FUNGI AS PEST CONTROLS

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Fungi as pest controls

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ABSTRACT

Fungi as pest controls are being studied intensively in many parts of the world. Success has been demonstrated against weeds, arthropods, fungal disease organisms of plants, and nematodes. To be selected for development, a fungus must be highly virulent against target species; it must be amenable to mass production and formulation; it must remain viable and virulent under conditions of extended storage in the formulated state; it must not be harmful to nontarget species; and it must not pose health hazards to man.

Fungi under commercial production include : Verticillium lecanii against aphids, whiteflies, and thrips in greenhouses; Hirsutella thompsonii against mites in citrus orchards; Phytophthora palmivora against a weed in citrus orchards; Beauveria bassiana and Metarhizium anisopliae against mainly arthropod pests in field crops; Trichoderma viride against disease organisms in commercial mushrooms, fruit and shade trees; and Peniophora gigantea against a rot disease organism in forest trees.

Fungi on the verge of commercial production include : Cercospora rodmanii against water hyacinth; Colletotrichum gloeosporioides against weeds in rice; and Colletotrichum malvorum and Alternaria macrospora against weeds in cotton.

Fungi for control of mosquitoes is an attractive idea. Several fungal species are promising larvicides. Each of these species, however, still has problems that need to be solved.

Control of fungal plant diseases with fungal antagonists can be approached by : modifying the microenvironment to favour antagonism; introducing antagonists; and inducing hypovirulence or host plant resistance. Induction of hypovirulence is successfully demonstrated by the introduction of hypovirulent strains of Endothia parasitica into lesions caused by virulent strains of the same fungus in American chestnut trees. The lesions heal as the disease organism loses its virulence.

Increased use of fungi for biological pest control, both as inoculations and as inundations, will depend on basic research into the bionomics of hosts, pests, and fungal agents, and a continuing search for new species and strains of fungal parasites and antagonists.

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I. INTRODUCTION

Pests are "living organisms that we regard as causing harm to our health or well-being" (Beirne, 1969). They include weeds, insects, mites, nematodes, plant pathogens, and vertebrates. Attempts to control pests usually involve chemical, physical, cultural, or biological means, and sometimes combinations of these.

The deliberate use of fungal pathogens as biological controls against pests was first considered in the latter part of the nineteenth century, with insect pests as targets. The early attempts mostly failed (Hall & Papierok, 1982). Fungi, unlike bacteria or viruses, usually invade their insect hosts through the cuticle. This mode of infection requires the presence of free water or high humidity, and warm temperatures (Roberts & Yendol, 1971). Because man can do very little about these meteorological factors, McCoy has observed (1974) that "the opinion of many insect pathologists is, fungi will not be used successfully in the field as a reliable control for insects."

Yet, in nature fungi continue to cause dramatic population crashes of insects (Burges & Hussey, 1971). Improved knowledge of fungal pathogens, target pests, and conditions for epizootics will undoubtedly ensure a better chance of success in the future. And, because of the stringent abiotic requirements for fungal infections, employment of fungal pathogens would be most

effective against pests that spend at least part of their life cycle in a moist or aquatic habitat. Alternatively, the ecosystem can sometimes be manipulated to favour the growth and spread of fungal pathogens (Baker & Cook, 1974; Ignoffo, 1981).

Recent reviews show that fungal pathogens have been used successfully against various pests in Brazil (Ferron, 1978; 1981), Chile (Templeton et al., 1979), China (Hussey & Tinsley, 1981), the USSR (Ferron, 1978; 1981), Australia (Cullen, 1978), Europe (Hall, 1981; Hall & Burges, 1979; Hall & Papierok, 1982), and the US (McCoy, 1981; Freeman et al., 1981; Templeton et al., 1979).

Progress in the past ten years has been most notable in exploring the potential of fungi to control weeds, arthropod vectors of diseases, microbial pathogens of plants, and greenhouse pests. Now, at least six fungal pathogens have been patented for use against various pests, five more are at the stage of commercial production and many others have been field tested.

Many of the recent successes in the control of pests with fungal pathogens have involved discoveries of fungal species and strains, adoption of new strategies, and the improvement of technology. This paper will review these advances, identify the problems and constraints of using fungi as control agents, and discuss some of the successes and failures.

II. CONTROL OF WEEDS

Fungal diseases can kill plants. Often the diseases are so efficient and pervasive that growing susceptible crops on contaminated land becomes uneconomical. Weeds are also subject to fungal attack. Weedy plants cause enormous losses in agricultural production. In the United States, the estimated annual direct loss to weeds is valued at more than $12 billion while farmers spend another $6.2 billion to control them (Shaw, 1982). Although chemicals are, and will remain, the most important method of weed control, "reliance on a single method of control is hazardous" (Wilson, 1969). The immediate danger is "ecological shifts to weed populations that are resistant to control by herbicides" (Shaw, 1982). Fungal pathogens can sometimes be more efficaceous than chemical herbicides (Templeton et al., 1979).

The idea of using fungi to control weeds was not seriously entertained until recently (Freeman et al., 1978). In the past ten years, there has been much activity to exploit this untapped resource and the results are very encouraging. Now, fungi are being seriously considered as control agents for some of the most troublesome weeds.

1. Aquatic weeds

Aquatic weeds are major problems in many parts of the world, particularly in the tropics and subtropics (Bennett, 1974). "They destroy fisheries, interfere with hydroelectric and irrigation schemes, stop navigation, and bring starvation and disease problems to riverine communities" (Holm et al., 1969).

Aquatic weeds can be controlled by chemical, physical, or biological means. Chemical control using herbicides is often not acceptable because of the danger of pollution. Physical control is expensive and is not practical when large river and lake systems are involved. Biological control is almost certainly the most desirable approach (Zettler & Freeman, 1972). It has been tried using insects, manatees, snails, fish, ducks, and goats. Fungal pathogens, long neglected, are particularly good candidates as biocontrol agents for aquatic weeds because they are "numerous and diverse, are frequently host specific, are easily disseminated and self-perpetuating, will not completely diminish a host species, and do not normally affect man or other animals" (Freeman et al., 1981).

To be considered for biological control, a fungal pathogen must have high virulence and infectivity; it must be easily cultured and formulated; it must have a long shelf-life in the formulated state; and it must be safe to use. Virulence is defined as the disease-producing intensity or power of a microorganism, and infectivity as the capacity of a pathogenic

microorganism to spread from one host to another (Steinhaus, 1949). The term 'safe to use' refers not only to causing no harm to man, his animals, or nontarget species, but also to the resolution of conflicts of interest. Conflicts of interest are particularly important in biological control of weeds.

Biological control with fungal pathogens is likely to be most effective where a single species of weed occurs in dense, pure stands, a condition that encourages a rapid increase of the pathogens with a resulting quick decline in the weed's abundance (Frick, 1974). In this respect, most of the world's pernicious aquatic weeds are good targets.

a. Water hyacinth

Of the many aquatic weeds, water hyacinth (Eichhornia crassipes (Mart.)Solms.) (Liliidae:Pontederiaceae) is the most noxious (Holm et al., 1969). Originally confined to South America, this weed is now found in most warm regions of the world. It has inflated petioles, forming dense floating mats where growing conditions are good. In Florida, most of the estimated $10-15 million spent annually to control aquatic weeds is on water hyacinth (Conway, 1976b). A control program was initiated in 1970 at Gainesville, Florida, with a search for pathogens (Gangstad, 1978). Both exotic and indigenous plant pathogens were surveyed. The most promising for water hyacinth are Cercospora rodmanii Conway, Acremonium (Cephalosporium)

zonatum (Sawada)Gams, and Uredo eichhorniae Fragoso and Ciferri (Freeman et al., 1981).

C. rodmanii is a recently discovered fungal pathogen (Conway, 1976a). It is an example of an indigenous fungus that has proved to be very effective against an introduced weed (Conway, 1976b). The fungus has been patented by the University of Florida and is being developed commercially by Abbott Laboratories, Chicago, Illinois (Freeman et al., 1981).

C. rodmanii causes chlorosis in water hyacinth. Infected plants have spindly petioles and do not produce offshoots. The final stage of infection is characterized by a root rot and the sinking of the whole plant (Conway, 1976b). The host tissues can be invaded either by mycelium or spores through stomatal openings. Secondary spores are produced which are wind disseminated and serve as inoculum for the spread of the disease. The sinking of killed plants is a key constraint on epidemic development of the fungus in nature because it greatly reduces the production of spores. As a result, the disease has a restricted geographical distribution, but is nevertheless capable of limited spread. Progression of the disease in a dense population of water hyacinth may take several weeks or months to complete (Freeman et al., 1981). Low inoculum and inefficient spread by spores can be overcome with a mycoherbicide tactic which involves the application of massive levels of host-specific pathogens to target weed populations. C. rodmanii is being developed for use as a mycoherbicide (Kenney et al.,

1979).

The efficacy of C. rodmanii appears to be closely associated with the physiological state of the host (Freeman et al., 1981). Under conditions that favour disease development and limit plant growth, C. rodmanii kills water hyacinth faster than it can regenerate (Conway, 1976b). When the water is highly eutrophic and temperatures are optimum for plant growth, water hyacinth can outgrow the disease. Additional stress is needed under such circumstances to keep the water hyacinth population in check. Integrated control was tested using C. rodmanii and A. zonatum with a weevil, Neochetina eichhorniae Warner and a moth, Arzama densa Walker. The four organisms had an additive effect (Conway & Freeman, 1977).

C. rodmanii grows readily on various solid or liquid fungal culture media. The standard solid medium is Difco potato dextrose agar (PDA) with the addition of 5 g/l of yeast extract(Y). For liquid culture, Difco potato dextrose broth (PDB) plus Y is generally used (Freeman et al., 1981). Conway (1976b) found that the fungus sporulated well in culture on V-8 agar. It will also sporulate on PDA plus Y. Sporulation is augmented by a cycle of 12h of near-ultraviolet (360nm) plus fluorescent light, followed by 12h of darkness (Conway, 1976b).

Dry formulations of conidia and fragmented mycelia of C. rodmanii are now available from Abbott Laboratories. Coarse and fine vermiculite, perlite, and wheat millings are used as carriers. A formulation was tested for viability and virulence

of the propagules by Freeman et al. (1981), who found them to be effective after six months of storage. Sanders and Theriot (1980), using a formulation containing 10^6 viable propagules/g, determined that at a rate of $5g/m^2$, an adequate infection of water hyacinth was produced even under less than optimum temperatures. The formulations can be applied using conventional sprayers. A low pressure system (25psi) and a mister-type nozzle (Delevan WR-25) are recommended (Sander & Theriot, 1980; Freeman et al., 1981).

C. rodmanii does not grow at 37C and is therefore not expected to be pathogenic on man (Freeman et al., 1981). It does not appear to be detrimental to any nontarget aquatic organisms. A standard 96h bioassay on the fish, Gambusia affinis, showed no adverse effects (Conway & Cullen, 1978).

C. rodmanii appears to be very host specific (Conway & Freeman, 1977). Based on tests involving 85 selected plants, both related to water hyacinth and unrelated species of economic value, only senescent leaves of squash, cucumber, and spinach were infected in the greenhouse. None of these plants was susceptible to C. rodmanii when grown in the field.

In culture, C. rodmanii produces cercosporin, a phytotoxin (Freeman et al., 1981). Cercosporin was implicated as a factor in necrosis of sugar beets (Balis & Payne, 1971). However, pathogenicity tests (Conway & Freeman, 1977) with C. rodmanii on table and sugar beets (varieties 'Detroit Dark Red' and 'Early Wonder') did not show any disease symptoms.

Conflict of interest has never been a question in the case of water hyacinth (Coulson, 1978). The plant has no great value to wildlife or livestock. It does have beautiful flowers, but because of its weedy nature, it is no longer regarded as a desirable ornamental.

Acremonium zonatum is another endemic foliar pathogen of water hyacinth found in Florida (Freeman et al., 1978). The fungus causes zonate spots on leaves and petioles, reducing the photosynthetic efficiency of the plant. Martyn and Freeman (1978) found that it could cause as much as 40% leaf necrosis in water hyacinth in 2 weeks.

Water hyacinth responds differently to infection by A. zonatum depending on its developmental stage. Small, young plants are believed to be more resistant than large plants because lesions on them are fewer. However, measured by the percentage of leaf surface damaged after two weeks, no significant difference could be found (Martyn & Freeman, 1978). To gain time, it was concluded that treatment with this fungal pathogen should take place in the spring when the water hyacinth plants are just beginning to grow. The disease is capable of secondary spread (Freeman, 1978). Study by Charudattan et al. (1978) showed that infection was greatly assisted by arthropod feeding.

A. zonatum can be mass cultured on Czapek-Dox broth amended with yeast extract(Y), and it is most pathogenic when grown on potato-dextrose broth with 5g/l Y added. Inocula can be prepared

by macerating mycelial mats collected after two weeks of culturing (Freeman, 1978).

A. zonatum appears to be host specific. A varietal test on 37 selected plants showed that it would probably pose no threat to agricultural and garden crops (Freeman, 1978).

Uredo eichhorniae is a rust pathogen of water hyacinth found in parts of Argentina, Uruguay, and Brazil (Charudattan et al., 1977). Rusts are highly host-specific and because of this, are desirable as biological control agents. However, it is not known whether U. eichhorniae is autoecious or heteroecious. No perfect stage (teliospores) of the rust has yet been discovered (Freeman, 1978).

U. eichhorniae is an obligate parasite and must be cultured on living materials. Lack of adequate inocula is limiting its study. A request to release it for field study in the United States has been denied on the ground that its life cycle is incompletely understood (Freeman et al., 1981).

Alternaria eichhorniae Nag Raj & Ponnappa was studied in India for its control potential on water hyacinth but was rejected because of its pathogenicity to maize and sorghum. Ponnappa (1974) suggested that the toxic metabolite of the fungus could be isolated and concentrated to produce a herbicide. Efforts to identify a metabolite or metabolites have not yet succeeded (Stevens et al., 1979).

