DEVELOPMENTS IN CULTURAL AND BIOLOGICAL CONTROL OF PHYTOPHTHORA DISEASES

by

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ABSTRACT

The ability of Phytophthora spp. to increase propagule density rapidly is the basis for their success as plant pathogens. Yet the sequence of events leading to the release and transmission of zoospores are complex and sensitive to small changes in the physical and biological environment. Similarly the susceptibility of many hosts varies with changes in the environment. There is thus the potential to use cultural techniques to modify the environment to disfavor the pathogens and increase the resistance of hosts.

There are a number of cultural procedures, for example, sanitation and drainage control, which have been used to lessen disease but there are a few examples where control has been achieved by biological or cultural methods. However, the absence of disease in some situations in nature, and in a few instances in crops, in the presence of the pathogen under environmental conditions normally suited for disease development indicates that control by ecological methods is possible.

Considerable progress has been made in understanding the biology of Phytophthora pathogens; but very little research has been done on the interaction between temporal variations in pathogen activity and host susceptibility in the environment where the disease is occurring. Elucidating these interactions is the major pre-requisite to the development of viable biological and/or cultural control methods.

The control of any soil-borne plant pathogen in a crop is difficult and Phytophthora diseases are no exception. Where control has been achieved, it has usually been based on the regular application of chemicals or the use of resistant species or cultivars. Cultural techniques, e.g. drainage, sanitation, clean stock, have been used successfully to lessen disease but there remain few instances where we can claim that a cultural technique, based on biological principles, has successfully been employed to achieve control.

However situations do exist in nature where susceptible vegetation in the presence of the pathogen is not diseased under climatic conditions which are normally suitable for disease development. These situations provide working models of successful biological and ecological control and as such are an invaluable aid to the development of control methods.

In this review we have excluded consideration of the use of chemicals and the development of resistant species to achieve control. The greatest potential for the development of control, however, may be in the integration of these two approaches with cultural treatments which create an environment which is physically, chemically and microbially unfavorable to the pathogen and which increases host resistance.

THE PATHOGENS

Identification and Quantification of Pathogens

Reliable and practical methods of identification and quantification of the pathogens is an obvious essential pre-requisite to the development of biological and cultural control techniques. But for many Phytophthora diseases this has not been achieved. Hickman (1958) commented on the difficulty of isolation and detection of Phytophthora spp. on diseased hosts because of their often transient occurrence on roots and in the soil. In one of the classic diseases caused Phytophthora cinnamomi, "Jarrah Dieback", recovery rates of the pathogen from soil and/or roots despite extensive sampling, was only ten per cent (Podger, 1968).

A variety of baiting, sieving and direct isolation techniques (Greenhalgh, 1978) are available for detecting Phytophthora in soil but most techniques fail to establish the type of propagule present and logistical restraints are considerable in assaying soils. Some methods for direct observation or tracing Phytophthora in soil and particularly in soil extracts are available (e.g. scanning electron microscopy, fluorescent antibody techniques (Malajczuk et al. 1978; MacDonald and Duniway, 1979), but they have little application in the field.

Failure to detect Phytophthora species in soil is often probably a consequence of inadequate sampling intensity in time and space rather than a failure of the isolation technique. Phytophthora species have the capacity to increase propagule density rapidly following a specific sequence of environmental events. Hence propagule density in soil can vary markedly

in time and space even in situations where disease intensity is high. Extensive and intensive soil sampling is required to detect these fluctuations in soil propagule density. Recent advances in the development of selective media by Masaga et al (1977) have alleviated logistical problems associated with quantification of Phytophthora propagules in soil and it is possible to document temporal variations in the type and density of propagules (Kliejunis and Nagata, 1979; Shea et al, 1980 A). Even though documentation of temporal and spacial variations in the type and number of propagules is difficult and time consuming, we suggest that little progress in the development of biological and/or cultural control methods or concepts will be made until this is achieved.

Even when the primary pathogen is identified it is possible that other pathogens may also be contributing to disease. Several different Phytophthora spp. have been detected on diseased roots of horticultural crops (Mircetich and Matheron, 1970; Mircetich and Matheron, 1976, Mircetich and Matheron, 1978; Mircetich et al, 1979).

Nematodes may predispose hosts to infection by Phytophthora cinnamomi by disrupting the fungal mantles of ectomycorrhizae (Barham, 1972; Barham et al, 1974).

Further research is required to determine the role of pathogens acting either independently or synergistically in Phytophthora diseases. This has particular relevance to research on biological and cultural control techniques since a control method for one species may favor an alternative pathogen. Halsall (1981) has found, for example, that soil microorganisms and chemical compounds in a forest soil suppressed sporangial formation by P. cinnamomi but stimulated P. cryptogea.

Saprophytism and Survival

Species of Phytophthora are generally considered to possess little competitive saprophytic ability sensu Garrett (1950). But some Phytophthora spp. e.g. P. cinnamomi and P. palmivora can invade organic matter readily in competition with other soil microorganisms. The longevity of mycelium outside root pieces is debatable (Reeves, 1975; Zentmyer and Mircetich, 1966; Turner, 1965). Marks et al (1975) classified P. cinnamomi as a 'saprophytic soil survivor' (sensu Griffin, 1972) based on field studies in eucalyptus forests in Victoria, Australia, implying that it is a parasite surviving in tissues that are colonised when the host is alive.

While many Phytophthora spp. can survive in soil as chlamydospores or oospores (Zentmyer and Erwin, 1970), zoospores (MacDonald and Duniway, 1979) sporangia (Sneh and McIntosh, 1974) and mycelium (Shea et al, 1979), alternative hosts (Cother and Griffin, 1973) and live host tissue may aid survival. The capacity of P. cinnamomi to invade large roots and the lower stem of Banksia grandis Willd. in the jarrah forest permits it to survive through the prolonged dry summer (Shea, 1979 B).

Prolonged drying of soil (Zentmyer and Erwin, 1970) and high soil temperatures (Hine et al, 1964) can reduce the degree of survival of Phytophthora spp. It is possible to destroy the inoculum of Phytophthora parasitica var. nicotianae by flooding fields and growing swamp rice in a tobacco and rice rotation system (Van Schreven, 1948).

Nitrogen, and particularly the form of nitrogen, has been implicated as a factor operating in a number of instances where biological control

of Phytophthora root rot is operating. Gilpatrick (1969 A) reported that soils amended with 5% alfalfa meal accumulated 60-197 p.p.m. ammonia within 7 days after amendment and this could be toxic to mycelium and zoospores of P. cinnamomi. Tsao and Oster (1981) and Tsao and Zentmyer (1979) implicated NH_3 and HNO_2 in suppression of Phytophthora in soils amended with chicken and urea.

Antagonism to Phytophthora propagules by a variety of soil microorganisms has been demonstrated in a number of studies (Broadbent et al 1971 A; Broadbent and Baker, 1974 A, 1974 B; Honour, 1974; Malajczuk et al 1977; Old, 1979; Shea and Malajczuk, 1977; Sneh et al, 1977; Ahmed and Ahmed, 1963; Pratt, 1971; Malajczuk and McComb, 1977 and Marx, 1973). This subject is reviewed in more detail in Chapter by Malajczuk.

Promotion of an antagonistic soil microbiota is the classical approach to biologicial control, but monitoring soil antagonists and assessing their significance is difficult. Techniques for measuring the size of microbial populations currently available involve direct counting, in which microorganisms are variously stained (Soderstrom, 1977; Babink and Paul, 1970) or soil extractions in which enzymes (Skujins, 1967) or components characteristic to living cells (e.g. ATP)(Eiland, 1979) are extracted and quantitatively analysed. Other methods include the disintegration of soil followed by separation and collection of cells (Balkiwill et al, 1975; Faegri et al, 1977) or respiration studies in which the addition of substrates are used to quantify the bacterial and fungal populations (Anderson and Domsch, 1973). In another method the carbon bound in the microbial biomass is released by microbial mineralisation and its weight can be calculated (Anderson and Domsch, 1978). However, these

methods do not permit identification of the specific groups of micro-organisms which are inhibitory to Phytophthora pathogens. Although where control of Phytophthora is achieved by cover cropping and mulching to attain a "balanced" state with improved soil chemical, physical and biological properties, a non-specific assemblage of organisms appears to be involved so microbial biomass measurements may be applicable.

