibility in soybean plants genetically resistant to Phytophthora megasperma var. sojae. Phytopathology 53:863-864.

KLARMAN, W.L., and J.W. GERDEMANN. 1963b. Resistance of soybeans to three Phytophthora species due to the production of phytoalexin. Phytopathology 53:1317-1320.

KLISIEWICZ, J.M., and L.B. JOHNSON. 1968. Host-parasite relationship in safflower resistant and susceptible to Phytophthora root-rot. Phytopathology 58:1022-1025.

KOUYEAS, V. 1964. An approach to the study of moisture relations of soil fungi. Pl. Soil 20:351-363.

KUHLMAN, E.G. 1964. Survival and pathogenicity of Phytophthora cinnamomi in several western Oregon soils. Forest Sci. 10:151-158.

LACEY, J. 1965. The infectivity of soils containing Phytophthora infestans. Ann. Appl. Biol. 56:363-380.

LAPIERRE, H., J.M. LEMAIRE, B. JOUAN, and G. MOLIN. 1970. Mise en évidence de particules virales associées à une perte de pathogenicité chez le Piétinéchaudage des céréales, Ophiobolus graminis Sacc. C.R. Acad. Sci. (Paris), Sér. D. 271:1833-1836.

LEGGE, BETTY J. 1953. Studies of species of Phytophthora. Ph.D. Thesis Univ. Birmingham. 136 p.

LOCKWOOD, J.L. 1977. Fungistasis in soils. Biol. Rev. 52:1-43.

MACDONALD, J.D., and J.M. DUNIWAY. 1979. Use of fluorescent antibodies to study the survival of Phytophthora megasperma and P. cinnamomi zoospores in soil. Phytopathology 69:436-441.

MALAJCZUK, N. 1979a. 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. Aust. J. Bot. 27:255-272.

MALAJCZUK, N. 1979b. Biological suppression of Phytophthora cinnamomi in eucalypts and avocados in Australia. Pages 653-652 in: B. Schippers and W. Gams, eds. Soil Borne Plant Pathogens. Academic Press, London, New York, San Francisco.

MALAJCZUK, N. 1981. Interaction between ectomycorrhizae of Eucalyptus calophylla R.Br and Eucalyptus marginata Donn ex. Sm. and Phytophthora cinnamomi Rands in soil suppressive and conducive to the pathogen. Aust. J. Bot. 29:

MALAJCZUK, N., and A.R. GLENN. 1981. Phytophthora cinnamomi - a threat to the heathlands. Pages 241-247 in: R.L. Specht, ed. Heathlands and Related Shrublands of the World. B. Analytical Studies. Elsevier, The Netherlands.

MALAJCZUK, N., and F.J. HINGSTON. 1981. Ectomycorrhizae of jarrah. Aust. J. Bot. 29:

MALAJCZUK, N., and B.B. LAMONT. 1980. Specialized roots of symbiotic origin in heathlands. Pages 165-182 in: R.L. Specht, ed. Heathlands and Related Shrublands of the World. B. Analytical Studies. Elsevier, The Netherlands.

MALAJCZUK, N., A.J. McCOMB, and C.A. PARKER. 1975. An immuno-fluorescence technique for detecting Phytophthora cinnamomi Rands. Aust. J. Bot. 23:289-309.

MALAJCZUK, N., and A.J. McCOMB. 1977. Root exudates from Eucalyptus calophylla R.Br. and Eucalyptus marginata Donn ex Sm. seedlings and their effect on Phytophthora cinnamomi Rands. Aust. J. Bot. 25:501-514.

MALAJCZUK, N., and A.J. McCOMB. 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. I. Rhizosphere bacteria, pectinomycetes and fungi. Aust. J. Bot. 27:235-254.

MALAJCZUK, N., A.J. McCOMB, and C.A. PARKER. 1977a. Infection by Phytophthora cinnamomi Rands of roots ofEucalyptus calophylla R. Br. and Eucalyptus marginata Donn. ex. Sm. Aust. J. Bot. 25:483-500.

MALAJCZUK, N., H.J. NESBITT, and A.R. GLENN. 1977b. A light and electron microscope study of the interaction of soil bacteria with Phytophthora cinnamomi Rands. Can. J. Microbiol. 23:1518-1525.

MALAJCZUK, N., and C.A. PARKER. 1981. Interaction between Phytophthora cinnamomi Rands and soil and rhizosphere microorganisms from Eucalyptus marginata Donn. ex Sm. and Eucalyptus calophylla R.Br. Aust. J. Bot. 29:

MALAJCZUK, N., and C. THEODOROU. 1979. Influence of water potential on growth and cultural characteristic of Phytophthora cinnamomi. Trans. Br. mycol. Soc. 72: 15-18.

MARAIS, L.J., and J.M. KOTZE. 1976. Ectomycorrhizae of Pinus patula as biological deterrents to Phytophthora cinnamomi. 5th Afr. For. Jour. 99:35-39.

MARKS, G.C., and R.C. FOSTER. 1973. Structure, morphygenesis and ultrastructure of ectomycorrhizae. Pages 1-44 in: G.C. Marks and T.T. Kozlowski, eds. Ectomycorrhizae: Their Ecology and Physiology. Academic Press, New York.

MARSHALL, K.C., and R.H. CRUIKSHANK. Cell surface hydrophobicity and the orientation of certain bacteria at interfaces. Arch. Microbial. 91:29-40.

MARX, D.H. 1969a. 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 59:153-63.

MARX, D.H. 1969b. The infleunce of mycorrhizal fungi on the resistance of pine roots to pathogenic infections. II. Production, identification, and biological activity of anitbiotics produced by Leucopaxillus cerealis var. piceina. Phytopathology 59:411-17.

MARX, D.H. 1972. Ectomycorrhizae as biological deterrents to pathogenic root infections. Annu. Rev. Phytopathol. 10:429-454.

MARX, D.H. 1973. Growth of ectomycorrhizal and nonmycorrhizal shortleaf pine seedlings in soil with Phytophthora cinnamomi. Phytopathology 63:18-23.

MARX, D.H., and BRYAN, W.C. 1969c. Scleroderma bovista, an extrophic mycorrhizal fungus of pecan. Phytopathology 59:1128-32.

MARX, D.H., and C.B. DAVEY. 1969a. The influence of ectrotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. III. Resistance of aseptically formed mycorrhizae to infection by Phytophthora cinnamomi. Phytopathology 59:549-58.

MARX, D.H., and C.B. DAVEY. 1969b. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. IV. Resistance of naturally occurrying mycorrhizae to infections by Phytophthora cinnamomi. Phytopathology 59:559-65.

MATARE, R., and M.J. HATTINGH. 1978. Effect of mycorrhizal status of avocado seedlings on root rot caused by Phytophthora cinnamomi. Pl. Soil 49:433-435.

MATTHEW, R.E.F. 1970. Plant Virology. Academic Press, New York. 350 pp.

MCINTOSH, D.L. 1972. Effects of soil water suction, soil temperature, carbon and nitrogen amendments, and host rootlets on survival of soil of zoospores of Phytophthora cactorum. Can. J. Bot. 50:269-272.

MEAGHER, J.W., R.H. BROWN, and A.D. RIVIRA. 1978. The effects of cereal cyst nematode (Heterodera avenae) and Rhizoctonia solani on growth and yield of wheat. Aust. J. Agric. Res. 29:1127-1137.

MEHROTRA, R.S. 1972. Behavior of zoospores of Phytophthora megasperma var. sojae and P. drechsleri in soil. Can. J. Bot. 50:2125-2130.

MIRCETICH, S.M., ZENTMYER, G.A., and J.B. KENDRICK. 1968. Physiology of germination of chlamydospores of Phytophthora cinnamomi. Phytopathology 58:666-671.

MUKERJEE, N., and A.B. ROY. 1962. Microbial influences on the formation of oospores in culture by Phytophthora parasitica var. subdariffae. Phytopathology 52:583-586.

NEAL, J.L., Jr., T.G. ATKINSON, and R.I. LARSON. 1970. Changes in the rhizosphere microflora of spring wheat induced by disomic substitution of a chromosome. Can. J. Microbiol. 16:153-158.

NESBITT, H.J., N. MALAJCZUK, and A.R. GLENN. 1978. Bacterial colonization of Phytophthora cinnamomi Rands. Pages 371-375 in: M.W. Loutit and J.A.R. Miles, eds. Microbial Ecology. Springer-Verlag, Berlin, Heidleberg.

NESBITT, H.J., N. MALAJCZUK, and A.R. GLENN. 1979. Effect of organic matter on the survival of Phytophthora cinnamomi Rands in soil. Soil Biol. Biochem. 11:133-136.

NESBITT, H.J., N. MALAJCZUK, and A.R. GLENN. 1981a. Bacterial colonization and lysis of Phytophthora cinnamomi Rands. Trans. Br. mycol. Soc.

NESBITT, H.J., N. MALAJCZUK and A.R. GLENN. 1981b. Translocation and exudation of matabolites in Phytophthora cinnamomi Rands. Trans. Br. mycol. Soc.