Other potential fungal pathogens for the control of water hyacinth include Myrothecium roridum Tode ex Fr. (Kasno &

Soerjani, 1980) and Rhizoctonia sp. (isolates RhEa and RhEc) (Freeman et al., 1982).

b. Hydrilla

Since its introduction around 1960, hydrilla (Hydrilla verticillata (L. fil.) Royle) has quickly become a major aquatic weed problem in Florida (Charudattan et al., 1981). In some areas, this submersed weed "fills waterways and lakes from the bottom to the surface" (Pieterse, 1977). Because it is submerged, the weed is difficult to control with chemicals. Biological control with the grass carp (Ctenophasyngodon indella (Val.) was initiated in 1970 (Sutton, 1977), but it appears that additional control measures are needed. The use of fungal pathogens has been considered, but none of the six species listed by Freeman (1977) as having biocontrol potential, is lethal to hydrilla.

An isolate from Holland of Fusarium roseum 'Culmorum' (Lk. ex Fr.) Snyder & Hansen (Dutch 'Culmorum') is the most virulent pathogen on hydrilla so far tested (Charudattan & McKinney, 1978). An inoculum of 2.5×10^4 spores/ml caused discoloration and rotting of the weed in 2 to 3 weeks. A bonus from the use of the Dutch 'Culmorum' isolate is that it also causes severe root rot in water hyacinth (Freeman et al., 1981).

The ultimate release of the Dutch 'Culmorum' for hydrilla control in Florida will hinge on the problem of safety. Isolates

of F. roseum 'Culmorum' can be seed pathogens (Charudattan et al.,1981). In host range studies, half of the 70 species and cultivars of nontarget terrestrial plants tested, had reduced germination. Castor bean, wheat cv. Hadden, and lima bean cv. Thorogreen were the most severely affected. The fungus is also lethal to some useful aquatics such as Vallisneria americana Michx. and Najas gudalupensis (Spreng.)Magnus (Charudattan et al., 1981; Sutton, 1977).

The Dutch 'Culmorum' grew between 15 and 30C in vitro with peak growth at 21C (Charudattan & McKinney, 1978). It did not survive at 40C beyond two days (Charudattan et al., 1981). It is argued that the propagules of the Dutch 'Culmorum' are unlikely to establish in the warm soils of Florida (Freeman et al., 1981). A 96h standard bioassay on Gambusia affinis indicated that the fungus caused no ill effects on these fish (Charudattan et al., 1981). Quarantine clearance of the fungus is being requested in the U.S. (Freeman et al., 1981).

c. Comment

Fungal pathogens for other serious aquatic weeds are being discovered and studied (Freeman, 1977; Ponnappa, 1977; Andrews, 1980; Colbaugh, 1981) but none has reached the development stage.

It is unlikely that fungal pathogens will be the answer to every aquatic weed problem. Not only may effective pathogens not

be found for every aquatic weed but also the choice of control method depends on the level of control required. Biological control by its very nature is not a method of eradication. Thus, in waters where complete freedom from vegetation is desired, other methods have to be used.

An argument against the use of pathogens on weeds in an aquatic environment is that it may result in replacing one weed with another. This is indeed a valid concern. Where the growth of water hyacinth was subdued with C. rodmanii in Lake Alice, Fla., water pennywort (Hydrocotyl umbellata L.) flourished (Conway, 1976b). Water pennywort, however, was itself parasitized by Cercospora hydrocotyles Ellis & Everhart and also by Puccinia hydrocotyles (Link)Cooke. It may therefore become necessary to use a combination of different pathogens or methods where a second weed is expected to be a nuisance after the dominant weed is supressed.

The use of fungal pathogens to control aquatic weeds is still in its infancy. The encouraging discovery and development of C. rodmanii will no doubt spur future efforts.

2. Annual weeds

Annuals are plants which complete their life cycle from seed-to-seed within a single growing season (Hay, 1966). These plants are generally recognized as difficult to control with biological agents (Andres et al., 1976; Haseler, 1981). They are

the most troublesome weeds of cultivated row crops. Baldwin and Santelmann (1980) estimated that most cultivated crops are subject to competition from about 200 weed species. Some of these weeds are refractory to chemical control because they are closely related to the crop plants or they are resistant to or tolerant of the herbicides used against them (Quimby & Walker, 1982) Alternative and supplementary methods are urgently needed.

Biological control with fungi is being actively pursued as a supplement to conventional weed control methods (Templeton et al., 1979). For annual weeds in cultivated crops, manipulation of endemic pathogens as bioherbicides probably holds the greatest promise (Daniel et al., 1973). The success of such a strategy has been clearly demonstrated in a number of cases but most notably in the control of northern jointvetch (Aeschynomene virginica (L.) B.S.P.) (Templeton et al., 1977; Boyette et al., 1979; Kirkpatrick et al., 1982). This is a member of the Leguminosae, not found in Canada.

a. Northern jointvetch

This weed is a serious problem to rice growers in eastern Arkansas (Smith, 1968). It reduces both the yield and quality of the rice. Control with chemicals, chiefly 2,4,5-T, is not very satisfactory (Daniel et al., 1973). However, the weed can be controlled with a fungus, Colletotrichum gloeosporioides (Penz.)Sacc. f. sp. aeschynomene.

This fungus was first isolated in 1969 by Daniel et al. (1973), and its use against northern jointvetch in rice was patented in 1974 by the University of Arkansas (Daniel et al., 1974). Packaged dry formulations are now available from the Upjohn Company of Kalamazoo, Michigan (Emge & Templeton, 1981).

The fungus and its host are both native to the southern United States (Smith et al., 1973; Templeton et al., 1977). Co-evolution has established a relationship which ensures a low incidence of the disease in nature (Templeton et al., 1979). The fungus overwinters in weed seeds. It produces only asexual spores which do not survive the growing season (TeBeest et al., 1978a). The spores are somewhat sticky and they are shielded from the wind by host tissues. Dissemination is by splashing rain and possibly by insects (Templeton et al., 1977). Low carryover and poor dissemination of inoculum are believed to be the reasons for the low incidence of the disease (TeBeest & Brumley, 1978).

The fungus has been found to be genetically stable with extreme virulence on northern jointvetch. It routinely killed 95-100% of the weed in greenhouse and field experiments (Templeton & Smith, 1977). Young plants from 5 to 30 cm tall are the most susceptible. Recommended spore concentrations are 10^5 to 10^6 spores /ml applied aerially in 94 l/ha of water (TeBeest et al., 1978b; Templeton et al.,1977). Optimum temperature for disease development is 28C but it will develop rapidly between 20 and 32C with 8h or more of dew. Plants are killed as a result

of the formation of lesions on the stems which are girdled as the lesions coalesce (TeBeest et al., 1978c).

Culturing the fungus is easy on most commercially available nutrient media. Submerged culture is used for commercial production. Maximum spore yields are obtained by continuous aeration with vigorous shaking (Daniel et al., 1973).

Tests with the fungus on animals indicated that it is probably safe (Beasley et al., 1975). In any case, there have been no reports of any adverse effects on man or animals since its first experimental use in 1970. The fungus is a facultative saprophyte with a very narrow host range (Templeton et al., 1979). Spore inoculations produced no infection on 165 crop and native plant species (Templeton et al., 1977).

b. Winged waterprimrose

Winged waterprimrose(Jussiaea decurrens (Walt.)DC.) (Onagraceae) is another native weed in the rice fields of Arkansas. The weed can be controlled with phenoxy herbicides along with northern jointvetch. But reduction of northern jointvetch with a fungal pathogen necessitated the search for a similar biological agent for winged waterprimrose. Identified in 1979, Colletotrichum gloeosporioides (Penz.) Sacc. f. sp. jussiaeae has been shown in greenhouse and field experiments to give more than 90% control of the weed with inoculum concentrations of 2×10^6 to 10^7 spores/ml. Initial tests with seven common crop plants and 14 weed species showed that this fungus was host-specific to winged waterprimrose (Boyette et al., 1979).

Most crops have a weed complex made up of several species. Effective reduction of a specific weed can result in weed species shifts (Baldwin & Santelmann, 1980). To compensate for the high degree of host specificity, biological control with fungal pathogens might have to involve a mixture of several pathogens to control a weed complex. This innovative idea was successfully demonstrated by Boyette et al. (1979) using two indigenous form species of C. gloeosporioides to control winged waterprimrose and northern jointvetch at the same time in rice fields.

c. Prickly sida

Prickly sida (Sida spinosa L.) is a troublesome and persistent malvaceous weed in cotton (Gossypium hirsutum L.) (Buchanan et al., 1977). Against this weed, the fungus Colletotrichum malvorum (A. Braun & Casp.) Southworth has been considered as a possible bioherbicide (Templeton, 1974). Again, the University of Arkansas pioneered this work and has patented the use of the fungus in agronomic crops (Templeton, 1976).

When the environmental conditions are favourable for epiphytotic development, the level of control of prickly sida with C. malvorum can be very high. Greenhouse tests indicated that the disease was most severe when host plants were exposed to a 16h dew period at 24C (Kirkpatrick et al., 1982). Field studies by the same researchers resulted in plant mortality ranging from 84 to 95%, 3 weeks after inoculation with 4×10^6 conidia/ml of water applied at 378 l/ha with a backpack plot sprayer.

The fungus appears to be nearly host specific. With the exception of prickly sida and hollyhock (Althaea rosea (L.)Cav.), all of 38 plant species tested were immune to the disease (Kirkpatrick et al., 1982). Hollyhock is an ornamental and it is anticipated that conflicts of interest may have to be settled between gardeners and cotton or possibly soybean growers before the fungus can be used.

d. Spurred anoda

Spurred anoda(Anoda cristata (L.)Schlecht.) is another economically important weed which is difficult to control with chemical herbicides because of its close taxonomic relationship to cotton (Chandler, 1977; Walker, 1981a). Control with a fungus, Alternaria macrospora Zimm., seems to have high potential (Ohr et al., 1977; Walker & Sciumbato, 1979; Walker, 1981a).

A. macrospora was responsible for a naturally occurring epiphytotic on spurred anoda in 1974 in the Mississippi Delta region (Ohr et al., 1977). The weed was severely stunted or killed but cotton and soybeans(Glycine max (L.) Merr.) were unaffected. Greenhouse and field studies by Walker (1981b) confirmed its pathogenicity to the weed. Control approached 100% in all test studies. Seedlings were the most susceptible although plants in all stages were infected. A minimum of 6h of dew period was required for 100% infection and the temperatures for greatest disease development ranged from 20 to 30C. The most effective concentration of inoculum for bioherbicide treatment was determined as 2.5 to 10 x 10^5 spores/ml applied at the rate of 225 l/ha

The fungus can be easily cultured in fermenter vessels and a method for large scale production of a granular formulation is available (Walker, 1981a). The dry formulation consists of

spores, mycelia, and vermiculite ; it was effective in greenhouse and field studies (Walker, 1981a).

Although A. macrospora has been reported in many parts of the world as a pathogen of cotton (Ellis, 1971; Sciumbato & Pinckard, 1974), the Mississippi isolate appears capable of doing severe damage only to spurred anoda. Host range studies (Walker & Sciumbato, 1979) showed that spurred anoda was the only plant severely stunted or killed, although under laboratory conditions, lesions of the hypersensitive type were observed on leaves of cotton. Overall injury on cotton was negligible with no defoliation or stem lesions. Cotton plants did not show infection under field conditions.

Still another fungal pathogen with potential as a biocontrol agent against weeds in cotton is Fusarium lateritium (Nees) emend. Snyder and Hansen. It is a highly variable fungus with worldwide distribution (Toussoun & Nelson, 1975) and a broad host range (Singh, 1973). An isolate discovered by Walker (1981c), however, appears to attack only malvaceous weeds including prickly sida, spurred anoda, velvetleaf (Abutilon theophrasti Medic.), and Venice mallow (Hibiscus trionum L.) Further ivestigation is justified.

e. Noogoora bur & Bathurst bur

Noogoora bur(Xanthium pungens Wallr.) and Bathurst bur(X. spinosum L.) are weeds (Compositae) of New World origin which

take over large areas of pastures in eastern Australia (Hasan, 1974b). The burs, heavily spined fruits, are an important contaminant of wool (Wapshere, 1974a). In addition, noogoora bur in the seed leaf stage is poisonous to livestock (Everist, 1974).

Puccinia xanthii Schw., an autoecious microcyclic rust, has been considered as a possible control against these two exotic weeds in Australia (Hasan, 1974b). The fungus, believed to originate in North America, was first recorded in Queensland in 1975. Its dispersal is now widespread with major damage reported to dense stands of its hosts (Haseler, 1981).

The Australian isolate of P. xanthii, however, is not host specific enough to warrant its use as a biocontrol agent. Alcorn found (1976) that it attacks sunflower(Helianthus annuus L.) and marigold(Calendula officinalis L.) under glasshouse conditions. An Italian isolate of the same fungus was reported (Hasan, 1974a) to cause no disease symptoms on Helianthus, Dahlia, or Zinnia. Further tests on this isolate are needed.

f. Ragweeds

Ragweeds (Compositae) are commonly found in cultivated fields, pastures, and meadows (Alex & Switzer, 1976). They are the main source of aeroallergenic pollen, an important cause of hayfever. Ragweeds can be controlled with cultural and chemical methods, but recently, the possibility of biological control has

been investigated.

A white rust fungus(Albugo tragopogi(Pers.)S.F. Gray, isolated in Quebec, appears to be highly damaging to common ragweed(Ambrosia artemisiifolia L.) (Hartmann & Watson, 1980a). Common ragweed is the most abundant of the ragweeds, which are native to North America. Host range studies by Hartmann & Watson (1980b) indicated that A. tragopogi did not infect nontarget plants. It was capable of reducing the pollen production of infected common ragweed plants by 99% when the plants were inoculated at the two-leaf stage (Hartmann & Watson, 1980a). However, only 14% of the inoculated plants became diseased. Research is needed to identify the constraints on disease development in the healthy plants. Perhaps a higher concentration of inoculum is needed than the 1.5×10^5 zoospores/ml used by Hartmann and Watson.