There have been few attempts to relate the activity of antagonistic microflora and/or fauna to the activity of the pathogen in the environment where the disease occurs. The important of the survival of Phytophthora phase in soil varies with the host susceptibility and soil conditions. For example, on free drained jarrah forest sites P. cinnamomi is a transient soil inhabitant, whereas on lowland sites it can be recovered consistently from the soil throughout the year. Shea et al (1980 B). Where the pathogen is a transient soil inhabitant control procedures based on biological antagonism of propagules in the soil are less likely to be successful. In these situations to be effective the antagonists must operate during the periods of the year when the pathogen is present in the soil. Even when the soil inhabiting phase is prolonged, it is unlikely that control by eradication of the fungus with other diseases (e.g. take-all of wheat caused by Gaeumannomyces graminis) that antagonism occurs only in response to live inoculum of the pathogen (Gerlagh, 1968).

Sporangial Formation and Zoospore Release and Germination

The ability of Phytophthora spp. to increase inoculum density rapidly

by asexual reproduction is probably the major factor contributing to their success as plant pathogens. Yet the sequence of events leading to the formation of sporangia and release and transmission of zoospores are complex and sensitive to small changes in the physical and microbiological environment. This sensitivity could be exploited by the use of cultural techniques to modify the soil environment.

Sporangial formation for many species only occurs at relatively narrow ranges of soil moisture potentials; release of zoospores will occur only when the soil is near saturation and zoospore transmission over significant distances is dependent on overland flow (Duniway, 1979). Similarly, fluctuation of soil temperature by a few degrees can affect sporangial formation (Chee and Newhook, 1964). The nature of the temperature regime can also affect sporulation significantly (Hyre and Ettinger, 1967).

A variety of chemical factors in the soil have been shown to affect sporangial formation, zoospore release and germination of Phytophthora spp. e.g. major soil nutrients (Tsao et al, 1979), trace elements (Halsall, 1977), sterols (Hendrix, 1964, 1965), chemicals orginating from decomposing plant roots (Whitfield et al, 1981) and organic matter (Gilpatrick, 1968). One of the most important chemical factors affecting sporangial formation and germination is the form and concentration of nitrogen in soil (Tsao and Oster, 1981; Tsao and Zentmyer, 1979; Broadbent, 1977; Gilpatrick, 1969A).

Soil microorganisms can affect zoospore production by causing plasmolysis or rupture of sporangia (Broadbent and Baker, 1974 B) or by affecting sporangial formation. Some Phytophthora species, such as

Phytophthora citrophthora (Sm. & Sm.) Leon. produce sporangia readily in axenic culture, but their number is increased in nonsterile soil leachate. Others (e.g. P. cinnamomi require the presence of living soil microorganisms (Mehrlich, 1935) for maximum production of sporangia. Prior to 1969, when Chen and Zentmyer (1970) produced sporangiae of P. cinnamomi under axenic conditions by washing mycelium in a salt solution, sporangial production was negligible on mycelia placed in sterile soil leachate. Living soil microorganisms, particularly Pseudomonas spp. (Marx and Haasis, 1965; Chee and Newhook, 1966; Manning and Crossan, 1966; Ayers, 1971; Ayers and Zentmyer, 1971) and Chromobacterium violaceum (Zentmyer, 1965) have been implicated in the production of sporangia by the fungus in nonsterile extracts.

The microbial factor in soils responsible for sporangial production appears to be ubiquitous and possibly nonspecific; the microbiota affecting stimulation are temperature-sensitive and are destroyed in soil by aerated steam at 49°C/30 min. (Broadbent and Baker, 1974 A). Variation in the formation of sporangia may be caused by differences in the numbers of stimulatory microorganisms or in the numbers of other microorganisms inhibitory to them or destructive to their stimulatory metabolities, or to differential sorption of bacteria or their metabolities by soil colloids.

It is possible that control of some Phytophthora species could be achieved by manipulation of the stimulatory microorganisms. When the pathogens are only transient soil inhabitants there are greater opportunities to manipulate the microorganisms which affect sporangial

stimulation than the pathogens. Broadbent (unpublished) has examined over 300 soils for suppression of Phytophthora root rot. While variations in sporangial production in soil extracts occurred, only two soils (Broadbent and Baker, 1974 A) have shown a sufficiently substantial inhibition of sporangial formation to have had epidemiological significence in terms of biological control. Halsall (1981) has shown consistent suppression of sporangial formation by P. cinnamomi in soil from a wet sclerophyll forest in New South Wales of Australia. Actinomycetes in this soil were antagonistic to a number of soil bacteria which had the capacity to stimulate sporangial formation and in addition a heat stable component of the soluble fraction of the soil contributed to suppression of sporulation. Shea and Malajczuk (1977) showed suppression of the stimulation factor in soil extracts from pots in which Acacia pulchella R. Br. had been grown. Saponin extracts (Alexander et al, 1978) root volatiles (Whitfield et al, 1981) and root extracts (Shea unpublished) from this species suppressed sporangial formation. However, soils collected at various times of the year from beneath A. pulchella stands, growing in the field, have not consistently suppressed P.cinnamomi sporulation. (Shea, unpublished).

Even if it is not possible to suppress the microorganisms which cause stimulation of sporangial production, it is essential to elucidate their role in disease epidemiology. For example, seasonal variations in soil stimulatory capacity (Chee and Newhook, 1966; Otrosina and Marx, 1975) probably have an important effect on temporal variations in pathogen propagule density in the soil. Is the relationship between

soil temperature and sporangial production affected by the nature and density of the stimulatory microorganisms?

The importance of the sporangial formation and germination phase of the life cycle of Phytophthora species and its demonstrated sensitivity to soil microorganisms suggests that manipulation of the soil microbiological environment to disfavor sporangial formation and/or germination is one of the most promising approaches to control. However, assessments of the effect of soil microorganisms on sporangial formation and germination must be based on realistic experimental techniques. It is unrealistic to expect that the soil microflora present in a soil extract which has been incubated for several days will be representative of the field situation from which the samples were collected. For example, there was no seasonal variation in sporangial stimulation in jarrah forest soil when a soil extract method was used, but marked seasonal variation was observed for the same soil when stimulatory capacity was tested in intact soil cores (McGann and Shea, unpublished). Blowes (1980) demonstrated that sporangial production on P. cinnamomi mycelial mats immersed in a sand suspension amended with an inorganic source of nitrogen was not comparable in successive experiments because of variation in the sporangial producing capacity of the P. cinnamomi cultures used.

The development of control methods based on manipulation of the soil microbiological, physical and chemical environment to disfavor survival

and reproduction by Phytophthora pathogens is handicapped by the absence of data on spacial and temporal variations in pathogen propagule density, data on the environment where the disease occurs and on the response of these pathogens to environmental regimes which is relevant to the field environment. To be effective, changes in the soil environment which are aimed at reducing survival and/or reproduction must operate during periods when the pathogens are present in the soil and/or are operating their asexual cycle. But there are almost no situations where the soil inhabiting phase of Phytophthora pathogens has been comprehensively documented. It is difficult to assess the potential of control methods based on manipulation of the soil environment without a detailed documentation of the environment where the disease occurs in relation to the temporal and spacial variation in pathogen propagule density. For example, in a disease situation where the soil moisture and temperature regime is only suitable for sporangial production for limited periods of the year, relatively small changes in the soil's physical environment can have a significant effect on pathogen propagule density. But when the pathogen is present in an environment where there are prolonged periods when soil moisture and temperature are suitable for survival and reproduction, major changes to the soil physical environment would be required to achieve a significant effect on the pathogen. Much of the data on the response of Phytophthora pathogens to changes in the environment has little relevance to the actual environment where the disease is occurring. For example, temperature, moisture, soil microbial activity, nitrogen form and concentration, etc. vary markedly over

time in the field. But most of the data which has been obtained on the effect of these factors on survival and reproduction has been obtained under constant conditions. Even if this data could be extrapolated to the field, very little research has been carried out to determine if the concentrations or levels of soil factors which have been shown to suppress Phytophthora survival and reproduction could be maintained in the field situation.