NEWHOOK, F.J. 1970. Phytophthora cinnamomi in New Zealand. Pages 173-176 in: T.A. Toussoun, R.V. Bega and P.E. Nelson, eds. Root diseases and Soil-Borne Pathogens. Univ. California Press.

NEWHOOK, F.J., and F.D. PODGER. 1972. The role of Phytophthora cinnamomi in Australian and New Zealand forests. Annnu. Rev. Phytopathol. 10:299-326.

OLD,.M. 1977. Giant soil amoebae cause perforation and lysis of spores of Cochliobolus sativus. Trans. Brit. mycol. Soc. 68:277-81.

OLD, K.M. 1978. Perforation and lysis of fungal spores by soil amoebae. Annu. Appl. Biol. 89:128-31.

OLD, K.M., and J.F. Darbyshire. 1978. Soil fungi as food for giant amoebae. Soil Biol. Biochem 10: 93-100.

OLD, K.M., and T.H. NICHOLSON. 1975. Electron microscopical studies of the microflora of rots of sand dune grasses. New Phytol. 74:51-58.

OLD, K.M., and Z.A. PATRICK. 1979. Giant soil amoebae potential biocontrol agents. Pages 617-628 in: B. Schippers and W. Gams, eds. Soil Boren Plant Pathogens. Academic Press, London, New York, San Francisco.

OLD, K.M., and J.M. ORDS. 1980. Mycophagous amoebae in Australian forest soils. Soil. Biol. Biochem. 12:169-175.

PALZER, C. 1976. Zoospore inoculum potential of Phytophthora cinnamomi. Ph.D. Thesis. University of Western Australia. 222 pp.

PARK, D. 1967. The importance of antibiotics and inhibiting substances. Pages 435-447 in: A Burges and F. Raw, eds. Soil Biology. Academic Press, London.

PAXTON, J.D., and D.W. CHAMBERLAIN. 1967. Acquired local resistance of soybean plants for Phytophthora species. Phytopathology 57: 352-353.

PEGG, K.G. 1977. Soil application of elemental sulphur as a control of Phytophthora cinnamomi root and heart rot of pineapple. Aust. J. Exp. Agric. Anim. Husb. 17:859-65.

PETO, S. 1953. A dose-respons equation for the invasion of micro-organisms. Biometrics 9:320-335.

PRATT, B.H. 1971. Isolation of Basidiomycetes from Australian eucalypt forest and assessment of their antagonism to Phytophthora cinnamomi. Trans. Brit. Mycol. Soc. 56:243-250.

PRATT, B.H., J.H. SEDGLEY, W.A. HEATHER, and C.J. SHEPHERD. 1972. Oospore production in Phytophthora cinnamomi in the presence of Trichoderma koningii. Aust. J. Biol. Sci. 25:861-863.

RAMBELLI, A. 1973. The rhizosphere of micorrhizae. Pages 299-349 in: G.C. Marks and T.S. Kozlowski, eds. Ectomycorrhizae: Their Ecology and Physiology. Academic Press, New York. RAMIREZ, B.N. 1974. Influence of endomycorrhizae on the relationship of inoculum density of Phytophthora palmivora in soil to infection of papaya roots. MS Thesis, Univ. of Florida, Gainesville. 45 p.

REEVES, R.J. 1975. Behaviour of Phytophthora cinnamomi Rands in different soils and soil water regimes. Soil Biology Biochem. 7:19-24.

REEVES, R.J., and R.M. JACKSON. 1972. Induction of Phytophthora cinnamomi oospores in soil by Trichoderma viride. Trans. Br. mycol. Soc. 59:156-159.

RIBEIRO, O.K. 1978. A Source Book of the Genus Phytophthora. Pub. J. Cramer, Germany. 417 pp.

ROBERTSON, G.I. 1973. Occurrence of Pythium spp. in New Zealand soils, sands, pumices, and peat, and on roots of container-grown plants. N.Z. J. Agric. Res. 16:357-365.

RODRIGUEZ-KABANA, R., and E.A. CURLE. 1980. Nontarget effects of pesticides on soil borne pathogens and disease. Annu. Rev. Phytopathol. 18:311-332.

ROSE, S.L., C.Y. LI, and A.S. HUTCHINS. 1980. A streptomycete antagonistic to Phellinus weirii, Fomes annosus and Phytophthora cinnamomi. Can. J. Microbiol. 26:583-587.

ROSS, E.W., and D.H. MARX. 1972. Susceptibility of sandpine to Phytophthora cinnamomi. Phytopathology 62:1197-1200.

ROVIRA, A.D. 1965. Plant root exudates and their influence upon soil microorganisms. Pages 170-186 in: K.F. Baker and W.C. Snyder, eds. Ecology of Soil Borne Plant Pathogens. Univ. California Press.

ROVIRA, A.D. 1969. Plant root exudates. Bot. Rev. 35:35-57.

SARBINI, G., and T. KOMMENDAHL. 1977. Effect of bacterial seed treatment on stand and yield of soybeans in Phytophthora-infested soil. Proc. Amer. Phytopathol. Soc. 4:146-147. (Abstr.).

SCHÖNBECK, F. 1979. Endomycorrhiza in relation to plant disease. Pages 271-280 in: B.S. Schippers and W. Gams, eds. Soil Borne Plant Pathogens. Academic Press, London, New York, San Francisco.

SCHROTH, M.N., and D.C. HILDEBRAND. 1964. Influence of plant exudates on root infecting fungi. Annu. Rev. Phytopathol. 2:101-132.

SHEA, S.R. 1975. Environmental factors of the northern jarrah forest in relation to pathogenicity and survival of Phytophthora cinnamomi. Bull. For. Dep. West. Aust. No. 85. 83 pp.

SHEA, S.R., J. McCORMACK, and C.C. PORTLOCK. 1979. The effect of fines on regeneration of leguminous species in the northern jarrah (Eucalyptus marginata Sm.) forests of Western Australia. Aust. J. Ecol. 4:195-205.

SHEA, S.R., and N. MALAJCZUK. 1977. Potential for control of eucalypt dieback in Western Australia. Pages 13-19 in: Seminar Papers of Annual Conference of Australian Nurserymen's Associtation Ltd., Hobart.

SHEW, H.D., and M.K. BEUTE. 1979. Evidence for the involvement of soil mites in Pythium pod rot of peanuts. Phytopathology 69:204-209.

SHIMONY, C., and J. FRIEND. 1975. Ultrastructure of the interaction between Phytophthora infestans and leaves of two cultivars of potato (Solanum tuberosum L.) Orion and Majestic. New Phytol. 74:59-65.

SKIDMORE, A.M. 1976. Interaction in relation to biological control of plant pathogens. Pages 507-528 in: C.H. Dickinson and T.F. Preece, eds. Microbiology of Aerial Plant Surfaces. Academic Press, London.

SMITH, W.H. 1977. Tree root exudates and the forest soil ecosystem: exudate chemistry, biological significance and alteration by stress. Pages 289-302 in: J.K. Marshall, ed. The Belowground Ecosystem: A Synthesis of Plant Associated Processes. Colorado State Univ.

SNEH, B., and D.L. McINTOSH. 1974. Studies on the behaviour and survival of Phytophthora cactorum in soil. Can. J. Bot. 52: 795-802.

SNEH, B., S.J. HUMBLE, and J.L. LOCKWOOD. 1977. Parasitism of oospores of Phytophtora megasperma var. sojae, P. cactorum. Phythium sp., and Aphanomyces euteiches in soil by oomycetes, chytridiomycetes, hyphomycetes, actinomycetes, and bacteria. Phytopathology 67:622-28.

SWIFT, M.J., O.W. HEAL, and J.M. ANDERSON. 1979. Decomposition in Terestrial Ecosystems. Studies in Ecology Vol. 5. Blackwell Sci. Pub. 372 pp.

TIPPETT, J.T., A.A. HOLLAND, G.C. MARKS, and T.P. O'BRIEN. 1976. Penetration of Phytophthora cinnamomi into disease tolerant and susceptible eucalypts. Arch. Microbiol. 10:231-242.

TIPPETT, J., and N. MALAJCZUK. Interaction of Phytophthora cinnamomi and a Resistant Host. Acacia pulchella. Phytopathology 69:764-777.

TOMIYAMA, K. 1971. Cytological and biochemical studies of the hypersensitive reaction of potato cells to Phytophthora infestans. Pages 387-401 in: S. Akai and S. Ouchi, eds. Morphological and Biochemical Events in Plant-Parasite Interactions. Phytopathol. Soc. Jpn., Tokyo.

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

TRINICK, M.J. 1970. The ecology of Rhizobium - interactions between Rhizobium strains and other microorganisms. Ph.D. Thesis, University of Western Australia. 353 pp.

TSAO, P.H. 1969a. Studies on the saprohytic behavior of Phytophthora parasitica in soil. Proc. 1st Inst. Citrus Symp. 3:1221-1230.

TSAO, P.H. 1969b. viral fluorescent labeling as applied to soil ecological studies of Phytophthora parasitica. Phytopathology 59:16-21.