Giant ragweed(Ambrosia trifida L.) is parasitized by Puccinia xanthii f.sp. ambrosia-trifidae(Batra, 1981). The rust was first recorded in 1978 in Beltsville, Maryland where it caused severe defoliation of the weed in an extraordinarily wet season. Preliminary tests showed that it did not infect any of 14 plant species belonging to the Compositae, including common ragweed and noogoora bur. However, in the same series of tests, only 22% of giant ragweed plants succumbed to the disease (Batra, 1981). Lack of uniform susceptibility of the host weed and unusual weather requirements for the pathogen may detract from the potential use of the fungus.

g. Comment

The control of annual weeds in intensely cultivated, high-value crops must, of necessity, be quick and effective to avoid loss through weed competition. Several fungal pathogens have been shown to be capable of providing this kind of control. All these fungi are highly pathogenic to the targeted weeds but are irregular in their occurrence as a result of poor overwintering capacity, weak saprophytic competitiveness, lack of vectors, or other constraints on dissemination (Templeton, 1982b). When used as bioherbicides, they are sometimes very effective. Repeated applications are necessary but even this has its blessings because repeated demand for a product means there is a constant market and a profit to be made. Private industry is becoming interested and thus the routine use of fungal pathogens in an integrated weed management system may some day become a reality.

3. Perennial weeds

These plants are generally most troublesome in pastures and orchards where the soil is relatively undisturbed. They also prosper under certain farming practices such as crop-fallow systems. With the advent of reduced tillage or no-tillage methods of cultivation, it is anticipated that problems of

perennial broadleaf weeds will increase in agricultural soils.

Biological control of perennial weeds has been spectacularly successful in some cases with insects (Dodd, 1940; Huffaker & Kennett, 1959; Hawkes, 1968). More recently, attempts have been made with fungal pathogens and these appear to be equally promising (Cullen, 1978; Ridings et al., 1982; Oehrens, 1977).

a. Rush skeleton weed

Native to Eurasia, the composite, rush skeleton weed(Chondrilla juncea L.), has become a serious weed in Australia (Wapshere et al., 1974) and a potentially serious weed in North America (Blanchette & Lee, 1981). The weed is perfectly adapted to wheat-fallow cultivation which is common in Australia (McVean, 1966) and northwestern North America (Emge et al., 1981). It is a strong competitor for moisture and nitrogen. Yield loss as a result of its competition may be as much as 50% in a wet season and 80% in a dry season (Cullen, 1978). Furthermore, the tough stems of the plant often cause mechanical problems with machine harvesting. Control with chemicals is costly and ineffective (McVean, 1966; Emge et al., 1981).

Rush skeleton weed , however, is not a serious problem in its native range. Its populations there are kept below economic levels by natural enemies (Wapshere et al., 1974; Wapshere et al., 1976). A project initiated in 1967 to search for biocontrol

agents came to fruition in 1971 with the introduction into Australia of a rust fungus, Puccinia chondrillina Bubak & Syd. from Vieste, Italy (Hasan, 1972).

P. chondrillina is an autoecious, macrocyclic rust specific to the genus Chondrilla(Hasan & Wapshere, 1973). It occurs wherever rush skeleton weed is found in Eurasia (Hasan, 1970). The rust is active throughout the year attacking seedlings, rosettes, and flowering stalks of the weed. Heavily attacked plants have spindly stems (Cullen, 1978) and their seeding is much reduced (Emge et al., 1981). The rust is disseminated by uredospores which are readily dispersed by wind and rain (Hasan, 1973). An introduction of nine infected plants resulted in an epidemic spread of the rust within a single year in southeastern Australia (Cullen et al., 1973; Hasan, 1974b). Greater than 50% reduction of the weed was recorded (Hasan & Wapshere, 1973). This translates into an estimated recurring annual saving in Australia of $25.96 million (Cullen, 1978).

Rush skeleton weed is an apomict with many morphological forms. Only three of these forms are present in Australia (Hull & Groves, 1973). The imported rust only attacks the narrow-leaved form which is by far the most common in Australia (Hasan, 1972). New strains of the rust are being sought that will attack the remaining two forms. One of these strains from Manisa, Turkey, is virulent against the intermediate form and has also been demonstrated to be host specific to rush skeleton weed. It has now been imported and released in Australia (Hasan,

1981a).

Rush skeleton weed presently occupies millions of acres of rangeland in California, Oregon, Washington, and Idaho (Blanchette & Lee, 1981). A cooperative effort amongst the states resulted in the release of four pathogenic strains of the rust against various forms of the weed (Emge et al., 1981). Uredospores were used as inocula and these were collected from rusted leaves and applied in water suspensions with hand dusters, powered dusters, helicopters, or fixed-wing aircraft (Emge et al., 1981). Released in 1978, the rust has successfully established and is taking its toll of the weed (Adams & Line, 1981).

Rusts are obligate parasites with very narrow host ranges. The strain imported into Australia was tested on 58 species of plants with no sign of infection in any of them (Hasan, 1972). The rust also remained host-specific when tested under many different climatic conditions (Hasan & Jenkins, 1972). Uredospores of the rust germinated between 0 and 36C, with optimum at 18C (Hasan & Wapshere, 1973). Blanchette and Lee (1981), working with an isolate from Eboli, Italy, found that the greatest number of infections occurred at 8 and 16C but the pustules developed faster at 24C than at lower temperatures. They also discovered that a dew period of 6h was required for maximum uredia development. On this basis, they recommended that applications of uredospores be made at dusk under cool temperatures when an extended dew period is expected.

Obligate parasites are generally considered to be poor candidates for biological control because they cannot afford to be too damaging to their hosts. By eliminating their hosts they drive themselves to extinction. However, they can sometimes greatly suppress their host populations, as demonstrated by Australia's successful control program against rush skeleton weed with a rust fungus.

b. Milkweed (strangler) vine

First recognized in 1957 (Swanson, 1975) as a problem in citrus groves in Florida, milkweed vine (Morrenia odorata Lindl.), a member of the Asclepiadeae, has persisted and continued to spread because of its resistance to chemical treatment (Tucker et al., 1971). In some infestations, more than 80 vines per tree have been reported (Ridings et al., 1978). The weed competes with citrus trees for light, water, and nutrients; it also interferes with spraying, harvesting, and irrigation practices (Ridings et al., 1977).

An indigenous fungus, Phytophthora palmivora Butler (formerly identified as P. citrophthora (R.E. Sm. & E. H. Sm.)Leonian) was isolated in 1972 in Orange county, Florida (Burnett et al., 1974). The isolate is highly efficacious against milkweed vine. When treated at 20 chlamydospores/cm^2 of soil, more than 90% of the vines died within 10 weeks (Ridings et al., 1982).

Phytophthora palmivora has an extensive host range (Chee, 1969; Ramirez & Mitchell, 1975; Ridings et al., 1978). It is capable of causing foot rot, gummosis of stems, blight of seedlings, and brown rot of fruit in various tropical plants, including citrus (Chee, 1969; Samson, 1980). The fungus, however, has distinct races and the milkweed vine pathotype is not pathogenic to citrus (Burnett et al., 1974). It is somewhat pathogenic to a few varieties of onion, cantaloupe, watermelon, tomato, okra, endive, cucumber, English pea, and carrot (Ridings et al., 1978). Some varieties showed close to 50% reduction in germination in greenhouse pre-emergence tests.

The milkweed vine pathotype is indigenous to Florida. It has a restricted distribution in nature, and was found only in Lake and Orange counties in a field survey carried out in 1975 (Ridings et al., 1978). Moreover, very low inoculum levels will provide effective control of the weed. Based on these considerations, Ridings et al. concluded that no significant contamination of nontarget areas or plants is to be expected from the use of this fungus.

The milkweed vine pathotype of P. palmivora has been registered by the Environmental Protection Agency (EPA) for use in Florida (Bowers, 1982). It is marketed as a mycoherbicide by Abbott Laboratories under the trade name DeVine (Kenney et al., 1979; Woodhead et al., 1981; Templeton, 1982b).

c. Curly dock

Curly dock(Rumex crispus L.) is a large, perennial, polygonaceous weed of considerable importance in pastures, roadsides, and ditchbanks of the United States and many other parts of the world (Hasan, 1973). Because of the extent of the infestation, control with chemicals is uneconomical. The weed is heavily attacked by a rust, Uromyces rumicis (Schum.)Wint. in Europe, where it is thought to originate (Inman, 1970). A project was initiated in 1966 to look into the possibility of introducing the rust into the United States.

Inman (1971) collected and tested under quarantine, various strains of the rust against curly dock from different parts of the United States. None of the strains tested significantly reduced seed production but the leaves were severely attacked which resulted in reduced vigour of the rootstocks and increased mortality of infected plants. In the plant community where every plant has to compete with many other plants and species to survive, the physiological stress on curly dock as a result of parasitism by U. rumicis may be enough to tip the balance against the weed.

The release of the rust in the United States, however, has not been approved because the rust is heteroecious and macrocyclic. Attempts to infect the recognized alternate host, Ranunculus ficaria L., the lesser celandine, have so far not succeeded (Frank, 1971). Otherwise, the rust appears safe, as

indicated by inoculum studies (Inman, 1971) with uredospores of the rust on 36 cultivated and 12 wild plant species.

Work on the alternate host is continuing (Spencer, 1981). Meanwhile, a computer-assisted search program (Spencer et al., 1981) funded by the USDA is in operation in Europe to expand the search for other pathogens and insects.

d. Wild blackberries

The edible berries of wild blackberries(Rubus spp.) are collected every year by many people to be eaten raw or made into jam. They are also a source of food to migrating birds. In some areas, however, they have become weeds by invading large areas of pastures. This is the case in Chile (Oehrens, 1977) and, to a lesser extent, Australia (Amor, 1973), and New Zealand.

In Chile, two species, Rubus constrictus Lef. & M. and Rubus ulmifolius Schott. occupied an estimated 5 million ha of grassland by 1973. In the same year, a rust, Phragmidium violaceum (Schultz) Winter, was imported from Europe to control them. Inoculation was made by rubbing infected leaves onto the underside of healthy leaves in the field. The inoculated leaves were then wrapped in polyethylene bags for three days. The disease became established and since then has spread through much of the blackberry infested areas of Chile.

The rust causes premature defoliation. The weakened canes are then destroyed by frost and secondary pathogens. Plants that

are severely attacked produce 45% fewer seeds than do healthy plants.

Phragmidium violaceum does not attack raspberry(Rubus idaeus L.) or loganberry(Rubus loganobaccus Bailey), both of which are grown as crops in Chile. It is also not very effective against the blackberry, Rubus ulmifolius. Strains of the rust virulent to R. ulmifolius are being sought (Hasan, 1981b).

e. Knapweeds

Although many weeds can be effectively controlled with chemicals, it is not always the most cost-effective approach. A case in point is the control of knapweeds (Compositae). There are three species of knapweeds in western North America: diffuse knapweed (Centaurea diffusa Lam.), spotted knapweed (Centaurea maculosa Lam.), and Russian knapweed (Centaurea repens L.). The first two species are of particular economic importance in North America (Anon., 1977). These Eurasian weeds, if not controlled, could cause an annual loss of $58 million to western Canada alone (Harris & Cranston, 1979). Chemical control with picloram(4-amino-3,5,6-trichloropicolinic acid) at about $37/ha is far too costly (Maddox, 1982). Two seed-head flies, Urophora affinis Frfld. and U. quadrifasciatus (Meig.) were introduced into British Columbia in 1970 and the western states in 1973. These are now well established but have not reduced the knapweeds below the desired economic threshold (Harris &

Cranston, 1979). More recently, a moth, *Metzneria paucipunctella* Zell. and a root-boring beetle, *Sphenoptera jugoslavica* Obenb. were released. It is expected that because of the very high reproductive potential of knapweeds, more natural enemies will be needed to provide added stress to reduce these weeds to an acceptable level. Two pathogenic rusts from Europe, *Puccinia centaureae* var. *diffusae* (Savile, 1973) and *P. jaceae* var. *diffusae* (Watson & Alkhoury, 1981) are being investigated as host-specific pathogens.

Preliminary studies showed that all samples of diffuse knapweed in western Canada were highly susceptible to a strain of *P. jaceae* collected from eastern Europe (Watson & Alkhoury, 1981). However, some cultivars of safflower(*Carthamus tinctorius* L.) were also susceptible. Safflower is grown in the United States as an oil crop and because of agreements between Canada and the United States on importation of exotic biological agents, the use of *P. jaceae* against diffuse knapweed in British Columbia is unlikely to proceed. "The use of exotic or indigenous biological control agents is practical only if they can be relied upon not to damage desirable plants" (Andres *et al.*, 1976). The potential and host range of *P. centaureae* should be further explored.

f. The dwarf mistletoes

These plants (Arceuthobium spp., Viscaceae) are weeds because they are damaging parasites of conifers. They cause considerable economic damage to forest trees in western North America (Kuijt, 1960; Hawksworth & Wiens, 1972). Trees parasitized typically develop abnormal clusters of branches known as witches' brooms. Another effect on trees is early decay because swellings and cankers caused by the mistletoes lead to invasions by secondary pathogens and insects.

Control of dwarf mistletoes is chiefly by silvicultural practices such as harvesting and thinning. Effective chemical treatments are not available (Knutson, 1978). Biological control using fungal pathogens has attracted much attention and has been discussed in several reviews (Kuijt, 1955; 1969; Wellman, 1964; Wicker & Shaw, 1968; Wilson, 1969; Knutson, 1978). But, to date, no fungal species is available for practical application. Investigations so far have concentrated on four species which are regarded as having some biocontrol potential. They are: Wallrothiella arceuthobii (Peck) Sacc., Cylindrocarpon gillii (Ellis) J.A. Muir, Colletotrichum gloeosporioides Penz., and Nectria macrospora (Wr.) Ouellette.

W. arceuthobii is an ascomycete which is indigenous to North America. It has been found parasitizing only spring-flowering dwarf mistletoes such as Arceuthobium

americanum Nuttall ex Engelmann, A. douglasii Engelmann, and A. pusillum Peck. Dwarf mistletoes are dioecious and the male and female plants are usually found close together on the same tree (Dowding, 1931). The fungus attacks female flowers only. Dispersal of ascospores is believed to be by insects, wind, and rain (Knutson & Hutchins, 1979). Parasitized flowers never produce viable seeds (Dowding, 1931; Kuijt, 1969). Although the fungus is believed to be of considerable importance in limiting the spread of spring-flowering dwarf mistletoes (Knutson, 1978), artificial inoculations have never achieved much success. Knutson and Hutchins (1979) obtained only 17% infections in their field trials with crushed perithecia and stroma tissue; they collected the perithecia from naturally infected shoots because no perithecia or ascospores have been produced in culture thus far (Parker, 1970; Knutson & Hutchins, 1979). A conidial stage of the fungus has also never been observed.