ENVIRONMENTAL FACTORS AFFECTING THE HOSTS

Host predisposition

The effect of non-genetic host factors on susceptibility to Phytophthora spp. has received little attention, possibly because the effect of stresses induced by the environment on the host-pathogen interaction are often difficult to separate from effects on the host itself (Schoeneweiss, 1975; Yarwood, 1959). But changes in susceptibility to Phytophthora spp. which are related to age and stage of development of the host have been commonly observed. Many species of plants are susceptible to Phytophthora spp. at the seedling stage but are resistant at later stages of development. The Pinus spp. are susceptible to Phytophthora cinnamomi during the initial and latter periods of tree development, but mortality rates during intermediate stages of development are low (Newhook, 1959; Campbell and Copeland, 1954).

The effect of environmental factors on host predisposition is to a degree determined by the capacity of the pathogen to invade host tissue.

When the host is highly susceptible and the pathogen can consistently and rapidly invade secondary tissue, it is unlikely that any cultural treatment will prevent death of the host. When the pathogen is restricted to primary tissue, for example, to fine feeder roots, the physiological status of the host through its effect, for example, on root regeneration or demand for water and nutrients; may have a major effect on disease development. In some hosts the rate of lesion extension by Phytophthora pathogens within secondary tissue is effected by host physiology. (Sewell and Wilson, 1973; Gates and Millikan, 1972).

Where Phytophthora pathogens cause disease by feeder root rot, timing of feeder root formation and the capacity to regenerate roots will effect susceptibility. For example, the period when jarrah trees form fine roots corresponds to periods when soil conditions are suitable for sporangial production by P. cinnamomi (Dudzinksi, Rockel and Shea, unpublished). Rough lemon (Citrus jambhiri Lush) is highly susceptible to P. citrophthora (Sm. & Sm.) Leon, but it often survives through its capacity to regenerate roots rapidly. (Broadbent, et al. 1971 B).

When the pathogen effects only part of the host, it is possible that cultural practices which maximise the capacity of the host to replace damaged tissue and minimize the stress induced by pathogens can be used to prevent development of the disease. Thus the favorable growing conditions provided by the red basaltic soils in which avocadoes are grown in Queensland, the coincidence of high light intensity, high temperature and high water status favors root regeneration and minimizes stress due to evapotranspiration (Pegg, 1977 A).

Intermittent waterlogging favors survival and reproduction of many Phytophthora species but it may also predispose the host to infection by altering its metabolism (Drew and Lynch, 1980) suppressing mycorrhizal formation (Khan, 1974; Zak, 1961), or affecting phytoalexin production (Cruickshank and Perrin, 1967). Water logging may also change the microbial population in the rhizosphere so that it is no longer antagonistic to P. cinnamomi or no longer confers resistance to the host. A water-saturated, oxygen-deficient soil may both predispose the weakened host to attack and permit infection at the water surface where there is sufficient oxygen for zoospore activity. Oxygen-stressed roots leak or exude greater amounts of soluble metabolites and also ethanol and these probably stimulate chemotactic movement of zoospores of P. cinnamomi along the concentration gradient to the root surface (Young et al, 1977); Kuan and Erwin, 1980). Plant water stress before infection predisposed safflower and rhododendron to root rot caused by Phytophthora pathogens. (Duniway, 1977; Blaker and MacDonald, 1981), and salinity stress significantly increased root rot of chrysanthemum by P. cryptogea. (MacDonald, 1981).

While infection of feeder roots and subsequent root rotting is largely dependent on soil conditions favoring zoospore production, the extension of the pathogen within a large root or stem canker is directly affected by host factors. The capacity of Phytophthora spp. to invade secondary plant tissue has often been neglected. Although P. cinnamomi was first identified by Rands as a stem canker of Cinnamomum burmannii (Nees) Blume (Rands, 1922), research on this pathogen has tended to

focus on its capacity to infect the fine root system. But in other hosts, e.g. macadamia (Macadamia integrifolia) Maiden and Betche), expansion of stem cankers caused by this pathogen is variable (Rands, 1922; Pegg, 1973) which suggests that a host factor may affect lesion extension within secondary tissue. Recent research on susceptible Eucalyptus and Pinus species suggests that the capacity of P. cinnamomi to invade secondary plant tissue is more important than was previously assumed and that environmental factors may predispose these hosts to secondary tissue invasion.

It has been assumed that Phytophthora cinnamomi causes death of jarrah by attrition of the fine feeder roots resulting in gradual starvation (Podger, 1968; Podger, 1972; Palzer, 1976; Shea and Dell, 1981). But a small proportion of trees in infected areas die rapidly and mass collapse of jarrah stands has occurred particularly in areas where there has been excessive soil disturbance and disruption of drainage (Bartle and Shea, 1979). Further extensive sampling has shown P. cinnamomi to be consistently present in large suberised roots and collars of trees in which this "rapid death" syndrome occurred (Shearer et al, 1981). Marks et al (1981) and Marks and Smith (1981) have recently isolated P. cinnamomi from the large roots and collar of E. sieberi, E. regans and E. obliqua growing in naturally infected sites in the coastal region in Victoria. Inoculation experiments confirmed that P. cinnamomi can kill susceptible Eucalyptus species by girdling the root collar and/or major roots (Marks et al, 1981).

P. cinnamomi has also been assumed to be a feeder root pathogen of

Pinus radiata D Donn. (Newhook, 1959). This species has been grown extensively in Australia and New Zealand but there have been no reports of significant mortality caused by P. cinnamomi except when it has been grown in shelterbelts (Newhook, 1959; Batini and Podger, 1968). However, P. cinnamomi and P. cryptogea have recently (Stukely and Boughton (pers. comm.) been consistently recovered from large roots and the collars of 8 year old P. radiata plants exhibiting a "rapid death" syndrome, growing in a plantation in south western Western Australia.

The diseases of these eucalyptus and pines have been characterized by periods when there has been a massive mortality followed by extended periods of sporadic deaths and in some situations slow crown decline. Most of these tree species have deep roots and are thus not dependent on surface feeder roots for uptake of moisture. Hence it is unlikely that rapid death could be caused solely by feeder root removal. It is therefore difficult not to conclude that rapid death results from invasion of the large roots and/or stem. If this hypothesis is correct then, since massive rapid mortality occurs periodically, the susceptibility of these hosts to pathogen invasion of secondary tissue must vary over time.

The extent and constancy of fluctuations in host resistance between seasons of the year has been shown for apples to collar rot caused by P. cactorum (Sewell and Wilson, 1973; Gates and Millikan, 1972). Citrus with young developing shoots (Rossetti, 1969) particularly where the leaves had attained their full size (Rossetti and Bitancourt, 1951) had larger collar rot lesions than those trees with no growth flush.

Similarly resistance to infection of apple cultivars to P. cactorum was least during the period of bud burst and flowering and increased sharply with the commencement of shoot extension growth (Dakwa and Sewell, 1981). This may be related to the carbohydrate status of the bark. Newly emerging citrus growth is heavily dependent on substrates stored in other part of the plant (Hildeman et al, 1967; Kriedemann, 1969).

Sewell and Wilson (1974) related infection by P. cactorum and P. syringae to seasonal variations in susceptibility of apple trees and suggested that outbreaks of disease occur in years when the pathogen is present in the soil during periods of the year when the hosts are susceptible. It is possible that the interaction between seasonal susceptibility of Pinus and Eucalyptus species and year to year variations in seasonal activity of P. cinnamomi accounts for the periodic mass decline of these species.

There are other examples of changes in relative susceptibility which are affected by host factors. Roots of seedlings from windfall fruit growing in dense shade beneath avocado trees are completely destroyed by P. cinnamomi whereas seedlings in sunlight remain vigorous. (Pegg, 1977A). Hartigan (quoted in Baker and Cook, 1974) showed that the sapwood starch content of Eucalyptus saligna Sm. in moist valleys near Gosford, New South Wales, Australia, was inversely correlated with severity of insect attack by psyllids (Glycaspis spp.) and that low starch appeared to be associated with the incidence of P. cinnamomi to which E. saligna normally is quite resistant. In horticultural crops the scion may have a modifying effect on rootstock susceptibility. Klotz et al (1966;1958) observed that lesion development on sweet orange rootstocks was larger

when Lisbon Lemon rather than "Washington Navel" orange was used as a scion.