TSAO, P.A. 1970. Selection media for isolation of pathogenic fungi. Annu. Rev. Phytopathol. 8:157-186.

TSAO, P.H. 1977. Prospects of biological control of citrus root disease fungi. Proc. Int. Soc. Agriculture 3:857-863.

TSAO, P.H., H.S. BHALLA and G.A. ZENTMYER. 1975. Effects of certain organic amendments on survival and activiyt of Phytophthora cinnamomi in soil. Proc. Amer. Phytopathol. Soc. 2:40 (Abstr.).

TSAO, P.H., and J.L. BRICKER. 1963. Growth inhibition of Phytophthora cinnamomi by soil diffusates on agar medium. Phytopathology 53:892. (Abstr.).

TSAO, P.H., and J.L. BRICKER. 1968. Germination of chlamydospores of Phytophthora parasitica in soil. Phytopathology 58:1070-1075.

TSAO, P.H., and G.A. ZENTMYER. 1979. Suppression of Phytophthora cinnamomi and Ph. parasitica in urea-amended soil. Pages 191-199 in: B. Schippers and W. Gams, Eds. Soil Borne Plant Pathogens. Academic Press, London, New York, San Francisco.

TU, J.C. 1978. Protection of soybean from severe Phytophthora root rot by rhizobium. Physiol. Plant Path. 12: 233-240.

TU. J.C. 1979. Evidence of differential tolerance among root rot fungi to rhizobial parasitism in vivo. Physiol. Plant Path. 14:171-177.

TU. J.C. 1980. Incidence of root rot and overwintering of alfalfa as influences by rhizobia. Phytopath. Z. 97:97-108.

TURNER, P.D. 1965. Bheavior of Phytophthora palmivora in soil. Plant Dis. Rep. 49:135-137.

TUZIMURA, K., and I. WATANABE. 1961. Estimate of number of root-nodule bacteria by the nodulation dibitum frequency method. Ecological studies Rhizobium in soil (Part 1). Soil Sci., Pl. Nutr. 7:61-65.

VAATAJA, O., R.E. PITBLADO, R.I. BUZZELL, and L.G. CRAWFORD. 1979. Chemical and biological control of Phytophthora root and stalk rot of soybean. Can. J. Plant Sci. 59-307-311.

VAN BRAGT, J., D.A.A. MOSSEL, R.L.M. PIERIK, and H. VELDSTRA. 1971. Effect of sterilization on components in nutrient media. Misc. Papers 9, Landbouwhogeschool Wageningen, The Netherlands. 146 pp.

VINCENT, J.M. 1965. Environmental factors in the fixation of nitrogen by the legume. Pages 384-435 in: W.B. Bartholemew and F.E. Clark, ed. Soil Nitrogen. Am. Soc. Agron., Madison, Wis.

VUJICK, R., and D. PARK. 1964. Behaviour of Phytophthora erthroseptica in soil. Trans. Br. Mycol. Soc. 47:455-460.

WATERHOUSE, G.M. 1940. A chytrid allied to Pleolpidium inflatum Butler. Trans. Br. mycol. Soc. 24:7-19.

WESTE, G. 1974. Phytophthora cinnamomi - the cause of severe disease in certain native communities in Victoria. Aust. J. Bot. 22:1-8.

WESTE, G., and K. VITHANAGE. 1977. Microbial populations of three forest soils: seasonal variations and changes associated with Phytophthora cinnamomi. Aust. J. Bot. 25:377-383.

WESTE, G., and K. VITHANAGE. 1979. Survival of chlamydospores of Phytophthora cinnamomi in several non-sterile, host-free soils and gravels at different soil water potentials. Aust. J. Bot. 27: 1-9.

WONG, R.T.W., and D.M. GRIFFIN. 1974. Effect of osmotic potential streptomycete growth, antibiotic production and antagonism to fungi. Soil Biol. Biochem. 6:319-325.

WYNN, A.R., and H.A.S. EPTON. 1979. Parasitism of oospores of Phytophthora erythroseptica in soil. Trans. Br. Mycol. Soc. 73: 255-259.

ZAK, B. 1964. Role of mycorrhizae in root disease. Annu. Rev. Phytopathol. 2:377-92.

ZAK, B. 1971. Characterization and classification of mycorrhizae of Douglas fir. II. Pseudotsuga menziesii + Rhizopogon vinicolor. Can. J. Bot. 49:1079-84.

ZAN, K. 1962. Activity of Phytophthora infestans in soil in relation to tuber infection. Trans. Br. mycol. Soc. 45:205-221.

ZENTMEYER, G.A. 1963. Biological control of Phytophthora root rot of avocado with alfalfa meal. Phytopathology 53:1383-1387.

ZENTMEYER, G.A. 1965. Bacterial stimulation of sporangium production in Phytophthora cinnamomi. Science 150:1178-1179.

ZENTMEYER, G.A. 1980. Phytophthora cinnamomi and the diseases it causes. Am. Phytopathol. Soc. Monogr. 10. 96 pp.

ZENTMEYER, G.A., and F.T. BINGHAM. 1956. The influence of nitrite on the development of Phytophthora root rot of Avocado. Phytopathology 46:121-124.

FIGURE LEGENDS

Fig. 1. Mycelial growth of Phytophthora parasitica in sterile (autoclaved) and natural soil, either amended with glucose or asparagine. (After Tsao, 1969).

Fig. 2. The correlation between Phytophthora cinnamomi hyphal lysis and log. (sporangium production). Data collected from hyphae incubated in three soil types at four temperatures. log (No. of sporangia) = -2.28 + 0.039 (%hyphal lysis) $r=0.785$ ($P<0.01$).

Fig. 3. Phytophthora cinnamomi zoospore survival in sterial and natural soil leachates when introduced into leachates as cysts.

Fig. 4. Phytophthora cinnamomi zoospore survival in sterile and natural soil leachates when introduced into leachates as mobile zoospores.

Fig. 5. The effect of increasing amounts Eucalyptus marginata decomposing leaf litter (organic matter = microbial populations) to lateritic soil on lysis of Phytophthora cinnamomi Hyphae (After Nesbitt et al., 1979.

Fig. 6. Bacterial colonization on lysed and viable hyphae of Phytophthora cinnamomi compared with autoclaved hyphae and inert glass fibre controls incubated in jarrah leaf litter leachates (After Nesbitt et al., 1981).

Fig. 7. Lysis of Phytophthora cinnamomi hyphae inoculated in sterile and natural soil leachates amended with different rates of Ridomil®.

PLATE LEGENDS

Plate A1. Lysed Phytophthora cinnamomi hyphae with bacteria (B) colonizing surface.

Plate A2. Lysed Phytophthora cinnamomi hyphae with bacteria colonies (B), actinomycete filaments (a), and fungal hyphae (F) colonizing surface.

Plate A3. Scanning electron micrograph (SEM) of Phytophthora cinnamomi hyphae and bacterial colony (BC) colonizing surface.

Plate A4. SEM of Phytophthora cinnamomi hyphae showing bacterial colinizes appressed against the surface.

Plate A5. SEM of Phytophthora cinnamomi hyphae showing end-on attachment of bacteria (B) and associated slime filaments.

Plate A6. SEM of bacterial colonies (B) associated with slime enveloping Phytophthora cinnamomi hyphae.

Plate B1. Transmission electron micrograph (TEM) showing bacteria (B) and mucopolysaccharide envelope attached to Phytophthora cinnamomi hypha.

Plate B2. Bacterial colony (B) on Phytophthora cinnamomi hyphal tip showing absence of Cytoplasm (C) immediately beneath colony.

Plate B3. Lysed (LH) and viable (VH) hypha of Phytophthora cinnamomi when mycelium incubated in soil leachates.

Plate B4. Antibiotic production by Streptomyces isolates from soil against Phytophthora cinnamomi showing inhibition zones.

Plate B5. TEM of Phytophthora cinnamomi hypha showing bacteria (B) invading and initiating cytoplasm (C) lysis.

Plate B6. Phytophthora cinnamomi viable sporangia showing zoospores prior to their release.

Plate C1. SEM of Phytophthora cinnamomi sporangia showing intense colonization of surface by bacteria.

Plate C2. TEM of Phytophthora cinnamomi sporangia showing lysis of cytoplasm immediately beneath colonizing bacteria.

Plate C3. SEM of Phytophthora cinnamomi zoospore prior to encystment showing gaps created immediately following loss of flagellae (arrowed).

Plate C4. SEM of abortive Phytophthora cinnamomi showing collapse of side walls.

Plate C5. Abortive Phytophthora cinnamomi sporangia showing collapsed cytoplasm.

Plate C6. SEM of abortive Phytophthora cinnamomi showing bacterial colonization.

Plate D1. Colonization of Phytophthora cinnamomi hypha by antagonistic Trichoderma sp. (T).

Plate D2. Colonization of Phytophthora cinnamomi sporangia by Chytrids (CH).

Plate D3. Intense development of protozoa colonies associated with lysed Phyto-cinnamomi hyphae incubated in suppressive soil.

Plate D4. SEM of Phytophthora cinnamomi hyphae incubated in suppressive soil showing intense colonization by bacteria and presence of parasitic protozoa (P).