Before attempts can be made to use the fungus for biological control, methods must be found, first, to mass produce infective propagules of the fungus, and second, to increase the rate of success of artificial inoculations.

Cylindrocarpon gillii is another fungus that has been associated with the premature death of some dwarf mistletoes. Species attacked include A. americanum (Gill, 1952; Mielke, 1959) and several forms of A. campylopodum (Ellis, 1939; 1946; Wicker & Shaw, 1968). This fungus parasitizes both male and female plants, but only the flowering shoots are attacked

(Ellis, 1946). Natural infections of mistletoes by the fungus are common in Washington and Oregon (Wicker & Shaw, 1968).

C. gillii grows best at 17C (Mielke, 1959). It produces abundant conidia which Wicker and Shaw (1968) found to germinate at 15C but not at room temperatures(22-23C). Artificial infections with conidia in water suspensions have not been very successful. Ellis (1946) obtained only 27% infections. Mielke (1959) had more success with inoculations (42 out of 50 trees), but the fungus died out from his experimental plots in three years. Knutson (1978) found fault with Mielke's experiments citing the latter's disregard for possible strain differences. Mielke collected C. gillii from A. campylopodum on pinon pine and used the spores to infect A. americanum on lodgepole pine.

The two fungi, W. arceuthobii and C. gillii, attack only the flowering shoots and not the endophytic system of dwarf mistletoes. The host is therefore not killed although its reproductive potential is reduced. Colletotrichum gloeosporioides, a blight disease of dwarf mistletoes, invades both the flowering shoots and the endophytic system (Wicker & Shaw, 1968). Field observations and early inoculation studies indicated that C. gloeosporioides was pathogenic to A. campylopodum , A. americanum, and A. douglasii (Parmeter et al., 1959; Scharpf, 1964; Wicker, 1967; Wicker & Shaw, 1968).

The fungus is easily grown on potato-dextrose agar (PDA). It also sporulates abundantly in potato-dextrose liquid medium at room temperatures (Parmeter et al., 1959). Based on cultural

characteristics, Scharpf (1964) identified several geographically distinct isolates of the fungus, but he showed, by successful cross inoculations, that these isolates were not restricted to parasitizing the species or forms of dwarf mistletoes on which they had been found.

Still another fungus that has been studied with an aim to biological control is Nectria macrospora (Smith & Funk, 1980). The fungus is found in British Columbia commonly associated with cankers caused by Arceuthobium tsugense (Rosendahl) G.N. Jones on western hemlock (Tsuga heterophylla (Raf.) Sarg.). The fungus is capable of reducing up to 30% of the flowering shoots of dwarf mistletoe (Funk et al., 1973).

N. macrospora is easily cultured with 2% malt extract broth or agar. It produces plenty of spores. Smith and Funk (1980) inoculated mistletoe swellings in field studies with spore suspensions of the fungus but could not increase the natural rate of infections. Further investigations are needed.

g. Canada thistle

This composite noxious weed (Cirsium arvense (L.) Scop.) is troublesome in all temperate regions of the world. The name Canada thistle is a misnomer because the weed is not native to Canada but was introduced from Europe in the 17th century (Moore, 1975).

Canada thistle is a pest of pastures and fodder, a good competitor, reproducing both by horizontal roots and seeds. The plant is dioecious and dense patches of male and female plants are common. It reduces crop yields and the quality of forage.

Thirteen species of fungi have been reported to attack Canada thistle but the damage is not great enough to warrant biological control with any of them (Moore, 1975). Two rusts, Puccinia punctiformis (Str.) Rohl. and P. obtegens (Link) Tul., have been the subjects of recent studies. Turner et al. (1981), through infections with P. obtegens on ten ecotypes of Canada thistle, found that host resistance is one factor limiting the rust disease. They suggested a systematic international collection of spores of P. obtegens to identify the virulent strains. Watson and Keogh (1981), working with P. punctiformis, found that the rust developed on 74.3% of inoculated leaves. The infected leaves died within two weeks but the disease did not spread and none of the infected plants was killed. On the basis of their findings, Watson and Keogh (1981) proposed multiple inoculations with uredospores of P. punctiformis as a biocontrol for Canada thistle.

h. Comment

Other attempts to control weeds with fungal pathogens include the use of Cercosporella adenophorum against pamakani (Eupatorium riparium) and a Cephalosporium sp. against kolomona

(*Cassia surattensis*) in Hawaii (Trujillo, 1976; Trujillo & Obrero, 1978; Anon., 1980a); the use of *Cephalosporium diospyri* against persimmon (*Diospyrus virginiana*) and *Ceratocystis fagacearum* against oak (*Quercus* spp.) in the US; the use of *Ganoderma pulverulentum* and *Ustulina zonata* against the legume marabu (*Dichrostachys nutans*) in Cuba; and the use of *Colletotrichum destructivum* and *Alternaria cuscutacidae* against dodder (*Cuscuta* spp.) in the US and the USSR respectively (Wilson, 1969). In California, Hildebrand and McCain (1978) studied the control of marijuana or hemp (*Cannabis sativa*) with *Fusarium oxysporum* f. sp. *cannabis*. In Australia, Dodd (1961) reported the successful, albeit fortuitous, control of the composite, crofton weed (*Eupatorium adenophorum*), by *Cercospora eupatorii*. And in Africa, Zummo (1977) identified several fungal diseases of giant witchweed (*Striga hermonthica*), an important parasitic plant on the staples, sorghum and millet.

Much interest is being generated in the use of fungal pathogens to control weeds. A regional cooperative research project entitled "Biological Control of Weeds with Fungal Plant Pathogens" was organized in 1978 in the United States, covering Alabama, Arizona, Arkansas, Florida, and Georgia (Freeman & Charudattan, 1981). This on-going project is a concerted effort to explore the practical applications of fungal pathogens.

III. CONTROL OF ARTHROPODS

"The literature on fungal parasites of insects and mites is extensive and long-established" (Brady, 1981). More than 400 species of entomogenous fungi have been recorded (Hall & Papierok, 1982). The subject has been discussed in books (Steinhaus, 1963; 1967; DeBach, 1964; Muller-Kogler, 1965; Cantwell, 1975; Burges & Hussey, 1971; Burges, 1981) as well as review papers (Baird, 1958; Madelin, 1966; Ferron, 1978; Brady, 1981; Hall & Papierok, 1982). It is generally agreed that the use of fungi to control arthropod pests is one of the most problematical areas in microbial control and that, in the past, failures have outnumbered successes. Many of the failures have been attributed to inadequate knowledge of the organisms and of the ecology of both the fungus and its target pest.

That fungi can be successfully used against arthropod pests is clearly demonstrated by the recent commercialization in some countries of Verticillium lecanii (Zimm.) Viegas and Hirsutella thompsonii Fisher, and the extensive use of Beauveria bassiana (Bal.)Vuill. and Metarhizium anisopliae (Metsch.)Sorokin. Cautious optimism was expressed in the use of fungal agents to control arthropod vectors of disease by the WHO Scientific Working Group on Biological Control of Vectors when they met in 1980 at Geneva (Anon., 1980b).

1. Greenhouse pests

"The glasshouse is an attractive environment in which to exploit entomogenous fungi since, up to a point, critical physical factors such as temperature and humidity are already favourable or can be manipulated" (Hall & Burges, 1979). It is therefore surprising to find so few recorded attempts to use fungal pathogens in greenhouses. It illustrates how successful the use of chemical pesticides has been up to now. Indeed, the distribution of the parasitic wasp, Encarsia formosa Gahan, for the control of the greenhouse whitefly, Trialeurodes vaporariorum Westwood, was discontinued after World War II when DDT became available (Hussey & Bravenboer, 1971).

Recently, the appearance of resistant strains and cumulative phytotoxicity associated with intensive use of pesticides has prompted a return to biological control agents. In Britain, growers are finding that switching to biological control is not only less hazardous to their health but also is financially more rewarding. The cost of biological control is approximately one sixth of that of equivalent chemical control and, as a result of the elimination of phytotoxicity, there has been a yield increase of 10 to 30% (Wyatt, 1974).

A wide range of arthropod pests affect the greenhouse industry, but the important ones are represented by only a few well-recognized, nearly cosmopolitan species: red spider mites (particularly Tetranychus urticae Koch), aphids (particularly

Myzus persicae Sulz.), whiteflies (particularly Trialeurodes vaporariorum Westw.), and a few Lepidoptera (particularly Trichoplusia ni Hubner) (Tauber & Helgesen, 1979). Effective biological control agents against these major pests are now available. These include: a predatory mite, Phytoseiulus persimilis Athias-Henriot , against spider mites; Encarsia formosa Gahan, against whiteflies; Bacillus thuringiensis, against caterpillars; and more recently, a fungus, Verticillium lecanii (Zimm.) Viegas, against aphids, whiteflies, and thrips.

a. Aphids

These are extremely serious pests worldwide which in recent years have developed multiple resistance to chemical pesticides (Hall, 1980b). The fungus, V. lecanii, is an efficient agent for control of aphids, especially the green peach aphid, M. persicae. A single spray was sufficient to give complete control for the duration of a crop of chrysanthemums (Hall & Burges, 1979).

The recommended dosage is 10^7 spores/ml in a phosphate buffer (pH 7.2) containing 0.02% Triton X100 as a wetting agent. Both conidia and blastospores can be used. V. lecanii produces conidia in aerial culture on agar and blastospores in submerged culture. Under greenhouse conditions, both spore-types exercise similar control on aphids (Hall, 1979).

Spores of V. lecanii are very sensitive to desiccation. Airborne conidia did not survive at 58% RH beyond 24h (Hall, 1981). Infection of hosts by airborne spores is unlikely to occur. V. lecanii sporulates in slime on live and dead insects (Hall, 1976), and is spread when aphids come into contact with spores on dead or diseased hosts.

Hall and Burges (1979) reported that control of two minor aphid pests, Macrosiphoniella sanborni Gill. and Brachycaudus helichrysi Kalt., was sometimes unsatisfactory. However, they could not find any inherent difference in susceptibility to V. lecanii among different aphid species. They believed that in large commercial greenhouses control would be better because of the higher humidities. The fungus has been observed to give satisfactory control of Aphis fabae Scop., Aphis gossypii Glover, and B. helichrysi in large greenhouses.

Genetic stability is an important feature of mycoinsecticides. Hall (1980c) tested the C-3 strain of V. lecanii and found that repeated subculturing on artificial media resulted in some physiological and morphological changes of the fungus but no attenuation of virulence. Conversely, virulence was not enhanced after passage through the aphid host, M. sanborni.

b. The greenhouse whitefly

This insect pest is a major problem in greenhouses worldwide (Vet et al., 1980). The pest induces wilting of plants by its feeding in the adult and scale stages. It produces honeydew in the same way as aphids. The accumulation of honeydew on leaves promotes the development of sooty mold which is unsightly on ornamentals, and reduces photosynthesis and plant respiration. In addition, the whitefly has been implicated as a vector of viral diseases in cucumber, lettuce, and ornamentals (Vet et al., 1980).

Encarsia formosa, a parasitic hymenopteran, has been used widely as an agent for biological control of this pest with considerable success. However, the parasite and host are differentially favoured by temperature (Wyatt, 1974). Failures have occurred when the greenhouse temperature is too low or the initial pest population too high (Hussey & Bravenboer, 1971; Kanagaratnam et al., 1982).

The fungus, V. lecanii, is a primary parasite of the greenhouse whitefly (Ekbom, 1979; Kanagaratnam et al., 1982). Low nightly temperatures with high humidities, disadvantageous to the parasitic wasp, are ideal conditions for the fungus. Spray trials using 10^7 spores/ml killed 85-98% of the scales (immature whiteflies) in three experiments (Kanagaratnam et al., 1982). It was discovered, however, that dispersal of the fungus

was inefficient among cucumber plants. Fortnightly or monthly sprays of the fungus are recommended.

Combined applications of V. lecanii and E. formosa to control the whitefly on cucumbers and tomatoes in the greenhouse are being investigated (Costello, per. comm., 1983).

V. lecanii is a species complex with many different strains (Ekbom, 1979; Hall, 1981). There is still controversy over the taxonomy of this fungus although most recent researchers tend to adopt the taxonomic grouping according to Gams (1971). Opponents to this grouping argue that it contains too many morphological differences to be included in one species. The fungus has been cited variously in literature as Cephalosporium lecanii Zimm. (Easwaramoorthy & Jayaraj, 1977), C. aphidicola Petch (Hussey, 1958; Wilding, 1972), and C. lefroyi Horne (Horne, 1915).

There are also differences in host specificity among various strains in virulence against E. formosa. A Swedish isolate tested by Ekbom (1979) is pathogenic towards the hymenopteran parasite. It killed the adult wasp 6-8 days after inoculation in infection trials. On the other hand, a British strain, isolated from the aphid M. sanborni has been reported to be innocuous to E. formosa (Hall, 1981).

Some British strains have been developed commercially as mycoinsecticides by the firm of Tate & Lyle, from work done at the Glasshouse Crops Research Institute, Littlehampton (Brady, 1982). The fungus is marketed as Vertalec, Mycotal, and Thriptal for the control of aphids, whiteflies, and thrips respectively.

These commercial formulations, to be applied as high-volume sprays, contain nutrients to encourage spore germination and fungal growth. Because of the added nutrients, it is possible and advisable to treat plants early so as to obtain best results. In the case of chrysanthemums, the preferred date of treatment is 2 weeks after planting out (Hall, 1982b).

The use of V. lecanii is compatible with some chemical pesticides. These include benodanil, oxycarboxin, iprodione, vinclozolin, dinocap, carbaryl, dicofol, dienochlor, pirimicarb, permethrin, white oil (Hall, 1981), and dimethirimol (Wilding, 1972). In vitro tests, however, indicate that most fungicides, acaricides, and insecticides, including the ones mentioned above, tend to be inhibitory to mycelial growth of V. lecanii (Hall, 1981; Olmert & Kenneth, 1974). The exceptions are dienchlor, white oil, and dimethirimol. Dimethirimol is used in Britain for the control of powdery mildew in greenhouse cucumbers. In North America, benomyl is commonly used for the same purpose. All studies indicate that benomyl is too fungitoxic to be used simultaneously with V. lecanii. But both Hall (1981) and Brady (1982) suggest that benomyl and V. lecanii could be used on the same crop if the systemic fungicide is applied only as a drench to the soil and the applications of the two products are carefully phased.