The mechanisms by which the condition of the host affect susceptibility are poorly understood. Chapman (1965) reported that "anything that tends to devitalize the tops of trees such as climatic extremes, insect infestation, insecticidal damage and nutrient deficiencies and excesses will lower the mortality of citrus roots and thus open them to destructive influences by both pathogenic and non-pathogenic soil organisms." However, the tendency to equate an increase in vigor with an increase in resistance needs to be approached with caution. Rapid growth rates or vigor per se does not necessarily indicate increased resistance. For example, Dakwa and Sewell (1981) found that the resistance of apple scions to P. cactorum diminished with increasing vigor of the root stock on which they were grafted.

Mycorrhizae

It has been proposed that ectomycorrhizal fungi contribute to the protection of plant roots from pathogens by providing a physical barrier to penetration by the pathogen, secreting antibodies inhibitory to pathogens, utilizing surplus carbohydrates, favoring protective phizosphere microorganisms and inducing in the host inhibitors to the pathogen (Zak, 1964; Marx, 1969A & B; Marx, 1972). In short term pot trials, with shortleaf pine (Pinus echinata Mill.)mortality and growth were significantly reduced in mycorrhizal plants in the presence of P. cinnamomi (Marx, 1973) Malajczuk (1975) found that mycorrhizal roots of jarrah resisted invasion by P. cinnamomi.

Ectomycorrhizae have been associated with reduced losses from root rot in a few instances in the field. Napier (1969) associated the development of disease with poor mycorrhizal development, while Newhook (1970) associated recovery of pines from root rot, following application of phosphate fertilizer, with development of mycorrhizal roots. The major difficulty in assessing the significance of these reports is that it is nearly impossible to separate cause from effect. One cannot be sure that the presence of mycorrhizae on seedlings or trees has not simply brought about a favorable physiological state in these plants which may cause a masking of symptoms of feeder root disease. Under field conditions comparisons of mycorrhizal with non-mycorrhizal plants are questionable. Conditions such as poor aeration and low organic matter contribute to feeder root disease and are inhibitory to mycorrhizal development (Marx, 1973).

In the suppressive loam soils of Western Australia, few mycorrhizal roots were formed in E. calophylla or E. marginata (Malajczuk, 1979B) but different types of mycorrhizae and their associated bacterial microflora may contribute to differential susceptibility of the two species to infection by P. cinnamomi in conducive soil (Malajczuk, 1979B). Marx (1969B) also reported that the differential susceptibility of two pine species to infection by P. cinnamomi may be attributed to specific mycorrhizal associations on loblolly pine (resistant host) roots which do not occur on shortleaf pine (susceptible host) in Phytophthora infested soil.

The effectiveness of ectomycorrhizal in preventing infection may depend on the physiological status of the mycorrhizal root in addition

to the type of mycorrhizal fungus. Klinac and Newhook (personal communication) found that while mature active ectomycorrhizae are capable of providing a high degree of rootlet protection against P. cinnamomi, many mycorrhizal roots in a given root system may be immature or senescent and much less resistant.

Disease development may also depend on the relative proportion of mycorrhizal and non-mycorrhizal roots. The timing of root initiation and colonization by mycorrhizal fungi, in relation to activity of P. cinnamomi could also be significant. Wilcox (1968) observed that rapidly growing roots especially those reaching dormancy, would outgrow ectomycorrhizal fungi and remain non-mycorrhizal for certain periods of time. Root initiation in jarrah trees corresponds to period when sporangial activity of P. cinnamomi is at a maximum and this may well precede mycorrhizal infection (Dudzinksi, Rockel and Shea, unpublished).

A major factor affecting the ability of mycorrhizal roots to confer resistance on tree species is the capacity of the pathogen to invade suberized roots. For example, although eucalyptus and pine trees commonly have root systems which are extensively mycorrhizal, P. cinnamomi has been consistantly recovered from suberized roots of these species. (Shearer et al, 1981; Stukely and Boughton, personal communication; Marks et al, 1981; Marks and Smith, 1981; Shea and Dell, 1981). Even if mycorrhizal roots are resistant to infection invasion of non-mycorrhizal roots and extension within large roots would bypass the mycorrhizal barrier.

A number of factors can affect the quantity and type of mycorrhizal root which is formed (Slankis, 1974). Factors such as levels of nutrients or soil organic matter can be regulated by cultural practices. Fire can

destroy mycorrhizal roots formed in the litter layer. (Malajczuk, 1979B). In horticultural crops or in plantation forestry it may be possible to protect tree seedlings by artificial inoculation with specific mycorrhizal fungi ecologically adapted to the forest site on which the seedlings are to be planted (Marx, 1975).

At this stage of research it is not possible to quantify the affect of mycorrhizal fungi on the development of Phytophthora diseases. However, the general beneficial effects of this symbiosis on plant growth is well documented. (Bowen, 1973). The adaption of cultural practices which favor mycorrhizal development could be justified on the general beneficial effects of the symbiotic effects on plant growth even if their significance in disease suppression is not certain.

Further research is required to identify the species of ectomycorrhizal fungi which prevent pathogenic infection and the mode of protection. It will be necessary to determine if it is possible to maintain these fungi as the dominant symbionts on the root system. Does the percentage of mycorrhizal roots correlate with the degree of control of root infection or can the production of antibiotics in mycorrhizal roots afford protection to adjacent non-mycorrhizal roots? Can a mycorrhizal fungus, highly efficient in water and nutrient uptake and present in a small portion of a root system, overcome the effects of root rot in the remainder of the root system? The association of ectomycorrhizae with other microorganisms also needs more study. Do the beneficial effects of mycorrhizal roots on host vigor contribute to resistance by reducing the capacity of the pathogens to invade the major root system and collar of susceptible species?

Endomycorrhizae

Evidence that endomycorrhizal plants are more resistant to Phytophthora diseases is sparse. No protection to P. cinnamomi was conferred on avocadoes infected with Glomus fasciculatus (Davis et al, 1978; Matare and Hattingh, 1978). Mycorrhizal roots of a nonresistant cultivar of soy-bean were more susceptible to Phytophthora megasperma sp. glycinera than were non-mycorrhizal roots (Ross, 1972).

Sweet orange seedlings infected by G. fasciculatus were susceptible to root rot by P. parasitica, but size, root health and phosphorus uptake were greater than in non-mycorrhizal plants (Davis and Menge, 1980). This tolerance may have been due to the ability of mycorrhizal roots to absorb more phosphorus and possibly other minerals than non-mycorrhizal roots (Davis and Menge, 1980). But vesicular-arbuscular mycorrhiza on citrus can also affect seedling stomatal conductance, phototsynthesis and proline accumulation, suggesting that the effect is on stomatal regulation rather than on root resistance (Levy and Krikun, 1980).

Most biological or cultural approaches to control of Phytophthora diseases have been directed to suppressing the pathogen. But comparatively recent research suggests that the environment may have a much greater affect on host susceptibility than has been previously assumed. However, identification of the host factors which affect infection and mycelial growth within host tissue by Phytophthora pathogens is required before it will be possible to determine if cultural procedures can be used to manipulate host susceptibility and lesser disease.

There is data which suggests that the physiological status of the

host will affect the composition and quantity of host exudates from roots and subsequently the number of zoospores attracted to the roots. But there is almost no information on the affect of root physiology and anatomy on the probability that a zoospore located at the root surface will penetrate host tissue. Seasonal variation in Phytophthora lesion extension within host tissue suggests that mycelial growth within host tissue is affected by host status but the processes responsible for this are not documented. Can hosts "compartmentalize" Phytophthora infections as has been demonstrated for wood decay fungi, (Shigo and Marx, 1977), and is the capacity to contain Phytophthora pathogens affected by host physiology?

There is circumstantial evidence that host factors such as growth rate, growth periodicity of roots and shoots, flowering and fruit formation, carbohydrate status of host tissue, root shoot ratios, etc., all affect host susceptibility. Most of these host characteristics can be modified by cultural procedures. There is, thus, considerable potential to lessen Phytophthora diseases by host manipulation but further research directed at determining the host factors which affect infection and mycelial extension is required before this potential can be realized.

SUPPRESSIVE SOILS

The occurrence of situations where susceptible vegetation is not diseased in the presence of pathogens, or where the probability of pathogen introduction is high, under climatic conditions which are normally suitable for disease development provides the best evidence of

the potential of biological and/or cultural control techniques. The inhospitability of certain soils to some plant pathogens is such that either the pathogens cannot establish, they establish but fail to produce disease or they initially establish and cause disease, but diminish in severity with continued culture of the crop (Baker and Cook, 1974). Such soils are referred to as "suppressive" soils as opposed to "conducive" soils where, given favorable climatic conditions and a susceptible host, the disease progresses unchecked. Suppressive soils have also been variously called resistant, immune, intolerant and antagonistic.