Plate D5. SEM of testate amoebae common in suppressive soil colonizing Phytophthora cinnamomi hypha.

Plate D6. SEM of Phytophthora cinnamomi hypha incubated in suppressive soil showing holes (H) typical of perforations initiated by amoebae.

Plate E1. SEM of Ecualyptus root showing zoospores (Z) of Phytophthora cinnamomi encysted on and penetrating epidermal cells.

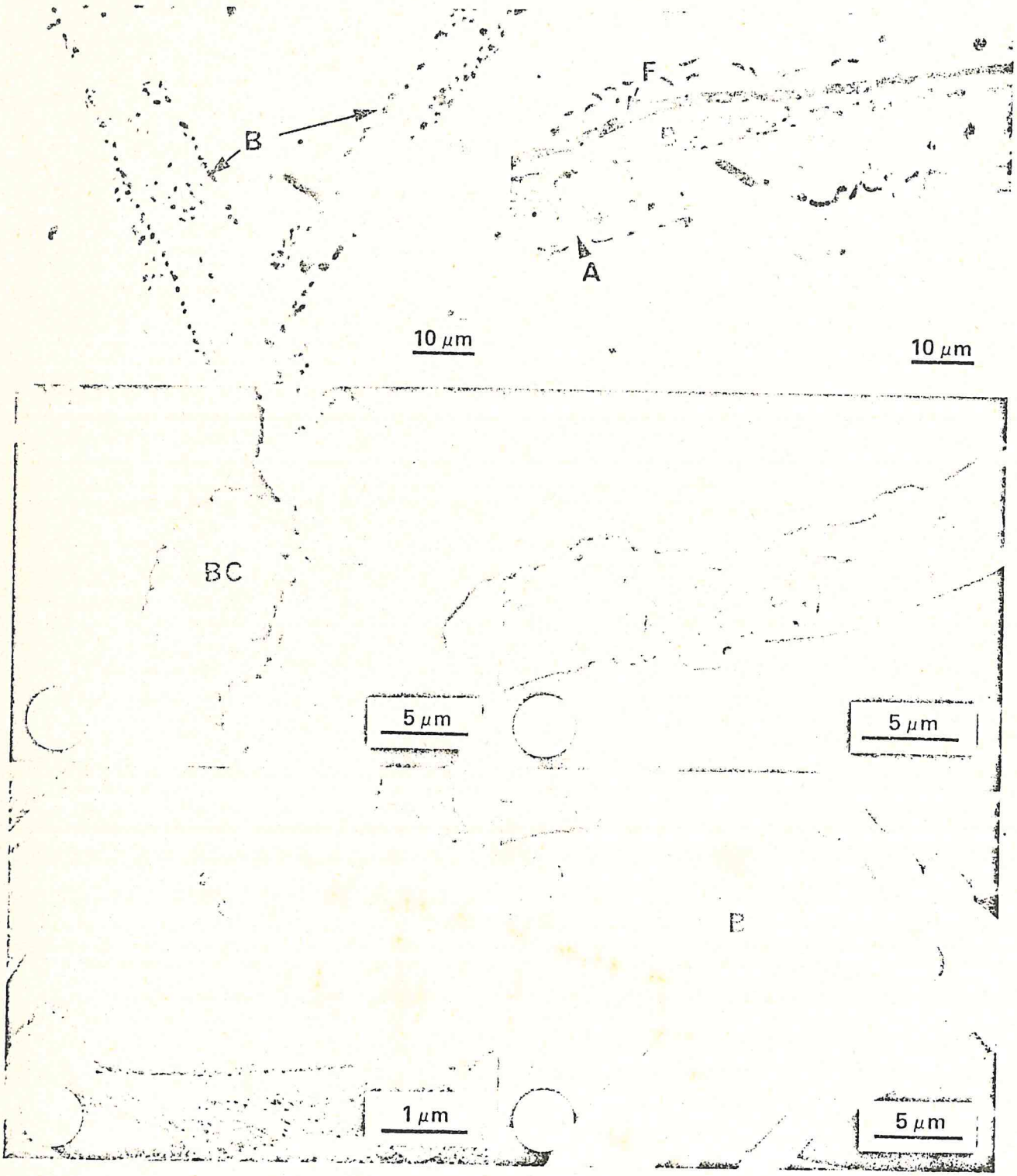
Plate E2. SEM of Phytophthora cinnamomi zoospore (Z) intensely colonized by bacteria and actinomycetes in the rhizosphere of a Eucalyptus root.

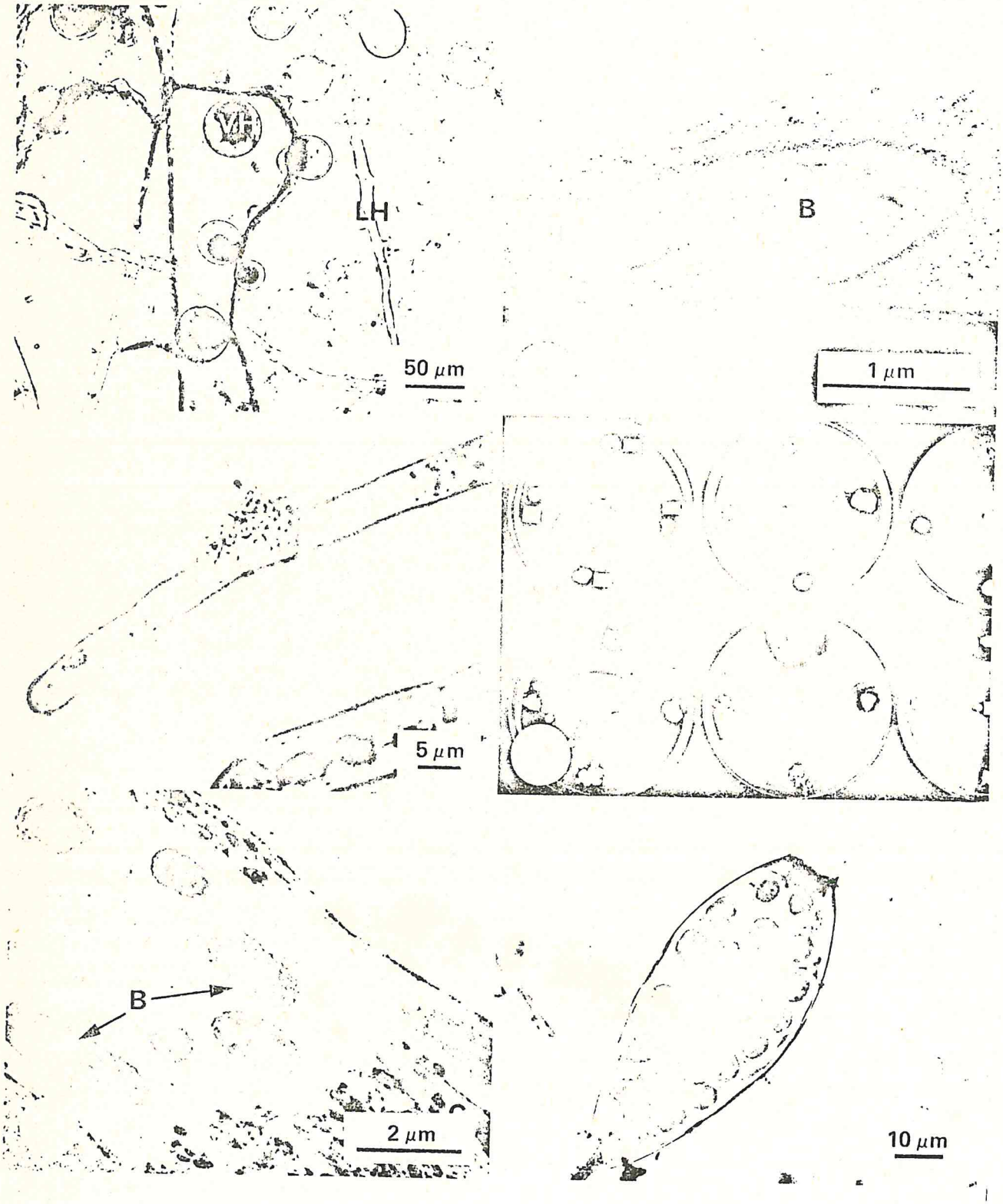
Plate E3. SEM of bacterial colonies in the rhizosphere of a Eucalyptus root infected with Phytophthora cinnamomi.