In the USSR, studies are also going on to control the greenhouse whitefly with fungal pathogens. Eleven species and forms of Aschersonia(Fungi Imperfecti) were introduced into

Russia from China, Japan, Vietnam, India, Mexico, Trinidad, and Cuba (Smetnik & Izhevsky, 1979). In 1978, Aschersonia was used on a total area of more than 100 ha. Control in the range of 65-85% was reported (Beglyarov, 1979). However, a standard technique for mass production of the fungus has not been perfected.

c. Thrips

These are not so serious as whiteflies, red spider mites, or aphids. They can be a problem when the major pests are controlled by host specific biological agents.

Thrips can also be controlled with fungal pathogens. V. lecanii is pathogenic to thrips and a commercial product of the fungus, Thriptal, is available on the market (Brady, 1982). Working with an undescribed species of Entomopthora in Switzerland, Carl (1975) reported that the fungus attacked Thrips tabaci Lind. on leek plants. Experiments showed that the fungus spread rapidly and caused reductions of thrips populations, from 500-800 individuals/leaf to 20/leaf, within one month. However, the parasite was not able to prevent oscillations of pest populations beyond an economic threshold. Investigations continue.

2. Field and row crop pests

With a few notable exceptions attempts to control pests in field and row crops with entomopathogenic fungi have not been very successful. One that failed was initiated in 1888 in Kansas, USA (Sweetman, 1958; DeBach, 1964). Over a period of eight years, large quantities of the fungus *Beauveria bassiana* (=*B. globulifera*) were disseminated in fields in an attempt to control the chinch bug *Blissus leucopterus* Say. The program was abandoned. As a result, many believed with Billings and Glenn (1911) that climatic factors were of overriding importance in fungal infections and that no amount of human interference could increase the incidences of fungal epizootics. Scientists in eastern Europe and the USSR were relatively unaffected by this negative attitude. Yet they were not particularly successful. The first commercial production of an entomopathogenic fungus for the control of field crop pests did not appear until the early 1970s. Now, two fungi are being produced and used routinely on an industrial scale against insect pests in field and row crops in three countries (Soper & Ward, 1981; Ferron 1981). The target pests are mainly of three taxomic groups: Coleoptera, Lepidoptera, and Homoptera.

a. Coleoptera

One coleopterous pest that has been studied more intensively than most is the Colorado beetle, Leptinotarsa decemlineata Say, on potato. It is often controlled in the USSR with Boverin (=Beauverin), a commercial product of the fungus B. bassiana containing 6 x 10^9 conidia/g (Samsinakova et al.,1981; Ferron, 1978; 1981).

Boverin is highly effective against the Colorado beetle. Lakhidov (1979) obtained 83% kill 5 days after spraying on artificially infested potato plants. In another Russian study, cited by Ferron (1981), consistently high mortality rates (85.7% to 97.6%) marked four consecutive years irrespective of climatic conditions.

Boverin in combination with a sublethal dosage of a chemical insecticide has been recommended (Lakhidov & Yanysheva, 1979; Beratlief, 1979). Some of the insecticides suggested include trichlorphon, dilor, parathion, parathion-methyl, DDT, and BHC. The rationale is that the pest, weakened through sublethal doses of pesticides, succumbs more easily to the attack of the pathogen (Schaerfenberg, 1964).

Samsinakova et al. (1981), on the other hand, argued against the combined use of Boverin and chemicals. They maintained that mortality rates of 80 to 100% on second and third instars of the Colorado beetle could be obtained by using the fungal preparation alone, results comparable to those

obtained with combined preparations with chemicals.

The combination of B. bassiana with a non-antagonistic control organism has also been suggested. The fungus Paecilomyces farinosus (Br. & Smith) is pathogenic to all larval instars of the Colorado beetle (Samsinakova & Kalalova, 1978). A concentration of 4.1 x 10^7 conidia suspended in 1 ml of water killed 70 to 96% of the beetle larvae. Studies in Poland (Bajan, 1980) established that the two species of fungi were not antagonistic. B. bassiana was most effective against the beetle in spring and P. farinosus in late autumn and winter. The Colorado beetle is also susceptible to the fungus B. tenella (Delacr.)Siem. and the nematode Pristionchus uniformis. Smirnov (1978) was able to show that a synergistic effect was produced when the two agents were used together.

According to MacLeod (1954), B. bassiana and B. tenella (=B. brongniartii) are the only two valid species in the genus Beauveria (Fungi Imperfecti). Both are entomopathogenic and between the two, almost 500 host species are known (Hall & Papierok, 1982). These belong mostly to the orders of Coleoptera and Lepidoptera. The disease caused by Beauveria is commonly known as the white muscardine because of the characteristic appearance of infected insect cadavers.

Beauveria can be cultured easily on artificial media. B. bassiana, the more common of the two species, has been grown on substrates of potato, pea, bean, oats, rice pulp, maize, bran, as well as Sabouraud's, maltose, and malt agar (Samsinakova,

1966). But for optimum sporulation, a medium containing 1.0% sorbitol and 0.8% peptone at pH 5 is recommended (Samsinakova *et al.*, 1981). In the USSR, *B. bassiana* is mass produced in submersed culture in fermenters (Globa *et al.*, 1982). The conidia are extracted with Nutsch filters, dried, and diluted with a dry filler powder such as kaolin. Adding calcium carbonate powder with particle size smaller than 50 microns to the culture fluid has been found to facilitate extraction of conidia. Maximum viability of spores can be achieved by hot-air drying and storing in a sealed pack at 5C.

Production methods for *B. tenella* have also been developed (Cordon & Schwartz, 1962; Fargues *et al.*, 1979). It was found that conidia of *B. tenella* could be formulated by coating the spores with bentonite clay and spray-drying at 150C. The method yielded 50-70% viable spores which could be stored without loss of activity for 18 months at 5C. Blastospores of the fungus were too sensitive for the spray drying but they could be lyophilized with powdered milk supplemented with glycerin, to produce 89% viable spores. Blastospores formulated in this way could be stored for 8 months at 5C without loss of activity.

Beauveria, particularly *B. bassiana* is one of the most studied of the entomogenous fungi. Its use, however, must be exercised with caution. Some strains of *B. bassiana*, for example, can cause mycoses in the silkworm *Bombyx mori* L. (Bell, 1974). Allergic reactions have also been reported during production of the fungal spores (Hall, 1954; York, 1958; Hsiao,

1981). But the fungus has been extensively used. It is considered safe because no mycoses have ever been recorded on hosts other than arthropods. Recent studies have confirmed that both species of Beauveria are nontoxic to vertebrates (Kachekova & Fralov, 1977; Donovan-Peluso et al., 1980).

With the exception of the Colorado beetle, attempted controls of beetles and weevils with entomopathogenic fungi have been marked by erratic results. Cram (per. comm.) explored the possibility of using B. bassiana or Metarhizium anisopliae to control the woods weevil Nemocestes incomptus Horn, a native pest of strawberries in British Columbia. He obtained high infection rates in the laboratory but field trials were unsuccessful. Interestingly, he discovered (unpublished results) that the fungicide captan, commonly used by strawberry growers, actually encouraged the increase of the weevil populations because it was fungitoxic to B. bassiana, a natural control of the weevil.

In Europe, the fungus B. tenella has been used against the cockchafer, Melolontha melolontha L., a beetle which is a serious pest of grasslands, at its larval stage (Franz, 1961; Ferron, 1977; Keller et al., 1979). Results indicate that it is not possible to control the pest with the fungus at the present time.

In Canada, the pathogenicity of M. anisopliae and B. bassiana to five species of wireworms (larval Elateridae) was the subject of study for many years (Rockwood, 1950; Fox &

Jaques, 1958; Fox, 1961; Tinline & Zacharuk, 1960; Zacharuk & Tinline, 1968). Although Zacharuk (1970a; 1970b; 1970c; 1973) did some excellent work in elucidating the infection mechanism of M. anisopliae on several species of wireworms, the practical use of the fungus for the control of these pests is generally regarded as remote.

Two weevils found in alfalfa or lucerne (Medicago sativa L.) have also been targeted for study because of the high incidences of natural fungal epizootics. They are the alfalfa weevil, Hypera postica (Gylh.), and the clover leaf weevil, H. punctata (Fabr.). The clover leaf weevil is attacked by Entomophthora phytonomi Arthur (=Empusa sphaerosperma Fres.) and a parasitic wasp Biolysia trisis Gravenhorst. Both these natural control agents usually make chemical control measures unnecessary (Davidson & Peairs, 1966). For control of the alfalfa weevil, an ichneumonid wasp, Bathyplectes curculionis Thomson, has been introduced into the United States. However, chemical insecticides are often needed to keep down the weevil populations. Recent discovery (Harcourt et al., 1974) that E. phytonomi is also pathogenic to the alfalfa weevil has generated much interest (Puttler et al., 1978; 1979; 1980; Barney et al., 1980; Barney & Armbrust, 1981; Ben-Ze'ev & Kenneth, 1980; Watson et al., 1981). Apparently two species of fungi are involved and they have been identified by Ben-Ze'ev and Kenneth (1980) as Zoothora (=Entomophthora) phytonomi (Arthur)Batko and Conidiobolus osmodes Drechsler. Rainfall and the resulting high

humidity is a key factor in seasonal larval infection rates (Barney & Armbrust, 1981). Larval mortality has been reported as 65-90% in Ontario (Harcourt et al., 1974), 10-93% in Illinois (Barney et al., 1980), and 27-81% in Missouri (Puttler et al., 1980). Recurrent epizootics have been observed and it is recognized that these fungi are key components in the control of the alfalfa weevil.

We have learned the hard way that natural biological control is an important factor in pest suppression. A good example was the use of broad-spectrum pesticides against the pests of cotton, which resulted in inadvertent elimination of natural enemies of hitherto unimportant pests. Without their natural enemies, the secondary pests, being more resistant to the chemicals, broke out in unprecedented numbers. "Indeed, much of the future of insect control in row crops should involve ways and means of preserving and augmenting naturally occurring biological control" (van den Bosch et al., 1976).

Besides the Colorado beetle, two other coleopteran pests have recently been shown as promising targets for deliberate introductions of entomopathogenic fungi. One of these is the weevil pest of rice in Cuba, Lissorhoptrus brevirostris (Suffr.). Meneses-Carbonell et al. (1980) obtained 66.3-95.8% kill of the adult weevils in rice fields within 4 days of application using a strain of B. bassiana imported from France. The other is the beet weevil in Romania, Bothynoderes punctiventris Germ. (=Cleonus punctiventris). Tested against 5

strains of B. bassiana, the weevil was killed at rates of 92-100% in the laboratory and 74% in the field (Beratlief, 1979). It appears that the control of coleopteran pests with entomopathogenic fungi can be improved by careful selection of virulent strains and continuing discovery of fungal species.

b. Lepidoptera

Control or attempted control with fungal pathogens has been carried out on several species of Lepidoptera in field and row crops, particluarly those in maize and in soybeans. Beauveria and Nomuraea (=Spicaria) are the commonly used or investigated fungi for this purpose. In China, for example, B. bassiana is being produced and used annually on 1 million ha against the European corn borer, Ostrinia nubilalis (Hb.) (Soper & Ward, 1981). In the U.S., Nomuraea rileyi (Farlow)Samson has been under intensive study for many years. N. rileyi has a host range that is almost exclusively lepidopteran (Ignoffo, 1981).

The European corn borer is a serious pest of maize. It also attacks chrysanthemum, dahlia, gladiolus, eggplant, pepper, beet, bean, potato, tomato, oat, soybean, and many kinds of weeds (Davidson & Peairs, 1966). Damage to maize is caused by the early larval instars chewing the leaves and later instars tunnelling all parts of the stalks and ears. Interest in the use of B. bassiana to control the corn borer began when Lefebvre (1931) noticed the fungus causing 80-100% mortality of the corn

borer larvae he had imported from northeastern China. Subsequent laboratory and field experiments confirmed the corn borer to be highly susceptible to the fungus (Barlett & Lefebvre, 1934; Beall et al., 1939; Brooks & Raun, 1965; Lynch & Lewis, 1978).

There was some interest in the U.S. to develop B. bassiana into a commercial product in the early 1960s (Dunn & Mechalas, 1963). Nutrilite Products Inc. (Buena Park, CA) mass-produced experimental quantities of a dust (5×10^8 spores/g) and a WP (5×10^9 spores/g) of the fungus for distribution. But an attempt by the company to register the fungus as Biotrol FBB did not succeed (Ignoffo et al., 1979).

B. bassiana is pathogenic to several caterpillar pests of cole crops. Ignoffo et al. tested Boverin against the imported cabbageworm, Pieris rapae (L.), the diamondback moth, Plutella xylostella (L.), and the cabbage looper, Trichoplusia ni (Hb.). All were susceptible. Field evaluations indicated that with 5.0% Boverin, about 50% of T. ni larvae were killed which resulted in about 87% reduction in leaf damage to a cabbage crop. The results were unsatisfactory, however, when compared with those obtained with chemical treatments. To be competitive, the specific activity of Boverin would have to be increased (Ignoffo et al., 1979).

Soybean (Glycine max (L.)) is an increasingly important crop in the United States (Turnipseed & Kogan, 1976). Much attention is being paid to improving its production. Most economic loss during growth is caused by outbreaks of leaf and

pod feeders of which the lepidopterous larvae are the most important group.

In nature, large populations of these larvae are often sharply reduced by the fungus, Nomuraea rileyi (Burleigh, 1972; Carner et al., 1974; 1975; Allen et al., 1971; Ignoffo et al., 1976). Unfortunately, the fungal epizootics usually peak after economic damage to the crop has already been done (Ignoffo et al., 1975a). It is therefore of interest to be able to induce epizootics earlier than they would occur in nature. Both Sprenkel and Brooks (1975) and Ignoffo et al. (1976) have demonstrated that it is possible to do so.