In Australia, there are a number of areas both in forests and avocado groves where Phytophthora cinnamomi Rands is present, but has not caused disease in susceptible vegetation and under climatic conditions which are normally suitable for disease development.

Forest Soils

(a) Western Australia

The jarrah (Eucalyptus marginata Sm) forest is a dry sclerophyllous evergreen forest occurring in the southwest of Australia. The climate is Mediterranean with the highest rainfall in the winter months and with little or none in the hot dry summer. The soils are predominantly lateritic and are extremely infertile when compared to the virgin rainforests and avocado groves of southeastern Queensland. They are low in organic matter, nitrogen and exchangeable cations (Malajczuk, 1979). Severe root rot, caused by P. cinnamomi, is invariably associated with these sandy and gravelly soils. The most susceptible sites occur along water courses or poorly drained areas but root rot has been found in most

jarrah forest communities, soil types and topographic situations, including free drained sites. (Podger, 1968; Shea, 1975), but the disease is not found in the vegetation on the more fertile red-brown loams of the steeper valleys which dissect the jarrah forest (Podger, 1968; Shea, 1975). Severe disease occurs on lateritic soils immediately upslope of these apparently resistant soils.

Malajczuk et al (1979A) compared the pathogenicity of P. cinnamomi to E. marginata and E. calophylla seedlings grown in lateritic soils and loam soils. Seedlings were grown in pots of sterile and non-sterile soil and inoculated with P. cinnamomi. In sterile loam and lateritic soil both eucalypt species were equally susceptible to infection. Using non-sterile soils, E. marginata was susceptible to infection only in the lateritic soils and E. calophylla was unaffected. This implies that the suppression of root rot exhibited by the loam soil involves a microbial factor and that resistance of the tolerant E. calophylla is not entirely due to innate resistance but also involves a microbial component in the rhizosphere.

(b) South Eastern Australia

Serious disease caused by P. cinnamomi has been recorded for duplex soils such as the shallow lateritic sands over impervious clays in the Brisbane Ranges (Weste and Taylor, 1971), deep sandy soils at Wilson's Promontory (Weste and Law, 1973) and infertile shallow soils with an impervious clay pan on the coastal plains of East Gippsland (Marks et al, 1975) in Victoria. However, although P. cinnamomi is widely distributed geographically in New South Wales (Pratt and Heather, 1973) disease caused by this fungus is restricted to moist gulley situations. Even

though the species which have been shown to be highly susceptible in Victoria are present there have been no major disease outbreaks. (Gerretson - Cornell and Dowden, 1978). Similarly, the disease situation in New South Wales constrasts with that in South Western Australia where soil physical environmental conditions at least on free drained sites are less favorable for pathogen reproduction and survival. Shea (1975).

The relative freedom from severe Phytophthora epidemics in south-eastern Australia may in part be due to microbial suppression of P. cinnamomi. Halsall (1981) described a soil from Tallaganda, New South Wales, which despite its low organic matter and nutrient levels, was suppressive to P. cinnamomi. P. cryptogea by contrast, was not inhibited. Blowes (1980) considered that the presence of a highly susceptible understorey in the jarrah forests of southwestern Australia which provided a large food base for P. cinnamomi and the absence of a corresponding species in New South Wales forests partially accounted for the differences in disease incidence between the two areas.

Blowes (1981) also suggested that the absence of severe seasonal drought stress in New South Wales may inhibit disease development. Pratt et al (1973) and Broadbent and Baker (1975) proposed that the location of Eucalyptus sieberi F. Muell, which is highly susceptible to P. cinnamomi, on deeper well drained ridges in New South Wales where pathogen activity is intermittent was a factor contributing to the absence of severe disease.

(c) Rainforest Soils

There have been few reports of P. cinnamomi in susceptible rain-

forest vegetation in Queensland (Q'ld) despite adequate opportunities for the spread of P. cinnamomi in drainage water from nearby infected plants like avocado and pineapple. (Newhook and Podger, 1972). "Patch death" in virgin rainforest in northern Queensland, which Brown (1976) attributed to P. cinnamomi, was associated with pig wallows which, because of heavy clay sub-soil close to the surface, retained water even when the soil under the apparently healthy rainforest was relatively dry.

Greenhouse pathogenicity tests were conducted on one hundred soils collected from various rainforest associations in New South Wales and south eastern Queensland. The soils were derived from shales and basalt and the texture varied from sand to clay. (Broadbent and Baker, 1974A; Broadbent, unpublished). These tests were carried out under a favorable temperature-moisture regime with a susceptible host (Eucalyptus sieberi F. Muell or Jacaranda acutifolia Humb. & Bonpl.) growing in small trays of soil infected with P. cinnamomi. The soils had been treated with aerated steam at 49°C or 60°C for 30 min. or with flowing steam at 100°C for 30 min. or were left untreated in an attempt to appraise the role of the microflora in the suppression. In soils conducive to root rot, seedlings developed root rot in all of the four treatments. In soils suppressive to root rot, seedlings were healthy and grew well in infected untreated soil but developed root rot in the steamed (100°C) soil. This suppression was removed by steam-air at 49°C or 60°C. Sporangium production of P. citrophthora and P. cinnamomi in untreated suppressive soils or leachates, was reduced to 10% of that in conducive soils (Broadbent and Baker, 1975).

Red basaltic soils suppressive to root rot have a high content of organic matter sometimes with a humus layer 9 inches deep, high exchangeable calcium levels (20-27 m.e.g.) with the calcium tied up in the organic cycle, a pH of 5.5-7.0, high total nitrogen levels, apparently locked in humic residues, and high biological activity. No association could be found between root rot suppression the clay mineral composition of the soil but the only soils found to be suppressive in these studies were derived from red basalts. "Patch death" of virgin rainforest, Brown (1976), was restricted to soils derived from granite-diorite-granodiorite parent material.

(d) Avocado Soils

The krasnozems of the north coast of New South Wales and south-eastern Queensland, prior to clearing, were vegetated with a sub-tropical rainforest. For a luxuriant rainforest to florish on soils poorly supplied with certain plant nutrients, there must be a rapid turnover of nutrients which is achieved by rapid decomposition of fallen leaf litter and softwood trees by saprophytic fungi and bacteria. Higher contents of organic carbon, nitrogen and exchangeable cations in upper horizons of the profile suggest a closed cycle in which the cation requirements of the virgin vegetation are supplied by leaf litter. The replacement of this vegetation with crops, e.g. avocadoes (Persea americana Miller) appears to have interrupted the cycle and replaced it with an exploitive system (Colwell, 1958; Nicholls and Tucker, 1956).

Surveys of avocado groves in northern New South Wales and south eastern Queensland coupled with soil tests to appraise the antagonistic potential to root rot, have shown that avocado soils, suppressive to root

rot, do exist and have similar physical, chemical and microbiological properties to those of nearby suppressive rainforest soils. These properties have been maintained principally by the use of organic amendments. Prior to planting and while the avocado trees are young, extensive cover cropping is practiced, using maize (Zea mays L.) and Dolichos lablab L.in summer and New Zealand blue lupin (Lupin angustifolius L.) and oats (Avena sativa L.)in winter, plus fowl manure, dolomite and synthetic fertilizers. When the tree canopies touch, mulches with a high carbon/nitrogen ratio e.g. barley straw, hay or Rhodes grass (Chloris gayana Kurth) or mixed native grass are added. Timing of the application of mulches may be important: mulches should be partially decomposed before the summer rains, otherwise they may be colonized by the P. cinnamomi fungus or retain too much soil moisture. Without the extensive application of organic amendments, the organic matter, the cation exchange capacity, and nitrogen levels fall, and the soils become conducive to root rot.