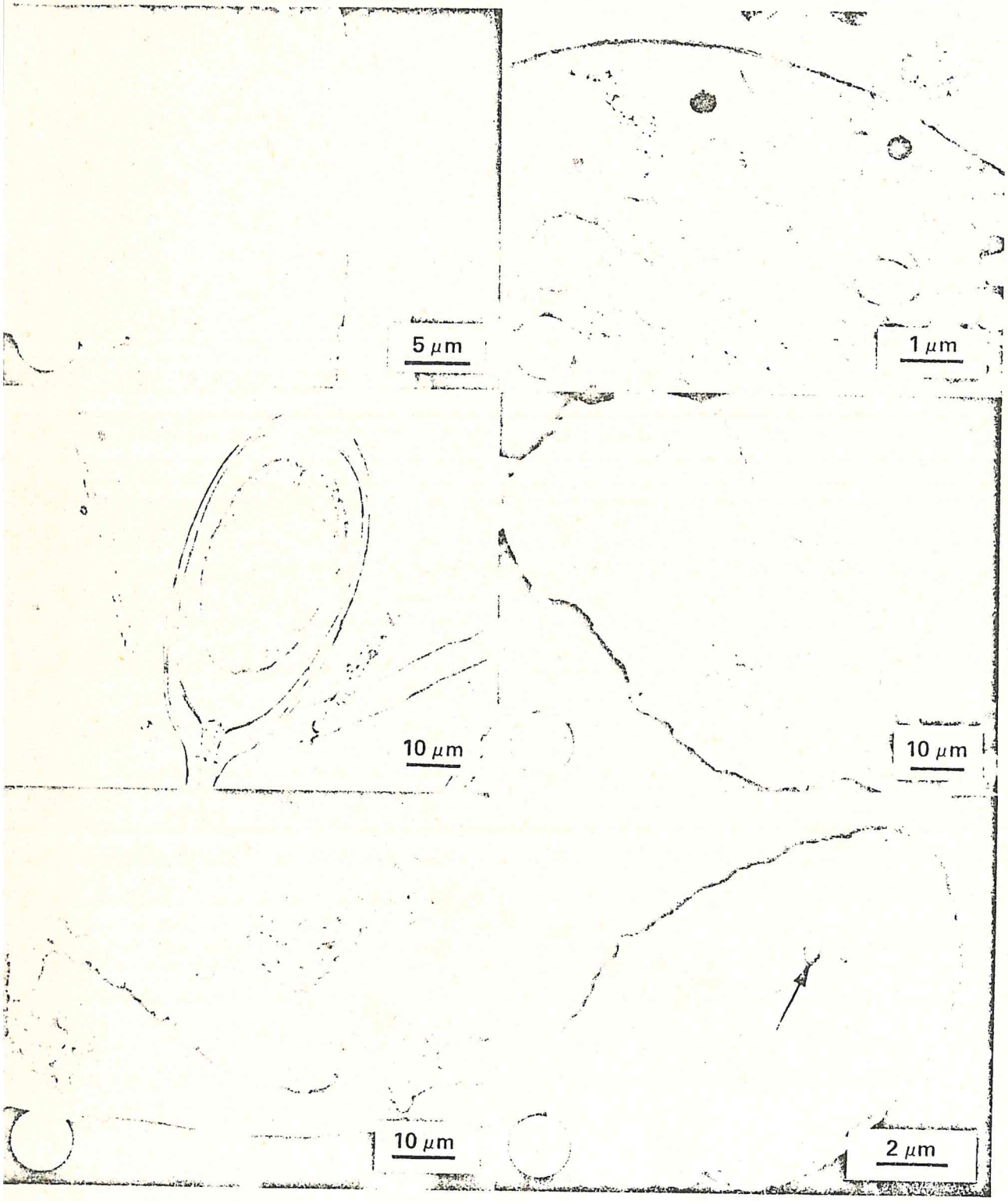
Plate E4. SEM of Eucalyptus ectomycorrhizal root surface showing intense covering of the epidermal cells by a fungal mantle.

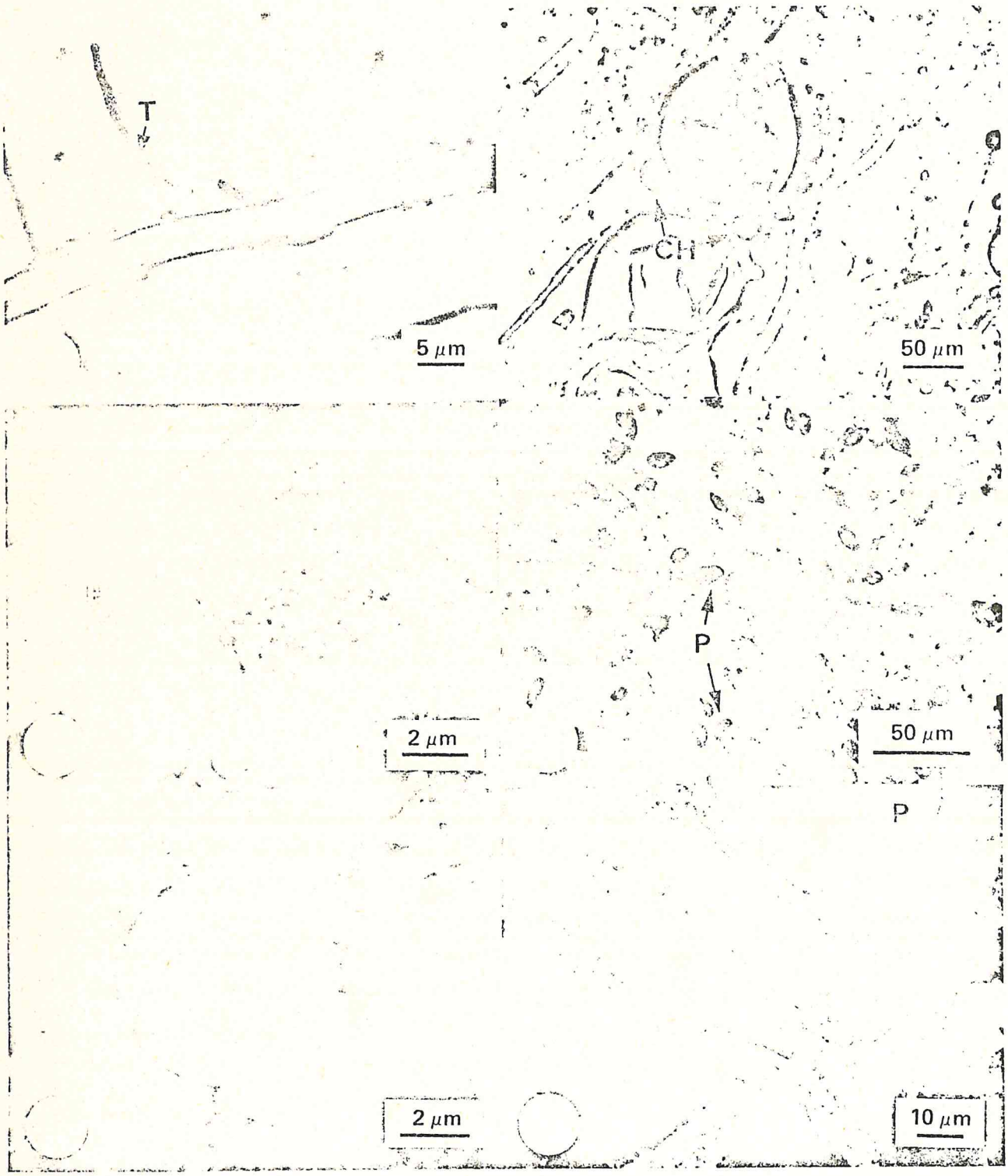
Plate E5. SEM of Eucalyptus ectomycorrhizal root surface showing a germinating zoospore (Z) with hyphae (H) growing at random on the mantle.