Sprenkel and Brooks (1975) distributed cut up pieces of cadavers of the tobacco budworm, Heliothis virescens (F.), killed by N. rileyi, among soybeans in North Carolina. Their results indicated that "early application (of inoculum) is of utmost importance, if an artificially induced epizootic is to be initiated earlier and be more intense than a natural epizootic." Ignoffo et al. (1976) came to a similar conclusion with their field experiments in Missouri. An early application of conidia at 1.1×10^{13} spores/acre produced an epizootic among larvae of the green cloverworm, Plathypena scabra (F.), 14 days before a natural epizootic broke out in untreated plots nearby. What was most important was that the peak of the induced epizootic occurred before and during the critical stages of soybean growth, thus providing the plant protection when it was most needed. Larval mortality in treated plots averaged 82.5%, much

higher than the 7.4% in the untreated plots. There is sufficient evidence that it would be of benefit to apply N. rileyi artificially to protect crops such as soybeans.

About 30 species of lepidopteran pests are susceptible to N. rileyi, including all the major caterpillars that feed on soybeans (Ignoffo et al., 1982; Carner et al., 1974). Pathogenicity studies in the laboratory have confirmed the field observations (Getzin, 1961; Gudauskas & Canerday, 1966; Behnke & Paschke, 1966). However, Getzin (1961) noted that the disease incubation period of N. rileyi was rather long, requiring 6 to 10 days as opposed to 3 to 4 days in the case of Beauveria or Metarhizium infection. The relatively long time of disease development is probably of little consequence because Mohamed (1982) showed that food consumption and utilization by larvae infected with N. rileyi are significantly reduced.

N. rileyi can be cultured with liquid or solid media, but only blastospores are produced in liquid media and these are not infective (Bell, 1975; Riba & Glandard, 1980). Because blastospores are more easily produced, Ignoffo (1981) suggested that they might be formulated with nutrients that promote development and sporulation of conidia in the field. Conidia are usually produced on solid media. A suitable substrate is Sabouraud maltose agar fortified with 1% yeast extract (Bell, 1975). A method for the mass collection of N. rileyi conidia has been proposed by Hamalle and Bell (1976). Cultures of N. rileyi are sometimes contaminated with bacteria; this can be prevented

by the use of most commonly available antibiotics or sulfonamides, many of which are not inhibitory to the growth of N. rileyi (Garcia & Ignoffo, 1979).

Several isolates of N. rileyi have been identified which differ in activity against some lepidopterous pests. The velvetbean caterpillar, Anticarsia gemmatalis Hb., for example, was resistant to some isolates of N. rileyi from Missouri, Florida, and Mississippi (Ignoffo et al., 1976; Puttler et al., 1976; Ignoffo et al., 1975a). In contrast, epizootics of the fungus among populations of the velvetbean caterpillar have been reported in some southern States (Allen et al., 1971; Johnson et al., 1976; Hinds & Osterberger, 1931; Moscardi et al., 1981). Boucias et al. (1982) demonstrated that at least two strains of N. rileyi existed: strain F178 was virulent to the velvetbean caterpillar but did not cause significant mortality of the fall armyworm, Spodoptera frugiperda (J.E. Smith); isolate F174 was virulent to the fall armyworm but caused only about 18% mortality of the velvetbean caterpillar. The recognition of such variations among isolates of N. rileyi is important when considering the practical use of the fungus against defined pest complexes.

The compatibility of N. rileyi with other pest control agents has been studied (Moscardi et al., 1981; Gardner et al., 1979; Ignoffo et al., 1975b; Johnson et al., 1976). The fungus is highly sensitive to almost all fungicides, and to some insecticides and herbicides that are registered for use on

soybeans. Because of the incompatibility of N. rileyi with other pest control agents and its proven ability to induce extensive epizootics in early instars of caterpillar pests on row and field crops, it "offers more potential if used as a prophylactic system in insect pest management programs" (Ignoffo, 1981).

Entomophthora gammae (Weiser) is another entomopathogenic fungus that has been reported to severely reduce natural populations of lepidopterous pests on soybeans (Carner et al., 1975; Newman & Carner, 1974; Harper & Carner, 1973; Livingston et al., 1981) The soybean looper, Pseudoplusia includens (Walker), is particularly susceptible. E. gammae is apparently resistant to benomyl: a natural epizootic of the fungus on the soybean looper was not significantly affected by field applications of benomyl at recommended rates (Livingston et al., 1981). The use of benomyl in soybean production has increased in recent years. The potential of this fungus as a biological control agent in an integrated pest management system deserves further investigation.

c. Homoptera

Aphids, leafhoppers, planthoppers and spittlebugs are serious pests of pastures, field and row crops. Many of these pests are important vectors of viruses and other diseases of plants (Harris, 1980). Entomophagous fungi, particularly species of Entomophthora on aphids, and Metarhizium on spittlebugs,

leafhoppers and planthoppers, often cause natural epizootics that dramatically reduce pest populations. Natural epizootics tend to be sporadic and unpredictable. To harness the forces of natural pest control, deliberate manipulation of these fungi has been attempted, with some success (Baird, 1958; Gustafsson, 1971; Ferron, 1978; 1981).

Aphids are common pests of clover and alfalfa (Haws, 1978). Some species can be found in large numbers without apparent injury to the plants, but with others, such as the spotted alfalfa aphid (SAA), a relatively small number can cause the plants to wilt and become stunted, resulting in very substantial loss of yield.

Originating in central Asia and discovered in California in 1954, SAA caused about US$81 million damage to alfalfa in the next two years (Haws, 1978). Surveys of natural enemies (Hall & Dietrick, 1955; Hall & Dunn, 1957) indicated that the aphid was parasitized by several species of fungi which sometimes caused epizootics that sharply reduced aphid numbers. But the fungi did not spread as fast as the aphid and it was decided to aid the fungal spread artificially.

Three fungi were selected: Conidiobolus thromboides Drechsler (=Entomophthora virulenta Hall & Dunn), Entomophthora exitialis Hall & Dunn, and Conidiobolus coronata (Cost.). The fungi were cultured on various artificial media (chiefly Sabouraud's dextrose agar) in 1/4 pint waxed food containers for placement in fields. Inoculation sites were carefully chosen to

ensure adequate moisture and a high aphid population. In all, 1,754 culture units were distributed in the San Joaquin and Sacramento valleys. Some limited success was claimed (Hall & Dunn, 1958). E. exitialis was the most pathogenic. It caused epizootics, mostly in the winter months (Hall, 1963).

In 1977, SAA and another aphid pest of alfalfa, the blue-green aphid (BGA), Acyrthosiphon kondoi Shinji, appeared for the first time in Australia (Milner et al., 1980). Because of the California experience, surveys were first conducted to identify fungal species that attacked the two exotic aphids. Results of the surveys (Milner & Bourne, 1983) showed that the BGA was heavily attacked by Conidiobolus obscurus (Hall & Dunn) Remaudiere & Keller, Entomophthora planchoniana Cornu, and Erynia neoaphidis Remaudiere & Hennebert during periods of high humidity and cool temperature. Populations of SAA, however, were relatively free of disease. Exotic pathogens were sought from America, Europe and Isreal (Grimm, 1979; Milner & Soper, 1981). It was found that Zoophthora radicans (Bretfeld) Batko (=Entomophthora sphaerosperma Fresenius) was the most pathogenic to the SAA strains in Australia. Tested against apterous adults, isolates of Z. radicans generally infected 80-100% of SAA in 3-7days with copious production of infective conidia.

Milner and Soper (1981) described a method for the production of Z. radicans. The fungus was first grown in a liquid medium made up of 20g yeast extract, 60ml sunflower oil, and 20g dextrose in 1 liter of distilled water. The culture was

incubated at 25C and shaken at 300rpm. After 2 or 3 days the mycelium was collected by filtration and then exposed to fluorescent light for 12-24h to stimulate spore production.

An isolate of Z. radicans from Israel, designated EM 539, was field tested (Milner et al., 1982). To provide suitable moisture conditions for the experiment, plastic garbage bins (45L), each with a hole cut in its bottom, were inverted over crop plants. Over the hole of each bin, the inoculum was introduced as a sporulating culture placed in a dish, or as infected aphids. Water was then sprayed into the bin and a large plastic bag was used to enclose the bin on the outside. The bin and the bag were kept in place overnight and removed the following morning. Five weeks after inoculation, the fungus succeeded in establishing at one site. Aphids within 3m of the point of release were infected up to 88%. It was noted that the spread of the disease was very slow and limited and that by the end of the experiment, the alfalfa was almost entirely destroyed by aphids.

Investigations into disease complexes of aphid pests of alfalfa were also carried out in New Zealand (Cameron & Milner, 1981; Hall et al., 1979). One survey (1980) in the Auckland region showed that 54% of the pea aphid, Acyrthosiphon pisum (Harris), was diseased with Zoophthora aphidis (Hoffman in Fresenius) Batko. The population of another aphid, the BGA, showed 11% infection with C. obscurus.

Entomogenous fungi controlling aphids on potatoes have long been studied (Shands et al., 1958; 1962; 1963; 1972). All the common species of aphids infesting potatoes in Maine are attacked by some species of fungi. An effort was made to use these fungi as mycoinsecticides. The fungus, Acrostalagmus aphidium Oud. was selected to test the idea because of its culturability. The fungus was grown on cooked slices of potato tubers or potato-infusion agar supplemented with 1% dry yeast, for 10 days at 24C. The culture material with fungal spores and mycelium was then mixed with water to prepare a spray suspension. The result of the spraying was unsatisfactory and few disease-killed specimens were collected afterwards.

The black bean aphid, Aphis fabae Scop., can cause heavy yield losses in field beans (Vicia faba L.) (Way, 1967; Gould & Graham, 1969). Fungal epizootics sometimes kill large numbers of this aphid (Missonnier et al., 1970; Dedryver, 1978). For this reason, surveys were made of the fungal species in Britain (Wilding & Perry, 1980) to identify candidates for possible use in biological control. Results showed that Conidiobolus obscurus, Entomophthora planchoniana, Erynia neoaphidis and Zoophthora radicans might have some potential. Wilding (1981b) carried out a series of five field experiments and showed that the rates of infection of aphids by these fungi could be raised from the natural or background infection rate of 1-2% up to 30-47% with a doubling of the crop yield as a result.

In France (Dedryver, 1978), the most common and effective fungal pathogen found on the black bean aphid is Neozygites fresenii (Nowak.) Remaud. & Kell. (=Entomophthora fresenii). Under greenhouse conditions, N. fresenii was able to cause 80-90% mortality of the bean aphid in 24-27 days (Dedryver, 1979).

The pea aphid, Acyrthosiphon pisum Harris, is another major pest of legumes that has been studied for possible control with Entomophthoraceae. Over a period of eight years (1962-1969), Voronina (1971) observed that the pea aphid populations in Leningrad Province, Russia, were held down annually by entomogenous fungi. Entomophthora ignobilis Hall & Dunn (=E. thaxteriana Petch) was identified as the key pathogen.

Cereal aphids are attracting increasing attention in Europe. The International Organization for Biological Control of Noxious Animals and Plants formed a subgroup recently to examine this problem and to explore various control methods. The two major cereal aphids in Europe are Sitobion arvense (F.) and Metopolophium dirhodum (Wlk.). In Czechoslovakia, another aphid species, Rhopalosiphium padi (L.), can also be of concern (Stary, 1976). C. obscurus, E. planchoniana and E. neoaphidis are the common fungal pathogens found on these aphids. Carter et al. (1982) noted, however, that natural control of cereal aphids by fungi was not a significant mortality factor in England. Dean and Wilding (1971) also reported that in spite of fungal infection of aphids, damage to a barley crop was not prevented.

Perhaps virulent strains of the fungi need to be identified. Papierok and Latge (1980) suggested that the strains most likely to be of use in biological control programs would be those possessing a low LC50, an ability to multiply quickly and abundantly, and a short infection cycle. Soper and Ward (1981) reported that the United States and France were working together to produce resting spores of C. obscurus . The spores produced were intended to be field tested on cereal crops in France (Latge & Perry, 1980).

In China, Aphis gossypii Glover is an important aphid pest of cultivated crops. It is claimed (Anon., 1976) that the aphid was successfully controlled with a fungus, E. neoaphidis (Wilding, 1981a; 1981b).

The production of rice in Asia is sometimes hampered by infestations of insects such as the brown planthopper, Nilaparvata lugens (Stal) (Sogawa, 1982). Because of the present socioeconomic conditions prevailing in many tropical countries in Asia, heavy reliance on chemical insecticides is impractical as well as undesirable. An integrated approach is being developed, exploiting resistant rice varieties and natural control agents. Among the agents being studied are the fungi Entomophthora delphaci Hori (Shimazu, 1977), Syncephalastrum racemosum Cohn ex Schroter and Penicillium oxalicum Currie & Thom (Phillip et al., 1981). Another pest, Cofano spectra (Dist.) (=Cicadella spectra), a leafhopper which occurs widely on rice in India, was also investigated to assess the

possibility of its control with S. racemosum (Mathai et al., 1979). Initial laboratory studies showed that the fungus was capable of causing more than 85% mortality of the leafhopper within 24-48h.

One of the few entomopathogens under commercial production is Metarhizium anisopliae (Metsch.) Sorokin. The product is known as Metaquino in Brazil (Ferron, 1978) and is used widely in that country against spittlebugs, particularly Mahanarva posticata (Stal), a major pest of pastures and sugarcane. The fungus is cultured on a boiled rice substrate at 26-29C for 15-20 days under high humidity. The culture is then dehydrated and ground into powder for distribution. The fungus is apparently very effective against M. posticata. Risco (1980) said that the use of Metaquino rose by 67% in 1980 over 1979, cutting the use of chemical insecticide to a mere 18.24% of the total area requiring protection. The fungus is also used to control Tomaspis (=Deois) flavopicta Stal and Zulia entreriana (Berg.), two important froghopper pests in pastures in Brazil (Naves, 1980). Ramiro and Cottas (1979) indicated, however, that the fungus might not be so highly effective against T. flavopicta and Z. entreriana as against M. posticata. Spraying control plots with 10^8 spores/ha against the two pasture pests, they could not obtain significant reductions of the pest populations when compared with untreated control plots.