Red basaltic soils conducive to root rot can be rendered suppressive in time (upward of 2 years) by the use of organic amendments. Pegg (1977A) demonstrated the effectiveness of these cultural practices with two examples; (i) many trees which declined following the 1972 deluge (1,750 mm rain in 3 days) when soils lost their suppressiveness due to prolonged waterlogging, have since been restored to health by using surface organic mulches and fowl manure; (ii) P. cinnamomi can no longer be recovered from a site at Mt. Tamborine at which declining avocado trees were removed in 1973 before restoration of the soil by intensive cover cropping,

frequent light dressings of dolomite and fowl manure prior to replanting with clean nursery stock. This demonstrates that the suppressive and conducive states of soil are relative and the balance can be readily tipped.

It appears to be the maintenance of a deep humus layer in the red basaltic soils which contributes to the suppression of root rot. The type of mulch or cover crop used is partly irrelevant (although the rate of breakdown, frequency of addition and requirement for additional nitrogenos amendments will vary with the mulch). 'Single shot' applications of fowl manure or sawdust or alfalfa, especially after a tree is showing visible signs of root rot will rarely work. A continuing program of mulching and for cover cropping and addition of nitrogenous calcareous amendments is essential to maintain the humus layer and the root rot suppression. Suppression of root rot is rarely, if ever, absolute and a degree of root rot can be tolerated by the avocado tree with no obvious effects on 'above-ground' tree health. A threshold can be reached where further loss of roots may result in irreparable damage to the tree and no amount of organic amendments will cause a response in tree health.

CULTURAL PROCEDURES

There are few examples in the literature where it can be shown that cultural procedures have been used to achieve control of Phytophthora diseases. There are, however, a number of techniques which can be used to reduce the severity of disease and there are some promising approaches

to control.

Control by Exclusion and Sanitation

In many areas Phytophthora species are not endemic and the simplest approach to control is to prevent their introduction. The recognition that quarantine and/or hygiene may ultimately be inadequate to prevent introduction and the capacity of Phytophthora spp. to rapidly increase in propagule density has caused this approach to control to be under-emphasized. Disputes as to the endemic or introduced status of some pathogens have also impeded the introduction of hygiene and/or quarantine (Shea, 1979). Mackenzie et al (Chapter) also warns that the value of sanitation has been underestimated.

In some disease situations, particularly in forests, the only viable long-term control strategy is based on manipulation of the existing vegetation. This option is not feasible if the pathogen has been introduced, has become widely dispersed, and has severely debilitated the forest. Hence even if hygiene and/or quarantine only delays disease development, it is justified. Even after the pathogen has been introduced the maintenance of hygiene procedures may still be justified, because the broadscale distribution of soil borne Phytophthora spp.(other than by water flow) after periods of natural quiescence, is limited. For example, although natural extension of P. cinnamomi infections in the jarrah forest upslope is less than 1 meter per year, uncontrolled road-making can transmit this pathogen over several kilometers in a few days (Shea et al, 1980A).

The importance of nursery hygiene in preventing the spread and intensification of Phytophthora diseases is well documented. Even when

nursery stock is destined for areas where pathogens are already present, disease control is greater if the plant is free of the pathogen at the time of establishment.

It is impossible to avoid transfer of inoculum to uninfected sites if the location of diseased areas, the sources of inoculum, are not accurately defined. For example, large scale aerial color photography has been used to identify and locate the disease based on symptoms on plants in the shrub and understorey layer of the jarrah forest in Western Australia. The objective of this program is to provide accurate maps of disease occurrence in over 500,000 hectares of forest. Identification of potential sources of inoculum in the forest makes it possible to minimize transfer of inoculum into healthy forest by activities such as logging and mining (Bradshaw 1974; Bradshaw and Chandler, 1978). Temporal as well as spacial variation in inoculum distribution can be used in hygiene management. For example, during the summer months the potential for spread of P. cinnamomi by vehicles in the Jarrah Forest on upland free drained sites is minimal because inoculum levels in the soil are low. (Shea et al, 1980A).

Spacial and temporal variations in receptivity of sites to inoculum should also be used in designing hygiene procedures. For example, the probability that transferred P. cinnamomi inoculum will remain viable on moisture gaining sites in the Jarrah forest is high throughout the year, but inoculum survival on dry upland free drained sites during the summer months is low (Shea, 1975).

Seasonal and year to year variations in inoculum levels and variation in host susceptibility with season and/or stage of development can be

exploited to achieve control. For example, Ko (1971) found that resistance of papaya roots to P. palmivora was directly correlated with the age of the plant. Awareness of this host factor led to a unique method of biological control. By filling the planting hole with pathogen free soil, the seedling escaped infection during its susceptible stage. By the time the roots reached the infested soil, they were resistant. Grainger (1968) proposed that timing of planting of potatoes in Scotland could be exploited to achieve control of late blight. Potatoes planted early in the season escape disease because environmental conditions are unfavorable for P. infestans (Mont.) De B. and at later stages of crop development when the fungus is active, the host is "unreceptive". Based on this, an index of host susceptibility, the Cp/Rs (weight of total carbohydrate in plant/ residual dry weight) ratio was proposed (Grainger, 1968). Phytophthora megasperma can cause major damage to early sown chickpeas in New South Wales, particularly on irrigated grey soils. Late March sowings were almost completely destroyed while plantings delayed until temperatures were cooler in May escaped the disease (Stovold, personal communication). This effect was attributed to temperature and illustrates how cultural practices can be modified to exploit differences in the timing of pathogen activity and host susceptibility to achieve a form of control by exclusion.

Where there are differences in susceptibility between trunk, major roots and feeder roots on such horticultural crops as citrus (Broadbent et al, 1971B) and peaches (Taylor, 1980) disease control may be achieved by management practices such as shallow planting, keeping the trunks dry (Taylor, 1980) and prevention of wounding of trunks and stems.

Sanitation involves reducing the inoculum level by removing infected host tissue. Turner (1965) recommended the removal of diseased cacao pods infected by P. palmivora and disposal of the cacao stubble as techniques which should be employed to reduce inoculum potential. To avoid tuber rot by Phytophthora infestans, potatoes should not be dug until the tops are either killed by frost or are treated with defoliant chemicals so that the possibility of spreading inoculum such as sporangia from on the tops to the tubers is prevented (Zentmyer and Bald, 1977). Reduction of the density of the Banksia grandis understorey in the Jarrah forest, which is highly susceptible to P. cinnamomi, has been proposed as one method of reducing inoculum potential. (Shea, 1975).

Manipulation of the Physical Environment

A number of cultural techniques can be used to change the physical environmental factors (e.g. temperature, moisture, aeration, light) in the soil to disfavor Phytophthora spp. Where the physical environment is only marginally favorable for the pathogen(s), relatively small changes could have a major effect on disease severity.

Careful site selection is important. In some sites the inherent structure of the soil profile or its position in the landscape may result in a soil moisture regime so favorable for survival and reproduction of Phytophthora that any cultural technique is unlikely to bring about control. Poorly drained soils are hazardous for avocadoes especially when the P. cinnamomi is present since there is a close correlation between root rot damage and soil type (Goodall, 1955). Soil drainage characteristics have been used to determine if specific soil series are suitable for

growing avocadoes in California (Zentmyer et al, 1967; Burns et al, 1960) and in South Africa (Wolstenholme and Le Roux, 1974).

One of the most important factors of the physical environment affecting the development of Phytophthora diseases is soil moisture regime. While root rotting may result from impedence to drainage and/or excessive rainfall, losses are accentuated by Phytophthora spp. In general any cultural practice which minimizes the period during which the soil is at a soil moisture potential less than 100mb and prevents overland flow of water, will reduce disease.

A number of management procedures can create a potential disease hazard by providing a favorable soils moisture regime. Evaluation of the effect of such practices as roadmaking, drain construction, logging track formation, etc. on soil drainage and subsequent disease can assist in the development of simple procedures to minimize disease. For example, the restriction of roads to lower topographical positions in the landscape will minimize the area predisposed to root rot. In New South Wales headland drains are used to prevent the entrance of run-off water into avocado orchards, while surface drains prevent excessive ponding and water soaking of the soil, and subsurface drains allow free water to percolate from the root zone (Chalker, 1974). Other helpful practices include ripping (Borst, 1975) and mounding of the beds on which the crop is planted. (Baker, 1938). Disease development can also be modified by regulation of the irrigation regime (Mircetich, 1978). For example, the dependence of many Phytophthora spp. on overland flow of water for widespread propagule dispersal emphasizes the advantage of drip irrigation and fine undertree sprinklers as opposed to furrow irrigation.