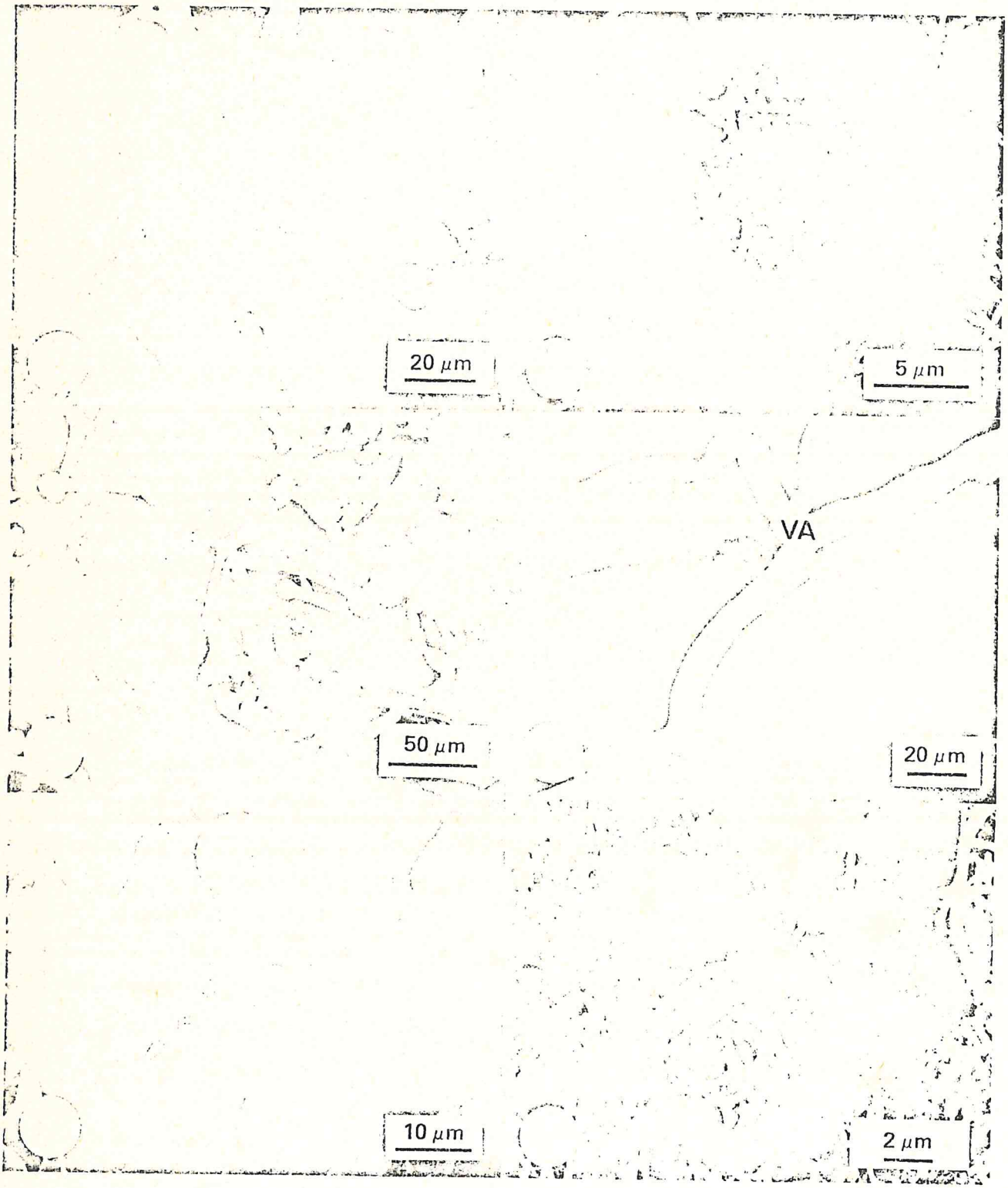
Plate E6. SEM of Trifolium subterraneum root surface showing typical vesicular arbuscular mycorrhizal fungal (VA) growth and penetrating between epidermal cells. Native lack of fungal mantle.