The genus Metarhizium (=Metarrhizium) contains two species: M. anisopliae and M. flavoviride (Tulloch, 1976; Samson, 1981).

M. anisopliae is the causal agent of the green muscardine disease of insects. Based on the spore size, M. anisopliae can be differentiated into M. anisopliae var. anisopliae, the short-spored taxon, and M. anisopliae var. major, the long-spored taxon. The short-spored type is the one used in Brazil against spittlebugs (Conti et al., 1980). The long-spored type has been used successfully in combination with a baculovirus against the rhinoceros beetle, a serious pest of coconut in the islands of the South Pacific (Marschall & Ioane, 1982; Beichle, 1979; Tulloch, 1976).

Insect pests other than coleopterans, lepidopterans, and homopterans are also subject to fungal attack. The black field cricket, Teleogryllus commodus (Wlk.), for example, is susceptible to M. anisopliae (Reinganum et al., 1981). The cricket is of some concern in southeastern Australia as a pest of pastures and a program is underway to test its control with the fungus. Grasshoppers in many parts of the world are often killed in large numbers by fungal diseases (Milner, 1978; Chapman & Page, 1979; Roffey, 1968; Nelson et al., 1982; MacLeod, 1963; Pickford & Reigert, 1964). Entomophthora grylli Fres. is the commonest fungus identified. Although this fungus has never been reported to cause heavy mortalities on Locusta migratoria L. or Schistocerca gregaria Forsk., it has been observed to cause extensive epizootics among Zonocerus variegatus L., a grasshopper that can sometimes become a serious pest of cultivated crops in Nigeria. Development of E. grylli as

a biocontrol agent will be difficult because it has not been successfully cultured on artificial media until recently (MacLeod *et al.*, 1980) and that only in protoplast form.

The cabbage maggot, *Hylemya brassicae* (Bouche), and the seedcorn maggot, *H. platura* (Meigen) (=*H. cilicrura* Rondani) are common pests of vegetables. Strong *et al.* (1960) discovered an unknown fungal disease of the seedcorn maggot while studying its biology and control in Wisconsin. Batko and Weiser (1965) named the unknown fungus *Strongwellsea castrans*. The fungus also attacks the adults of the cabbage maggot on rutabagas (Nair & McEwen, 1973). Infected flies which are characterized by the presence of one or two ventral abdominal holes, become completely sterile , but capable of normal feeding and flying. Further studies on the fungus, however, are hampered by the inability to culture it *in vitro*.

Most fungi pathogenic to insect pests on cultivated crops are members of Entomophthorales. This group of fungi has been extensively reviewed (King & Humber, 1981; Wilding, 1981a; MacLeod, 1963; Ferron, 1978; Gustafsson, 1969; Rockwood, 1950). Taxonomically it is a difficult group and it has undergone many redefinitions (King & Humber, 1981; Milner, 1981; Latge *et al.*, 1980; Remaudiere & Hennebert, 1980; King, 1976; Remaudiere & Keller, 1980; Ben-Ze'ev & Kenneth, 1981). Many species formerly grouped under the generic name of *Empusa* (MacLeod, 1956) have been renamed *Entomophthora* . The following is a list of the major changes that have been adopted recently (from Milner,

1981; King & Humber, 1981):

Old name	New name
Entomophthora aphidis Hoffman *sensu* Thaxter	*Erynia neoaphidis* Remaudiere & Hennebert
Entomophthora aphidis (Nowakowski) Gustafsson	*Neozygites fresenii* (Nowakowski) Remaudiere & Keller
Entomophthora obscura Hall & Dunn	*Conidiobolus obscurus* (Hall & Dunn) Remaudiere & Keller
Entomophthora phalloides (Batko)Remaudiere, Keller, Papierok & Latge	*Zoophthora phalloides* Batko
Entomophthora sphaerosperma Fresenius	*Zoophthora radicans* (Brefeld)Batko
Entomophthora virulenta Hall & Dunn	*Conidiobolus thromboides* Drechsler
Entomophthora thaxteriana Petch	*Entomophthora ignobilis* Hall & Dunn
Entomophthora coronata (Cost.) Kev.	*Conidiobolus coronata* (Cost.) Tyrrell & MacLeod

One species, *Entomophthora exitialis* Hall & Dunn, has been confused with *Erynia neoaphidis*, *Zoophthora aphidis*, and *Erynia nouryi* in existing literature (Milner, 1981). More taxonomic work is needed to clarify the identity of this fungus.

Deliberate manipulations of Entomophthorales for the control of insect pests in cultivated crops have been few and far between. Of the few attempts, success has been evasive. The outstanding success claimed by China in the control of the cotton aphid (Anon., 1976) has yet to be confirmed (Wilding, 1981a). Field observations reported over the years, however, indicate that these fungi are quite capable of reducing large

populations of insect pests to very small numbers. Much effort, therefore, has been directed to preserve these natural control agents in cultivated crops--an effort that is reflected in the large number of research papers on the effects of insecticides and fungicides on this group of entomopathogenic fungi (Nanne & Radcliffe, 1971; Radcliffe et al., 1976; Sagenmuller, 1976; Wilding & Brobyn, 1980; Hall & Dunn, 1959; Wilding, 1981b; 1982; Bailiss et al., 1978; Soper et al., 1974; Delorme & Fritz, 1978).

There is potential for some of these fungi being developed into effective biological control agents. Progress is being made to elucidate the often fastidious environmental requirements of these fungi in order to germinate, spread, and cause epizootics (Newman & Carner, 1975; Yendol, 1968; Wilding, 1969; 1971; 1981a; Milner, 1981; Dedryver, 1979; Robert et al., 1973; Pady et al., 1971; Milner & Bourne, 1983). In general, it appears that saturated or near-saturated air is required. Other important factors are inoculum concentration, host density and distribution (Robert et al., 1973; Wilding & Perry, 1980).

An obstacle to commercial development of Entomophthora species is their inability to persist as conidia. Although many produce resting spores which are long-lived, these spores are characterized by very low germinability (Krejzova, 1978). Several approaches are being taken to increase their rate of germination, and these include selection for high germinating strains, chemical and physical treatment of resting spores, and

biochemical studies of the germination process (Roberts, 1973).

3. Forest, plantation and orchard pests

Modern biological control began in California with the management of an orchard pest (Doutt, 1967). It was so successful that citrus production doubled in a single year. The vedalia, a beautiful, predacious, ladybird beetle, introduced from Australia in 1888, became permanently established and kept populations of the cottony cushion scale, *Icerya purchasi* (Maskell), down to non-pest levels. Growers are still reaping the benefits of that introduction.

Entomopathogenic fungi are biological control agents. Their potential use to control pests on trees was recognized early when Speare and Colley (1912) tried to curb populations of browntail moth, *Nygmia phaeorrhoea* (Donov.), in Massachusetts with the fungus *Entomophthora aulicae* (Reich.) Sorok.

Recent development in the applied control of arthropods with fungal pathogens has made it possible to obtain commercial products such as Mycar (*Hirsutella thompsonii* Fisher) and Boverin (*Beauveria bassiana* (Bals.) Vuill. It appears that increased efforts are being made to incorporate fungi and fungal toxins into an expanding arsenal against forest, plantation and orchard pests.

a. Forest

Defoliators and bark beetles are very serious pests of forest and shade trees. Heavy reliance on chemicals to solve these pest problems is becoming both unpopular and costly. A good example is the chemical control program against spruce budworm, Choristoneura fumiferana Clem., in New Brunswick. Environmental constraints and socioeconomic needs require development toward biological control.

Entomophthora species have been cited as ecologically acceptable agents for development as microbial controls (Weatherston & Retnakaran, 1975). Two such fungi are under intensive study for spruce budworm control (Dunphy & Nolan 1981, 1982a, 1982b; Vandenberg & Soper 1975, 1978, 1979). The two fungi, Zoophthora radicans (Bref.) Batko and Entomophaga (=Entomophthora) egressa MacLeod & Tyrrell, are also virulent to larvae of the eastern hemlock looper, Lambdina fiscellaria fiscellaria (Guen.).

The looper attacks many species of forest trees in Newfoundland although its principal host is balsam fir, Abies balsamea (L.) Miller. Otvos et al. (1973) noticed that Z. radicans and E. egressa were often the primary cause of collapse in looper infestations. To test the possibility of artificially initiating epizootics, they distributed sporulating cadavers of the looper in naturally occurring host populations and achieved moderate success.

Gypsy moth, Lymantria (=Porthetria) dispar (L.), is a major defoliator of forest and shade trees in the eastern United States and southeastern Canada (Wasti & Hartmann, 1975). Included in present control programmes are a variety of methods such as: chemical insecticides, artificial pheromones and lures, and bacterial insecticide. The use of viruses and fungi are being investigated. Fungi that have been identified as possible candidates include Conidiobolus coronatus (Cost.) Batko (Hartmann & Wasti, 1974), C. thromboides Drechsler (=Entomophthora virulenta) (Hartmann & Wasti, 1976), Beauveria bassiana (Bals.) Vuill. (Wasti & Hartmann, 1975), Nomuraea rileyi (Farlow) Samson (Wasti & Hartmann, 1978a), Metarhizium anisopliae (Metsch.) Sorokin and Paecilomyces fumoso-roseus (Wize) Brown & Smith (Wasti et al., 1980), Entomophthora aulicae (Reich.) Sorok. and P. canadensis (Vuill.) Brown & Smith (Aoki, 1974).

Wasti and Hartmann (1978b) also discussed the possible use of mycotoxins from B. bassiana, P. fumoso-roseus and N. rileyi as insecticides against the gypsy moth. They described a modified method from Hamill et al. (1969) for the laboratory extraction of fungal toxins. Toxins of Beauveria can also be obtained commercially from Eli Lilly Company (Indianapolis, Indiana). Results of topical applications of the mycotoxins on gypsy moth larvae showed that they were less effective than conidial applications.

Tent caterpillars are common pests of deciduous trees. The forest tent caterpillar, Malacosoma disstria, Hbn., in particular, is widely distributed in North America (Stairs, 1972). Fungi, primarily B. bassiana, and Erynia (=Entomophthora) crustosa (MacLeod & Tyrrell) are found in most forest tent caterpillar populations (Stairs, 1972, MacLeod & Tyrrell, 1979, Retnakaran et al., 1982). Abrahamson and Harper (1973) sprayed resting spores of E. crustosa (=Entomophthora megasperma Cohn) at 4.2×10^6 spores/acre to one plot of water tupelo (Nyssa aquatica L.) in southwestern Alabama but were unable to save the trees from defoliation. Probably the dosage they applied was too low to have any effect.

In China, the pine caterpillar, Dendrolimus punctatus Wlk., is one of the most serious leaf-feeding insects of Pinus massoniana Lamb. (Hsiao, 1981). Various methods, including the use of ants, parasitic wasps, bacteria and viruses are used to control it. The fungus, Beauveria bassiana, is used on a large-scale. In 1978, more than 587,000 ha of pine stands in the southern eight provinces were treated with preparations of the fungus. B. bassiana has proved particularly effective against the overwintering larvae, achieving 86-99% kill in some areas. No adverse effect on the silkworm (Bombyx mori L.) was recorded.

The fungus Cordyceps militaris (L.) Link is a well-recognized entomopathogen. In the Pacific Forest Research Centre, Victoria, B.C., studies were made to test it for the control of forest defoliators, particularly the green-striped

forest looper, Melanolophia imitata Wlk. (Ilnytzky & Funk, 1976). Infection was 100% in an experiment carried out in northern Vancouver Island that involved spraying homogenized hyphae and conidia of the fungus onto infested trees with a mist blower.

Funk (1977) investigated methods of mass producing the fungus and proposed an inexpensive procedure of liquid culture using polythene bags. Field tests with the fungal preparations against western hemlock looper (Lambdina fiscellaria fiscellaria), false hemlock looper (Nepytia freemani Monroe), and black-headed budworm (Acleris gloverana Powell), were not successful.

Whereas forest Lepidoptera are serious defoliators, bark beetles girdle trees and are also important vectors of plant pathogens. In the southern United States and in Central America, the southern pine beetle, Dendroctonus frontalis Zimm., is a serious killer of pines. Sample studies in the United States indicated that one-third to one-fifth of the beetle populations died of diseases every year (Moore 1971, Sikorowski et al. 1979). Amongst the disease-causing organisms are the fungi Beauveria bassiana, Aspergillus flavus Link, Fusarium solani (Martius) Appel & Wollenweber, Paecilomyces viridis Segretain ex Samson, and Metarhizium anisopliae.

Both the adult beetles and the late instar larvae are susceptible to fungal infections. Pabst and Sikorowski (1980) and Moore (1973) tested the effectiveness of these fungi. All

proved pathogenic under laboratory conditions. Working with Beauveria, Aspergillus, and Fusarium against adult beetles, Moore noted that varying RH of 55%, 75%, and 94%, did not significantly affect mortality rates, but temperatures did. The optimum range of temperatures for fungal infections was between 15 and 25C. Pabst and Sikorowski (1980) also found relative humidity an unimportant factor in the infection of late instar larvae. They treated the larvae topically with conidia of B. bassiana , P. viridis, and M. anisopliae separately and incubated them for 10 days in the dark at 26%RH and 22-25C. An average mortality rate of 90% was obtained with 2.2×10^4 viable spores/larva for Beauveria or Paecilomyces. With Metarhizium, a dosage of 1.1×10^5 viable spores/larva was needed to obtain the same level of kill. Germination tests for M. anisopliae (25%) and P. viridis (2.7%) showed that most conidia were not viable or failed to germinate. Reasons for the low germination were not investigated.

In the Pacific Northwest, the mountain pine beetle, Dendroctonus ponderosae Hopkins, is a serious pest of mature pines (Wood & VanSickle, 1983). The Pacific Forest Research Centre, Victoria, B. C., is exploring the possible control of this beetle with B. bassiana. The white muscardine fungus is highly pathogenic to the mountain pine beetle. In a master's research paper, Hunt (1983) stated that he consistently obtained high mortalities amongst his inoculated control insects with B. bassiana although he could not observe germinating or

penetrating conidia on the external cuticle of experimental insects. He found that saturated air or free water enhanced conidial germination. But even at 100% RH, the percentage of Beauveria conidia that germinated averaged below 2.5%. He demonstrated that lack of nutrients was probably the limiting factor, in agreement with the findings of Smith and Grula (1981).