Although vertical drainage is a critical factor that favors Phytophthora root disease, there are large areas in the severely diseased jarrah forest in Australia where the water table is more than 10 meters in depth, and there is minimal impedence to water flow in the upper 50cm of the soil profile (Shea, 1975). Even where susceptible vegetation is growing on freely drained sites with coarse textured soils there may be times when high rainfall or frequent rainfall favors sporangial formation and release of zoospores. In these situations the soil moisture regime can only be modified by cultural treatments which effect the density and composition of the vegetation and the surface litter. (Newhook, 1970; Shea, 1975).

Temperature also has a marked effect on survival and reproduction of Phytophthora pathogens. Soil temperature regimes can be modified by changing the canopy and the litter cover. Coincidence of relatively high temperatures and low matric potential are required for the sporulation by P. cinnamomi. Roth and Kulman (1963) postulated that P. cinnamomi was unlikely to be a threat to Douglas Fir forests in Oregon because of the absence of periods when there was a coincidence of high soil moisture and temperature regimes suitable for sporangial formation. Similarly an unfavorable soil temperature regime was cited as the principal factor preventing survival in, and colonization of, mountain soils in eastern Victoria by P. cinnamomi (Kassaby et al, 1977). Shea (1975) suggested that the promotion of a dense canopy, which lowered soil temperatures on freely drained sites in the jarrah forest, would decrease the periods during which sporangial formation could take place.

Identification of the upper temperature limits for survival and reproduction of P. cinnamomi permitted the identification of low hazard

sites for Phytophthora root rot of pineapple (Ananas comosus L.) Hine et al, 1964). High temperature treatments of nursery stock can be used to eradicate P. cinnamomi (Baker, 1962; Benson, 1978).

Fire

Fire is a natural factor of the environment in many regions of the world. Prescribed fire has been extensively used in some forests for the purpose of removing litter and brush, which is a fire hazard, and regeneration. The effect of fire on a forest depends on its frequency and intensity, and the season during which the burn is carried out (Shea et al, 1980C). By varying these factors it is possible to manipulate the structure and composition of forests and the nature of the litter layer. This, together with the fact that it can be used over large areas at a relatively low cost, makes prescribed fire potentially one of the most practical tools available to the forest manager to modify the forest environment.

Changes in the fire regime, however, may have both beneficial and detrimental effects. It is possible that periodic removal of the litter layer by fire could significantly increase the susceptibility of a forest to Phytophthora root rot by allowing soil temperatures to increase and by decreasing the interception of rainfall, thus prolonging the period when the soil moisture and temperature regimes are suitable for sporangial production by P. cinnamomi. (Shea, 1975).

The microbiological effects of periodic litter removal by fire are not well understood (Warcup, 1981). Differences in soil organic matter

levels between regularly burned and unburned E. marginata forest sites were found to be insignificant (Hatch, 1959). P. cinnamomi causes disease in unburned areas (Podger, 1968), and a high level of sporangial production was observed in forest soils bearing a 7-year accumulation of litter (Shea et al, 1979). Nesbitt et al (1979A) found that soils into which jarrah forest litter had recently been incorporated caused lysis of P. cinnamomi mycelium and abortion of sporangia, but it is unlikely that these treatment were relevant to the field situation.

Malajczuk (1979A) stated that "the development of ectomycorrhizae of jarrah appears to be strongly associated with an increased organic matter or litter component beneath trees". Since ectomycorrhizal roots are resistant to infection, removal by fire of that proportion of the ectomycorrhizal roots which are present in the litter layer would, by inference, increase the proportion of the fine root system which is susceptible to infection. The significance of this to disease development would depend on the relative importance of the ectomycorrhizal roots removed by fire to total nutrient uptake. This is not known.

The intensity, frequency and season of burn can markedly affect the structure and composition of the understorey. For example, periodic (5-9 year cycle) low-intensity fire carried out to reduce fuel accumulation and protection from fire in the jarrah forest favors the maintenance of an understorey dominated by Banksia grandis Willd. which is highly susceptible to P. cinnamomi (Shea, 1975; Shea 1979A). Moderate to high

intensity fire causes regeneration of leguminous species and reduces the density of the susceptible Banksia grandis. Acacia pulchella, a common legume species, is resistant to root invasion by P. cinnamomi (Shea, 1975; Shea et al, 1976; Shea and Malajczuk, 1977; Tippett and Malajczuk, 1979). There is some evidence that the microbiological and physical environment in soil under legume stands is less suitable for sporangial production and survival of P. cinnamomi. (Shea et al, 1979; Shea and Malajczuk, 1977) and that chemical exudates from A. pulchella depress sporangial production and germination and mycelial growth (Whitfield et al, 1981; Alexander et al, 1978).

Fire can stimulate growth of Eucalyptus species and affect flowering and seeding cycles (Kimber, 1978) and this may affect host susceptibility. Fire is also an important method by which regeneration of eucalypt species is achieved. There is considerable potential to increase the diversity of mixed eucalypt forests by direct seeding of selected tree species following regeneration burns. For example,mixtures of P. cinnamomi - tolerant and susceptible species of trees have been successfully established on P. cinnamomi-infected coastal forest areas in south-eastern Victoria (Shea, 1979A).

Fire has the capacity to affect the host, the pathogen and the environment, but little progress will be made in elucidating its effect on disease development and its potential for control until the processes by which it affects each of these factors is understood and evaluated in the context of epidemiology.

Organic Amendments

High levels of organic matter in soil have been associated with some soils which are suppressive to P. cinnamomi (Broadbent and Baker, 1974A; 1974B), and manipulation of organic matter levels in forest soils has been proposed as a potential method of control of this pathogen (Malajczuk, 1979; Nesbitt et al, 1978). Organic matter can effect vigor of the host by improving soil structure and moisture and nutrient holding capacity, but the principal effect is to provide a more complex and antagonistic soil microflora and fauna (Broadbent and Baker, 1975).

When high value agricultural and horticultural crops are grown in short rotations, soil organic matter levels can be manipulated by direct additions of organic matter and/or cover cropping. Even in forests it may be possible to regulate organic matter directly by protection from fire (Malajczuk, 1979A), or fire may be used to change the species composition of the understorey to favor species of plants from which soil organic matter levels are increased (Shea, 1979A).

A good example of control of Phytophthora root rot by organic amendments exists in Australia where some avocado growers add copious amounts of plant residues and chicken manure each year to their orchard soils to build up the organic matter levels or to maintain them at a level near that of the surrounding undisturbed rainforest(see "Suppressive Soils".) Orchards managed in this way have little root rot caused by Phytophthora cinnamomi whereas those orchards where tillage has reduced the organic matter levels have severe root rot (Broadbent and Baker, 1975).

The potential for control of Phytophthora pathogens by the use of organic amendments has its most likely application innurseries in which

plants are grown in containers. Hardwood bark composts have been used to eliminate Phytophthora pathogens during the composting phase thus eliminating the necessity for steam sterilization (Hointink et al, 1977; Hointink, 1980). In addition these composts suppress the activity of Phytophthora pathogens after they are introduced. Hointink's studies demonstrated that the type of organic matter and the control of the composting process were critical. Control was not achieved if the hardwood bark component was excessively diluted.

There have been a number of other studies which have shown that Phytophthora diseases can be controlled in pots by regulation of the quantity and composition of the organic matter (Gerretson-Cornell et al, 1976; Zentmyer, 1963; Gilpatrick, 1969 B; Tsao et al, 1975).

Although control of Phytophthora diseases can be achieved by regulation of the media used to grow container grown plants, and there is a correlation between high organic matter levels and lower levels of disease in some field situation, it cannot be assumed that organic matter amendments per se will always contribute to a reduction of incidence or severity of disease. Some types of organic amendments may lead to an increase in diseases caused by Phytophthora species. The rate at which P. cinnamomi affected (Pinus echinata Mill.) and the rate of decline was increased by the addition of forest litter, but compost and horse manure had little effect. (Roth et al, 1948).