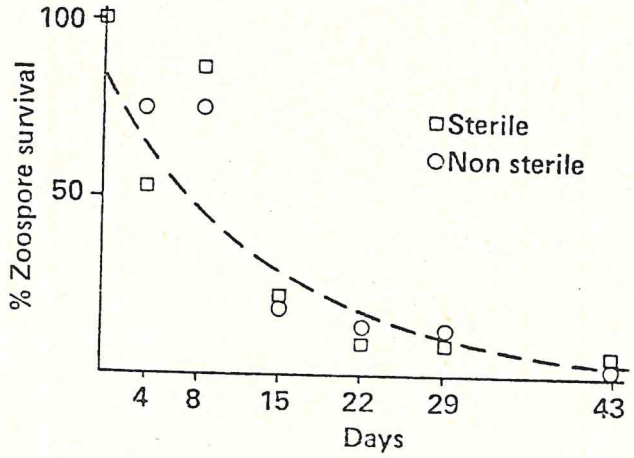

B
F
A
10 μm
10 μm
BC
5 μm
5 μm
B
1 μm
5 μm

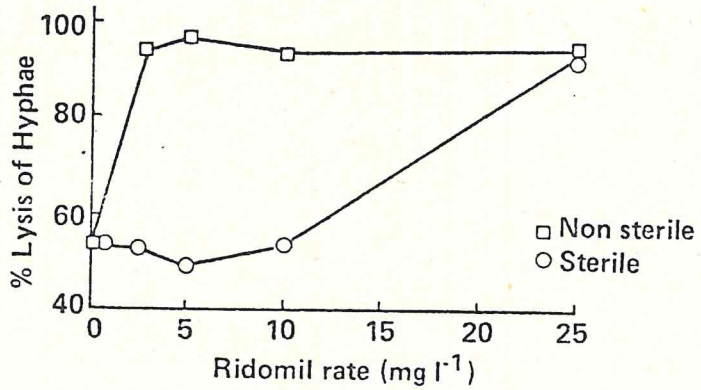

VH
LH
50 μm
B
1 μm
5 μm
B
2 μm
10 μm

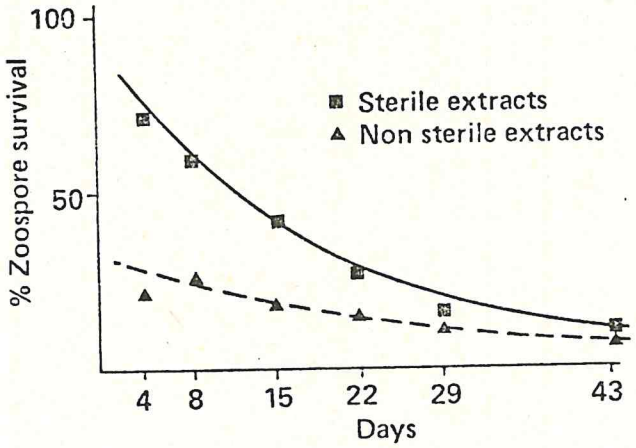

5 μm
1 μm
10 μm
10 μm
10 μm
2 μm

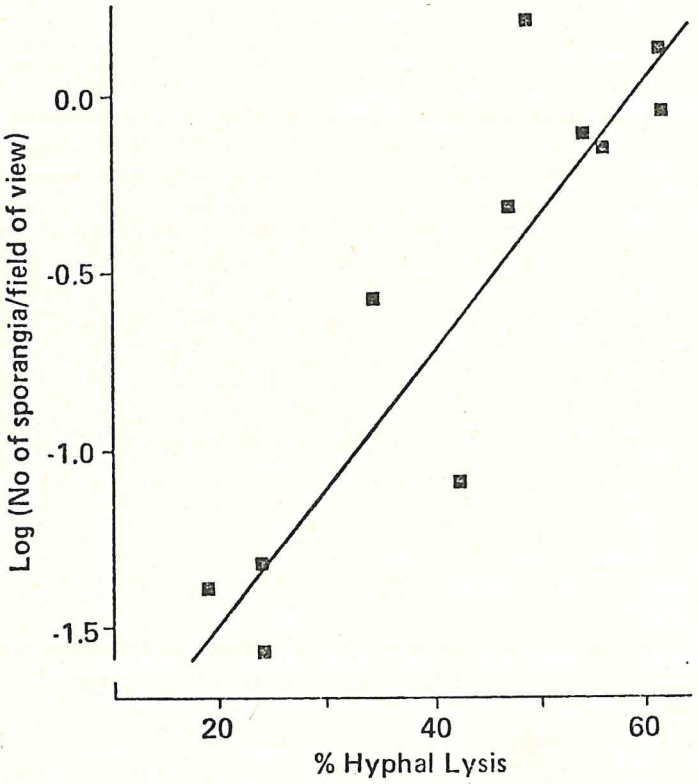

T
5 μm
CH
50 μm
P
2 μm
50 μm
P
2 μm
10 μm

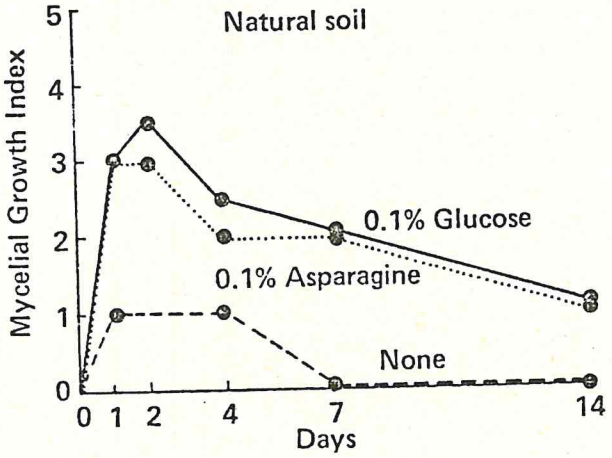

20 μm
5 μm
VA
50 μm
20 μm
10 μm
2 μm

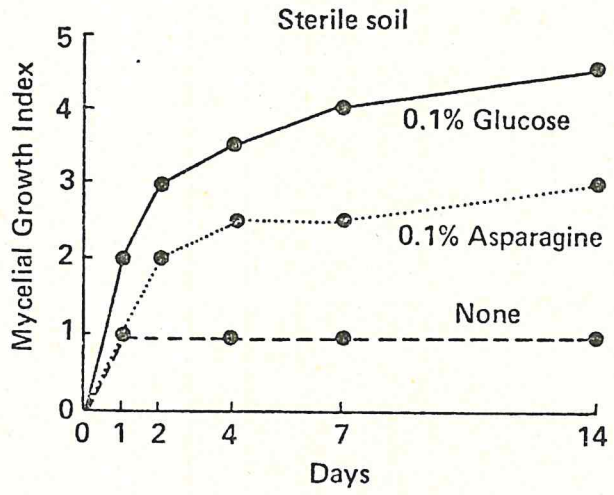

100
50
% Zoospore survival
Sterile
Non sterile
4
8
15
22
29
43
Days

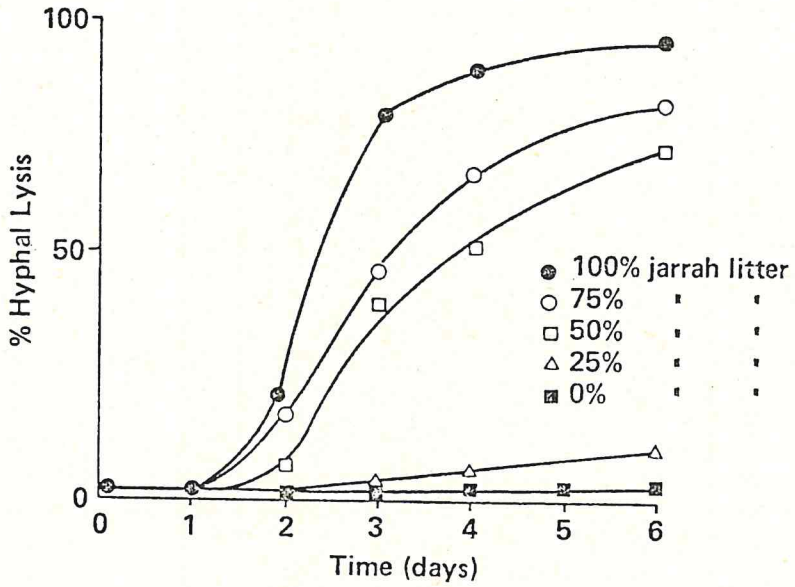

100
80
60
40
% Lysis of Hyphae
0
5
10
15
20
25
Ridomil rate (mg l-1)
Non sterile
Sterile

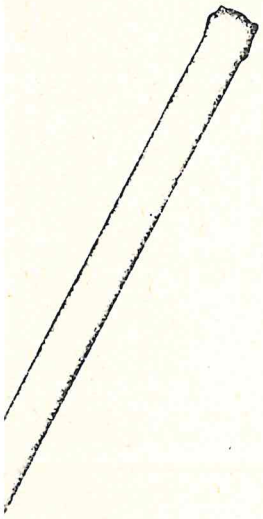

100
50
% Zoospore survival
Sterile extracts
Non sterile extracts
4
8
15
22
29
43
Days


0.0
-0.5
-1.0
-1.5
Log (No of sporangia/field of view)
20
40
60
% Hyphal Lysis


Natural soil
Mycelial Growth Index
5
4
3
2
1
0
0.1% Glucose
0.1% Asparagine
None
0 1 2 4 7 14
Days


Sterile soil
Mycelial Growth Index
5
4
3
2
1
0
0.1% Glucose
0.1% Asparagine
None
0 1 2 4 7 14
Days


100
50
0
% Hyphal Lysis
0
1
2
3
4
5
6
Time (days)
100% jarrah litter
75%
50%
25%
0%



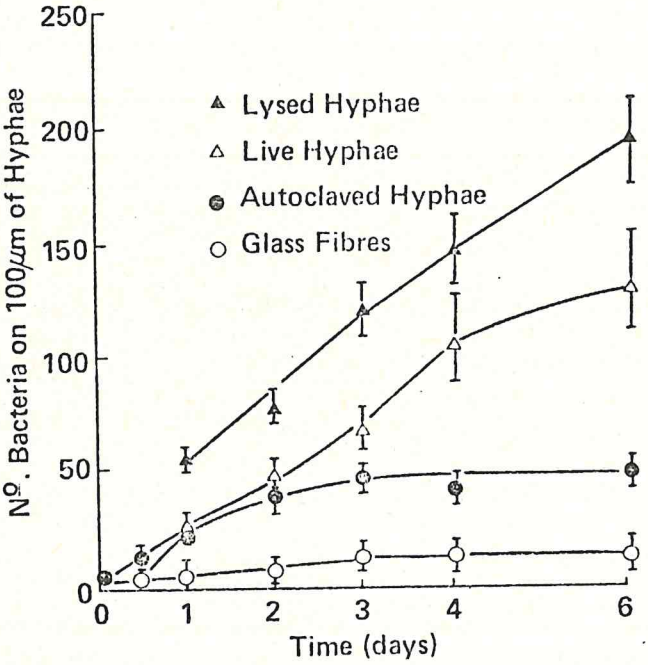

250
200
150
100
50
0
Nº. Bacteria on 100μm of Hyphae
Lysed Hyphae
Live Hyphae
Autoclaved Hyphae
Glass Fibres
0
1
2
3
4
6
Time (days)

TABLE 1. Survival periods of *Phytophthora* propagules in soil and key literature citations.

Phytophthora sp.	Propagule, survival time (approximate No. days), references[1]			
	mycelium	zoospores/sporangia	chlamydospores	oospores
Ph. cactorum	3–14[1,2]	7–35[1]	>105[2]	>365[3]
Ph. cinnamomi	1–60[4,5,6]	3–42[4,7]	84–365[4,8,9]	
Ph. cryptogea		14[10]		
Ph. dreschleri	10–12 (non sterile)[11] > 30 (sterile)	15[12]/35[13]		
Ph. infestans	poor growth (non sterile)[14] good growth (sterile)	>63/77[15]		
Ph. megasperma	7–8[11]	5–14[7,11,16]	>210[17]	
Ph. palmivora		10–180[18]		
Ph. parasitica	< 7 (non sterile)[19,20] > 14 (sterile)[19,20]			

[1]References: 1 = Sneh and McIntosh, 1974; 2 = Gisi and Myer, 1973; 3 = Legge, 1953; 4 = Hwang and Ko, 1978; 5 = Reeves, 1975; 6 = Malajczuk and Theodorou, 1978; 7 = MacDonald and Duniway, 1979; 8 = Kassaby *et al.*, 1977; 9 = Weste and Vithanage, 1979; 10 = Bumbieris, 1979; 11 = Mehrotra, 1972; 12 = Hickman, 1970; 13 = Duniway, 1975; 14 = Lacey, 1965; 15 = Zan, 1962; 16 = Ho, 1969; 17 = Basu, 1980; 18 = Turner, 1965; 19 = Tsao, 1969a; 20 = Tsao, 1969b.

TABLE 2. Estimate of total populations of bacteria and actinomycetes in suppressive loam and conducive lateritic soils and in the rhizosphere of *Eucalyptus calophylla* (resistant) and *Eucalyptus marginata* (susceptible) seedlings growing in these soils (After Malajczuk 1979b)

	Soil	Rhizosphere of *E. calophylla*	Rhizosphere of *E. marginata*
Loam:			
Bacteria	32.8×10^5	18.8×10^7	14.5×10^6
Actinomycetes	11.2×10^6	22.2×10^6	69.8×10^6
% Antagonists	4.2	10.68	15.92
Laterite:			
Bacteria	52.4×10^5	72.5×10^6	36.6×10^6
Actinomycetes	13.6×10^5	32.3×10^6	16.3×10^6
% Antagonists	0.75	11.68	2.00

TABLE 3. Antagonism of bacteria and actinomycete towards *Phytophthoras*.

Phytophthora sp.	Antagonistic bacteria	Reaction recorded	Reference
Ph. cactorium	*Rhizobium*	antibiotic production	Drapeau *et al.* 1973
Ph. cinnamomi	*Bacillus*	antibiotic production	Malajczuk *et al.* 1977
	fluorescent *Pseudomonas*	hyphal lysis	Broadbent *et al.* 1971
	Streptomyces	sporangium abortion	Broadbent and Baker 1974a,b
	Streptomyces griseoloalbus	antibiotic production	Rose *et al.* 1980
Ph. crytogea	*Bacillus subtilis*	antibiotic production	El-Goorani *et al.* 1976
	Arthrobacter	antibiotic production	Erwin and Katz-Nelson 1961
Ph. citrophthora	*Bacillus*	antibiotic production	Broadbent *et al.* 1971
	fluorescent *Pseudomonas*	hyphal lysis	Broadbent and Baker 1974a
	Streptomyces	sporangium abortion	
Ph. erythroseptica	bacterial isolate	oospore parasitism (?)	Wynn and Epton 1979
Ph. infestans	*Streptomyces*	antibiotic production	Lacey 1965
Ph. megasperma var. *sojae*	*Rhizobium*	hyphal lysis	Tu 1978, 1979
	bacterial isolates	antibiotic production	Vaartaja *et al.* 1979
	Pseudomonas	oospore parasitism (?)	Sneh *et al.* 1977
	Actinoplanes missouriensis		
Ph. nicotianae var. *parasitica*	*Bacillus*	antibiotic production	Broadbent *et al.* 1971
	Streptomyces		
Ph. parasitica	*Streptomyces*	parasitism of oospore	Honour and Tsao 1973
	Pseudomonas	antibiotic production	Sarbini and Kommedahl 1977
	Bacillus		

TABLE 4. Antagonism of *Phytophthoras* by fungi.