At what stage of the breakdown of organic matter is Phytophthora suppressed? Nesbitt et al (1979A) added varying quantities of fresh jarrah litter to a lateritic soil and increased the lysis of hyphae and sporangia of P. cinnamomi which they attributed to increased concentrations

of nutrients and microbes. However the number of viable sporangia was greater in the organic matter treatments because organic matter stimulated greater sporangial production. Undecomposed leaf litter piled around a citrus tree can act as a substrate for Phytophthora and may retain moisture so that collar rot losses may be increased (Fawcett, 1923). Broadbent (unpublished data) has isolated P. cinnamomi from decomposed sorghum mulch and mixed native grass hay around avocado trees. Leachates from these mulches may stimulate the formation of sporangia.

Fertilizer application

The application of fertilizer is one of the most common cultural techniques appied to the management of agricultural and forest crops. But our knowledge of the interactions between fertilizer application, plant growth and Phytophthora diseases is inadequate and often contradictory. Part of this confusion can be attributed to the difficulty of spearating the effect of fertilizers on the host and on the pathogen.

The addition of large quantites of nitrate or ammoniacal fertilizers was generally effective in reducing the incidence of little leaf among healthy pine trees, and in improvement of many trees which were already diseased (Roth et al, 1948). However, the addition of a large number of other elements (Na, P, K, S, Ca, Zu, Mg, Mn, Cu, Mo, Co, Ni, B, Fe), had no beneficial effect. Broadbent and Baker (1974A) and Pegg (1977A) have implicated nitrogen as a factor which influences the suppression of root rot of avocadoes in red basaltic soils.

A number of studies have shown that the form of nitrogen has an important effect on survival and reproduction of Phytophthora pathogens.

(Tsao and Oster, 1981; Gilpatrick, 1969A; Broadbent, 1977). Soil pH can affect both the form of nitrogen, the pathogen directly and the antagonistic microflora as has been demonstrated by Smiley (1978) with take-all of wheat. Form and concentration of nitrogen may also affect host susceptibility. (Hornby and Goring, 1972). In a model system, Brown (1975) found that the amount of take-all disease of wheat depended on a complicated interaction between host nutrition, form of nitrogen on which the pathogen was grown and the activity of the microbial flora of the roots. It is probable that such an interaction must also occur for Phytophthora root rot.

Newhook (1970) by applying superphosphate to a forest of Pinus radiata in New Zealand to correct a phosphate deficiency and improved the crown density, root growth and mycorrhizal development. The increased tree growth in fertilized plots led to a greater removal of water from the soil, which contributed to a reduction in Phytophthora root rot.

Soil applications of elemental sulphur in replant pineapple culture have been effective in controlling pineapple root and heart rot caused by P. cinnamomi (Pegg, 1977B; Kewcock, 1935). This result was attributed to a lowering of the soil pH below 3.8 which markedly reduced sporangium formation (Chee and Newhook, 1964; Pegg, 1977A). Fortunately, the pH values that were limiting to the sporulation of P. cinnamomi were favorable for the growth of the pineapple. The population of Trichoderma spp. explodes in sulphured soils (Pegg, 1977A) but its role in reduction of Phytophthora caused disease has yet to be determined.

Fertilizer application in some instances may increase disease. In field trials fertilization of Eucalyptus spp. primarily with N,P and K (applied as a mixture) has increased disease or at least had no significant effect (Marks et al, 1973).

The effect of fertilization of plants with minor elements on Phytophthora caused disease has received comparatively little attention. However, a number of studies have suggested that calcium may have a positive effect on disease control. Avocado soils suppressive to Phytophthora root rot in eastern Australia are high in exchangeable cations, particularly calcium and magnesium (Broadbent and Baker, 1975). The maintenance of high calcium levels in soil and the addition of calcareous amendments may affect root rot by improving soil structure, but in addition there appears to be a complex relationship between soil drainage, and aeration, calcium supply and resistance to fungal attack. (Borst, 1970). Chapman (1965) found that in nutrient solution experiments with citrus, root rotting in areas of low oxygen supply is much reduced in the presence of a high concentration of calcium. Zentmyer and Lewis (1975) reduced root rot of avocado and Persea indica seedlings by drenching with calcium salts. Lee (1979) found that seedlings of Persea indica grown in Hoagland's solution No. 1 containing 160 ppm Ca^{++} were more resistant to infection or tissue colonisation by P. cinnamomi than those grown at lower Ca^{++} levels. Bellamy et al, (1971) found that calcium chloride reduced the rate of spread of P. cinnamomi in the roots of New Zealand blue lupin. Calcium carbonate markedly increased the proportion of healthy fine roots and almost suppressed infection of jarrah roots by P. cinnamomi. This was attributed to an increase in the

development of ectomycorrhizal fungi on roots. (Boughton et al, 1978). However, Halsall (1980) found that calcium did not reduce mortality nor reduce the growth suppression associated with infection of susceptible eucalypt seedlings by P. cinnamomi. The addition of gypsum or lime at varying rates to avocado seedlings in pots of conducive soil infested with P. cinnamomi reduced root rot very slightly; the response was more marked in the presence of NH_4^+ (Broadbent, unpublished). Gypsum applied in addition to cover cropping (Lablab purpureus L. and Lupinus angustifolius L.) and application of fowl manure to avocado trees in a soil management trial on red basaltic soil at Alstonville, New South Wales, Australia, increased the availability of and improved vigor and yields of trees (Trochoulias and Broadbent, 1978).

Fertilization, like fire, is cultural procedure which has great potential to be used in control of Phytophthora diseases because it can be controlled by the manager or farmer and fertilizers have been shown to affect pathogens and disease development. But also, like fire, fertilizers affect host, pathogens and environment. Further research is required to elucidate these interactions and the processes involved before it will be possible to determine if cultural procedures based on fertilizers applications can be used to reduce Phytophthora diseases.

CONCLUSIONS

Grainger (1979) observed that "It is easy ..... for plant pathologists ..... to concentrate on our desire for scientific understanding and to neglect our duty to be useful to farmers". While such

progress has been made in understanding the biology of Phytophthora pathogens and the hosts they attack, this has rarely been translated into viable control procedures. We suggest that this a primarily a consequence of our failure to integrate our research findings and apply the principles of integrated control to the field.

Although the dynamic nature of the interactions between host, Phytophthora pathogens and the environment are recognized, most research has examined only the effect of single factors on host and on the pathogen. Almost no research has been carried out on the interaction between temporal variations in pathogen activity and host susceptibility, induced by changes in the environment, on disease development. We suggest that many of the puzzling variations in Phytophthora disease intensity in time and space could be resolved by contemporous analysis of pathogen activity and host receptivity together with the principal factors of the environment which effect pathogen and host.

Although the data base is small in those situations where we have some knowledge of the basic epidemiology of Phytophthora diseases, disease outbreaks appear to occur during periods when a number of factors of the environment favor the pathogen during periods when the host has minimal resistance. It is unlikely that biological or cultural control techniques which are directed at manipulating one or even a few of these factors, without consideration of the temporal variations in pathogen activity and host resistance, will significantly lessen disease. For example, the potential for successful biological or cultural control is negligible if there are unavoidable periods during which host susceptibility is insensitive to inoculum potential.

In the relatively few instances where successful control of Phytophthora diseases has been achieved by biological and/or cultural methods and where Phytophthora diseases are suppressed in natural ecosystems, a number of the factors of the environment which disfavor the pathogens and increase the resistance of the hosts appear to be operating. We suggest that biological and/or cultural control is most likely to succeed when the various techniques which can be used to manipulate pathogens and hosts are integrated to reduce pathogen activity and increase host resistance during the critical periods when disease outbreaks occur.

An understanding of the basic epidemiology of Phytophthora diseases however, is an essential pre-requisite to the development of integrated biological and/or cultural control procedures. We conclude, therefore, that effective control by these methods is likely to be achieved only if more of our research effort is directed towards studies which elucidate the interactions between host and pathogen over time in the environment where the disease is occurring.

Our failure to undertake this type of research in the past can be in part attributed to the difficulty of making a meaningful analysis of the data which is derived. But as Mackenzie et al Chapter have observed, computer simulation has had the potential to remove this constraint. A more serious problem is our inability to develop integrated research programs. Elucidation of the basic epidemiology of Phytophthora diseases requires specialized knowledge in a number of disciplines and there are considerable logistical problems.

But most of our plant pathological research programs are structured around a single research scientist with limited technical support staff. The premium placed on the quantity of published papers produced by plant pathologists also is a disincentive. In view of our limited success in developing methods to control Phytophthora diseases we suggest that it may be appropriate to examine the institutional constraints on the development of integrated research programs.

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