Antagonistic fungi	*Phytophthora* sp.[1], Reaction[2], Reference[3]
Chytridiales	
Canteriomycetes stigeoclonii	*Ph. meg.*[5.C]
Hyphochytrium catenoides	*Ph. cac.*[5.A], *Ph. ery.*[5.J], *Ph. meg.*[5.C]
Pleolpidium inflatum	*Ph. ery.*[5.H], *Ph. meg.*[3.H]
Rhizidiomycopsis japonicus	*Ph. ery.*[5.H], *Ph. meg.*[5.C]
Oomycetales	
Leptolegnia sp.	*Ph. meg.*[5.C]
Pythium sp.	*Ph. meg.*[5.C]
Mucorales	
Mucor spinosus	*Ph. inf.*[1.K]
Moniliales (= Hyphomycetes)	
Alternaria alternata	*Ph. ery.*[5.H], *Ph. meg.*[5.C]
Cephalosporium sp.	*Ph. meg.*[5.C]
Cladosporium herbarum	*Ph. inf.*[1.K]
Dactylella spermatophaga	*Ph. cac.*[2,5.C], *Ph. cinn.*[2,5.C], *Ph. meg.*[2,5.A,C]
Diheterospora chlamydosporia	*Ph. meg.*[5.C]
Fusarium oxysporum	*Ph. ery.*[5.H], *Ph. meg.*[5.C]
Gliocladium roseum	*Ph. ery.*[5.H], *Ph. meg.*[1.L]
Humicola fuscoatra	*Ph. ery.*[5.H], *Ph. meg.*[5.C]
Monosporium sylvaticum	*P. inf.*[1.K]
Penicillium patulum	*Ph. cry.*[1.I]
Rhizoctonia	*Ph. inf.*[1.K]
Trichoderma harzianum	*Ph. cinn.*[1.D]
Trichoderma lignorum	*Ph. meg.*[2.M]
Trichoderma polysporum	*Ph. cinn.*[6.E]
Trichoderma viride	*Ph. cac.*[2.B], *Ph. cinn.*[1,2.F,G], *Ph. ery.*[2.B]

[1] *Phytophthora* abbreviations: *cac. = cactorum; cinn. = cinnamomi; cry. = cryptogea; ery. = erythroseptica; inf. = infestans; meg. = megasperma; par. = parasitica.*

[2] *Phytophthora* reaction to antagonism: 1 = hyphal lysis due to antibiotic production; 2 = hyphal parasitism; 3 = zoospore/sporangia parasitism; 4 = chlamydospore parasitism; 5 = oospore parasitism; 6 = stimulation of fungus.

[3] A = Dreshsler 1938; B = Dennis and Webster 1971c; C = Sneh *et al.* 1977; D = Kelly and Rodriguez-Kabana 1976; E = Kelly 1976; F = Brasier 1975a; G = Reeves 1975; H = Waterhouse 1939; I = El-Goorangi *et al.* 1976; J = Wynn and Epton 1979; K = Lacey 1965; L = Vaartaja *et al.* 1979; M = Durrell 1966.

TABLE 5. Zoospore infection probability of lupin (*Lupinus angustifolius*) roots with and without rhizosphere population (After Palzer 1976).

Experiment	Rhizosphere microorganisms	Dose (average No. of zoospores)	No. of lupins inoculated/infected		Probability of single spore infecting*
1	absent	3.1	11	1	0.030
	present	15.5	11	0	<0.006
2	absent	8.6	40	21	0.087
	present	71.6	26	16	0.013
3	absent	12.3	34	19	0.066
	present	111.8	40	33	0.016

* Based on exponential model detailed by Bald (1937) and Peto (1953).

TABLE 6. Interaction between rhizobia (*Rhizobium japonicum*) and root rot fungus *Phytophthora megasperma*, tested at different levels of rhizobial and fungal concentrations, on average root rot severity of soybean (*Glycine max*) (After Tu 1978).

Concentration of fungal inoculum in soil (v/v)	Population of *Rhizobium* per cm^3 of soil				
	10^4	10^3	10^2	10^1	0
0	0*	0	0	0	0
10^4	0.2	0.5	1.5	2.2	2.5
10^3	2.0	3.8	4.2	6.3	7.2
10^2	5.5	6.5	7.2	8.0	8.5
10^1	6.1	7.5	8.0	8.3	9.0

* Root rot rating from 0 to 9, zero is free from root rot, 9 is extensive root rot.

TABLE 7. Effect of vesicular-arbuscular mycorrhizae on disease caused by *Phytophthora* species.

Phytophthora sp.	Host	Resistance response by mycorrhizal plant	Reference
Ph. cinnamomi	avocado	no difference	Mataré and Hattingh 1978
Ph. cinnamomi	avocado	decreased	Davis *et al.* 1978
Ph. megasperma	soybean	decreased	Ross 1972
Ph. megasperma	soybean	slight increase	Chou and Schmitthenner 1974
Ph. megasperma	soybean	no difference	Davis *et al.* 1978
Ph. palmivora	papaya	no response	Ramirez 1974
Ph. parasitica	citrus	increased	Schenck *et al.* 1977
Ph. parasitica	citrus	increased	Davis *et al.* 1978
Ph. parasitica	citrus	increased (influenced by nutrients)	Davis and Menge 1980

TABLE 8. Antagonism of *Phytophthoras* by basidiomycetes.

Basidiomycete	*Phytophthora* sp.[1] and reference[2]
Agaricus langei	*Ph. cinn.*[A]
Suillus luteus	*Ph. cac.*[D], *Ph. cam.*[D], *Ph. cinn.*[A,D], *Ph. cry.*[D], *Ph. pal.*[D], *Ph. par.*[D]
Bovista brunnea	*Ph. cinn.*[A]
Clavulina amethystina	*Ph. cinn.*[A]
Clitocybe eucalyptorum	*Ph. cinn.*[A]
Clitocybe infundibuliformis	*Ph. cinn.*[A]
Collybia abutyracea	*Ph. cinn.*[A]
Collybia sp.	*Ph. cinn.*[A]
Cortinarius austro-venetus	*Ph. cinn.*[A]
Cortinarius walkeri	*Ph. cinn.*[A]
Geastrum	*Ph. cinn.*[A]
Gymnopilus	*Ph. cinn.*[A]
Hyprophoropsis aurantiaca	*Ph. cinn.*[A]
Hygrophorus niveus	*Ph. cinn.*[A]
Laccaria laccata	*Ph. hev.*[D]
Lactarius deliciosus	*Ph. cac.*[D], *Ph. cam.*[D], *Ph. cinn.*[A,D], *Ph. pal.*[D], *Ph. par.*[D]
Leucopaxillus cerealis var. *piceina*	*Ph. cac.*[D], *Ph. cam.*[D], *Ph. cinn.*[D], *Ph. Cit.*[D] *Ph. cry.*[D], *Ph. dre.*[D], *Ph. hev.*[D], *Ph. pal.*[D], *Ph. par.*[D]
Naematoloma fasciculare	*Ph. cinn.*[A]
Omphalina sp.	*Ph. cinn.*[A]
Rhizopogon vinicolor	*Ph. cinn.*[B]
Scleroderma bovista	*Ph. cac.*[C], *Ph. cinn.*[C], *Ph. citc.*[C], *Ph. dre.*[D], *Ph. hev.*[C]

[1] *Phytophthora* abbreviation: *cac.* = *cactorum*; *cam.* = *cambivora*; *cinn.* = *cinnamomi*; *citc.* = *citricola*; *cit.* = *citrophthora*; *cry.* = *cryptogea*; *dre.* = *dreschleri*; *hev.* = *hevea*; *pal.* = *palmivora*; *par.* = *parasitica*

[2] A = Pratt 1971; B = Zak 1971; C = Marx and Bryan 1969c; D = Marx 1969

TABLE 9. The effect of root inoculation with bacteria on total plant dry weight and disease severity of *Eucalyptus marginata* and *Eucalyptus calophylla* seedlings grown in sterile soil infested with *Phytophthora cinnamomi*.

Isolate	Plant age (weeks)	*E. calophylla* Mean plant dry wt (mg)	*E. calophylla* Mean root rot index[a]	*E. marginata* Mean plant dry wt (mg)	*E. marginata* Mean root rot index[a]
Streptomyces #1	4	7.00	0.5	2.22	2.5
	12	16.75	0.5	5.43	3.5
Streptomyces #3	4	4.03	0.5	2.82	2.0
	12	9.00	3.5	3.55	4.0
Bacillus #5	4	4.09	1.5	1.29	5.0
	12	17.35	2.0	3.16	4.5
Pseudomonas #7	4	2.24	4.5	1.78	3.5
	12	6.78	4.5	4.21	4.5
Bacterial isolate #8	4	2.44	4.5	3.80	1.5
	12	4.73	5.0	14.02	1.0
Control (No *Ph. cinnamomi* inoculum)	4	7.54	0.0	5.08	0.0
	12	19.65	0.0	19.39	0.0
Control (*Ph. cinnamomi* inoculated)	4	2.03	5.0	0.16	5.0
	12	1.47	5.0	3.92	5.0

[a] Mean of five replicates based on a scale of 0-5.
0 = uninfected; 5 = 81-100% root rot.