To improve the efficacy and reliability of B. bassiana as a mycoinsecticide against the mountain pine beetle, Hunt suggested that the conidia could be formulated with some type of nutrient mixture. The problem is, however, that with added nutrients, the fungus tends to proliferate on the surface of the insect cuticle instead of penetrating it, a fact that Hunt also demonstrated in his experiment.

In Russia, Gusteleva (1980) reported that Boverin (B. bassiana) was used effectively against the larch bark beetle, Ips subelongatus Motsch. The fungus reduced both the rate of development and viability of the adult beetles.

The large (Scolytus scolytus F.) and the small (S. multistriatus Marsham) elm bark beetles are vectors of Dutch elm disease. Doane (1959) recorded that the small elm bark beetle was frequently infected by B. bassiana. Epizootics could kill up to 97% of the beetle larvae on infested trees in the shade but only 4% on trees in the open nearby. B. bassiana is also highly pathogenic against the final instar larvae of the large elm bark beetle (Barson, 1977). A dose of 6.5×10^7 spores/ml gave a

rapid kill of 100% of the larvae within 5 days when incubated at 23C and at 100% RH. In laboratory experiments, another fungus, Verticillium lecanii (Zimm.) Viegas, was also able to cause high mortalities amongst the large elm bark beetle larvae (Barson, 1976). However, it has been observed that fungal pathogens did not appear to be important factors in the natural regulation of the numbers of either the large or the small elm bark beetle (Beaver, 1966; Barson, 1977). Selection of virulent fungal strains and the study of infection requirements have been undertaken recently (Doberski, 1981a; 1981b).

The introduced pine sawfly, Diprion similis (Hartig), is found in the central and eastern United States, and in parts of Ontario and Quebec (Johnson & Lyon, 1979). It feeds on a wide range of pines including white, red, Scots, and jack. Klein and Coppel (1973) reported a fungal epizootic on the sawfly which killed nearly 100% of the sawfly larvae sampled in Wisconsin. The fungus was identified as Entomophthora tenthredinis Fres. but they could not culture it on artificial media.

The pales weevil, Hylobius pales (Hbst.), is one of the most serious insect enemies of pine regeneration in eastern North America (Schabel, 1976). It kills seedlings by girdling them. B. bassiana and M. anisopliae are both effective pathogens of the weevil but field experiment (Walstad & Anderson, 1971) indicated that very large dosages were needed to achieve satisfactory control. Schabel (1982) discovered two phoretic mites which could act as carriers of M. anisopliae. Possible use

of the mites to increase the efficacy of the fungus in the field was discussed.

Cone and seed production by trees is often cyclic. For white spruce , Picea glauca (Moench) Voss, each cycle is approximately 7 years (Waldron, 1965). To maintain the supply of pulp and lumber, adequate forest regeneration is needed. In British Columbia, seed crops are sometimes drastically reduced by insect infestations (Hedlin, 1973). The spruce cone maggot, Hylemya (=Lasiomma) anthracina (Czerny), is particularly damaging to spruce. A single maggot may destroy more than half of the seeds in one cone. This pest is widely distributed and, where infestations are severe, is capable of destroying 100% of the seeds (Hedlin et al., 1980).

When seeds are collected from natural stands, chemical control of insect pests is often unsatisfactory because of the large acreage involved (Timonin et al., 1980). The possibility of using white and green muscardine fungi was explored. Timonin et al. found that the muscardine fungi could be very effective. They noted also that the virulence of the fungi could be improved by serially passaging the fungi through the host or related insects, a phenomenon that was also reported by Hartmann and Wasti (1974).

b. Plantation

Very few investigations have been made into fungal control of arthropod pests on tropical fruits and nuts (Bennett *et al.*, 1976) and fibre crops. The available records show that more study is warranted. Smith and Prior (1980, quoted in Smith, 1981) used *Beauveria bassiana* against *Pantorhytes plutus* Oberthur, a weevil pest of cocoa in Papua New Guinea. They obtained infection rates of more than 90% under laboratory conditions. In India (Srivastava & Tandon, 1980), *B. bassiana* and *Aspergillus flavus* were tested against the mango leaf webber, *Orthaga euadrusalis* Wlk. *Beauveria* caused 100% mortality in 4 days when the larvae were allowed to crawl over the fungus. *Aspergillus* also caused 100% mortality within 4-8 days. In Guadeloupe (Delattre & Jean-Bart, 1978), the banana weevil, *Cosmopolites sordidus* (Germ.), was found to be highly susceptible to strains of *B. bassiana* and *M. anisopliae*. Treatments under both laboratory and field conditions showed that the fungi were capable of causing infection. A survey conducted in southern Iraq (Al-Hassan *et al.*, 1980) on populations of a stem-borer on date palms, *Pseudophilus testaceus* Gah., revealed that many larvae were killed in their tunnels by *B. bassiana*. Laboratory tests in which sprays of spore suspensions of the fungus were applied to larvae confirmed the pathogenicity of *B. bassiana* to the cerambycid. In the South

Pacific Islands, M. anisopliae is often used in combination with a baculovirus to control the rhinoceros beetle, Oryctes rhinoceros L. on coconut palms (Beichle, 1979, Marschall & Ioane, 1982). The fungus is particularly useful in treating breeding sites of the beetle.

c. Orchard

The commercial pecan, Carya illinoensis Koch, is an important nut crop to many southeastern and midwestern states (Boethel & Eikenbary, 1979). A serious economic pest often found in pecan orchards is the pecan weevil, Curculio caryae (Horn). Swingle and Seal (1931) first reported that two entomopathogenic fungi, Metarhizium anisopliae and Beauveria bassiana, were notable in their control of the pecan weevil. Recently, interest in the two fungi was renewed because of a movement to reduce reliance on chemical pesticides (Neel & Sikorowski, 1972; Tedders et al., 1973; Boethel & Eikenbary, 1979; Champlin et al., 1981; Gottwald & Tedders, 1982; 1983). These studies indicate that Beauveria is more pathogenic than Metarhizium to the pecan weevil and produces more secondary inoculum on insect cadavers. But even with B. bassiana, tests against weevil larvae were disappointing (Gottwald & Tedders, 1983). Their results in field trials against adult weevils were better, with an average mortality of 79.6%; this compared with a natural disease background of 7.6%. They noted that diseased weevils failed to

produce viable eggs.

Neither B. bassiana nor M. anisopliae are compatible with common fungicides used to control phytopathogens on pecans (Tedders, 1981). Triphenyltin hydroxide, the most common and widely used fungicide on pecans, is especially toxic to the two entomopathogens.

In many apple orchards, the codling moth, Laspeyresia pomonella (L.), is a major pest. Against this insect, the sterile male technique has been used successfully in the Okanagan Valley of British Columbia. However, the operating costs of rearing moths and sterilizing them for release are high. The use of fungi pathogenic to the moth has been explored in France (Ferron & Vincent, 1977) and the Soviet Union (Simchuk, 1979). Simchuk suggested that the effectiveness of B. bassiana against the codling moth could be enhanced if it were used in conjunction with a protozoan, Nosema carpocapsae Paillot.

The periodical cicada, Magicicada septendecim (L.), is an occasional pest of orchards and woodlands (Lloyd et al., 1982). It can, for example, reduce yield in an apple crop although the trees are not killed (White & Lloyd, 1975). Massospora cicadina Peck is a specific pathogen of the periodical cicada. The fungus attacks the abdominal portion of adult insects which continue to fly, dispersing conidia and resting spores as terminal abdominal sclerites break off.

A closely related species, Massospora levispora, was discovered by Soper (1963). This fungus is a specific parasite of the northern cicada, Okanagana rimosa (Say). The biology and epizootiology of this fungal species in cicada populations have been studied (Soper, 1976a; 1976b).

Being obligate parasites, Massospora spp. are difficult to culture on artificial media but Tyrrell and Welton (1983) succeeded with M. levispora, though only in the protoplast form.

Mites and whiteflies are among the most important pests of citrus (Boyce, 1950). In Florida, the major species are citrus rust mite, Phyllocoptruta oleivora (Ashm.), citrus red mite, Panonychus citri (McG.), and citrus whitefly, Dialeurodes citri (Ashm.). Populations of citrus rust mite were often observed to fluctuate dramatically and it was suspected (Speare & Yothers, 1924; Fisher et al., 1949; Fisher, 1950) and later confirmed (McCoy & Kanavel, 1969) that the mite was being attacked by an entomogenous fungus, Hirsutella thompsonii Fisher.

H. thompsonii is a facultative parasite which grows readily on common mycological media (McCoy & Kanavel, 1969; Yen, 1974; McCoy et al., 1972; 1975; Gerson et al., 1979). A simple and economical method of mass producing the fungus was proposed by McCoy et al. (1978). Using this method, the fungus is grown in a liquid culture containing 2.0% molasses and 8.0% soybean meal adjusted to 7.5 pH. However, H. thompsonii does not produce conidia in liquid culture and it is necessary to transfer the mycelial mat to semi-solid substrates for conidiation (McCoy &

Couch, 1978). Conidia are considered superior to mycelia as inoculum because they can be handled, formulated and stored more easily.

H. thompsonii attacks a number of species of Acarina, primarily eriophyid mites inhabiting citrus. Besides citrus rust mite, the fungus is also pathogenic to Panonychus citri (McG.), Eriophyes sheldoni (Ewing.), Acalitus vaccinii (Keifer), Eutetranychus banksi (McG.), Eutetranychus sexmanculatus (Riley), Tetranychus cinnabarinus (Boisduval) and Eutetranychus orientalis (Klein). Only one species of predatory mite, Tyhlodromalus pereqrinus Muma, has so far been recorded as susceptible to H. thompsonii (McCoy & Couch, 1978).

H. thompsonii requires 90-100% RH or free water to be infectious. Once started, however, the infection process is quite rapid, often killing the host in less than 48h at 26-27C.

Abbott Laboratories' (North Chicago, Illinois) has developed and produced H. thompsonii as a commercial product under the trade name Mycar (McCoy & Couch, 1982). The fungus is available both as a dust and as a wettable powder.

Several adjuvants are recommended to be mixed with Mycar in the spray tank. Adjuvants such as oil (FC-435), Docagin, Nu-Film 17, and Ortho X-77, appeared to delay conidial germination in the first 1 to 3 hours. This is a very desirable effect because conidia will be germinating on the body of the host instead of in the mixing tank. After the initial inhibition, it is interesting that some adjuvants (oil, Docagin) actually

stimulate conidial germination (McCoy & Couch, 1982). Oil is a particularly good adjuvant because it also serves for the initial knockdown of mites and as a prophylactic spray for greasy spot disease on citrus fruits.

Product tests conducted by Abbott Laboratories in orange groves located in central and south Florida in 1979 and 1980 showed excellent crop protection. It was found that substances formulated with H. thompsonii were able to act as a substrate for mycelial growth and subsequent conidiogenesis by the fungi in the field.

The safety of H. thompsonii to mammals and the honey bee has been investigated. Ignoffo et al. (1973) performed a series of tests, including eye irritation, acute inhalation toxicity, primary skin irritation, acute dermal toxicity, and acute oral toxicity on several vertebrates, using massive doses of mycelia and conidia of the fungus. They could not detect any adverse effect on a single animal. Honey bees, fed with conidia, also showed no effect (Cantwell & Lehnert, 1979). In addition, McCoy et al. (1978) noted that the researchers had handled the fungus for several years with no signs of allergy or toxicity.

H. thompsonii, however, is not compatible with most chemical fungicides and some chemical insecticides. The fungicides benomyl, captafol, captan, daconil, ferbam, maneb, and zineb, in particular, are strongly fungistatic to this entomopathogen at recommended rates (McCoy, 1981).

Another serious pest of citrus, citrus whitefly, was the target of early attempts at biological control with fungi in the United States (Boyce, 1950). For a few years beginning in about 1915, the Florida State Plant Board produced cultures of Aschersonia spp. on sweet potato strips and supplied them to growers at cost. The practice was stopped in the midst of controversy over the effectiveness of artificial dissemination of fungi to control pests. Recently, reports (Smotnik & Izhersky, 1979) indicate that species of Aschersonia are produced on solid or in liquid media and used regularly as sprays against whiteflies in citrus groves in central Asia.

In many parts of the world, particularly the tropics and subtropics, termites (Isoptera) are important insect pests. They damage mainly wooden structures but sometimes also trees and plantation crops (Harris 1969; Hickin 1971; Ko et al. 1982).

The exoskeleton of termites is associated with many species of fungi (Blackwell & Kimbrough, 1979). Except for two Penicillium spp. mentioned in Smythe and Coppel (1966), none of them seems to do any harm to its host (Khan & Kimbrough, 1974; Blackwell & Kimbrough, 1976; Blackwell, 1980).

A few species of fungi are reported to be pathogenic to termites. These include Aspergillus flavus, Beauveria bassiana, Metarhizium anisopliae, Conidiobolus coronatus, and Gliocladium virens (Ko et al., 1982; Kramm et al., 1982; Kramm & West, 1982). The Koppers Company Inc., which specializes in wood products, carried out a number of field tests over a period of 8

years against subterranean termites (Reticulitermes spp.) with pathogen and attractant-toxicant combinations (Lund, 1971). One of the pathogens tested was the fungus A. flavus. Results were not encouraging.

Ko et al. recently (1982) discovered that two fungi, C. coronatus and M. anisopliae, appeared to play a significant role in soils which are pernicious to the subterranean termite, Coptotermes formosanus Shiraki. C. formosanus is an important pest of wood structures and sugarcane in Hawaii. The control potential of the two pathogenic fungi deserves further study.

4. Vectors of human and animal diseases

The use of chemical insecticides, particularly DDT, has revoluntionized the control of disease vectors and brought about a period of unprecedented protection of public health (Brown, 1980) at a high level. For example, malaria, a mosquito-transmitted disease, has been nearly eradicated or reduced to a fraction of its previous prevalence in many parts of the world (Wright et al., 1972). But, after many years of use, malaria appears to be resurgent and it has become increasingly clear that chemicals have their limit of usefulness. Public concerns for environmental protection are mounting; costs are escalating; and under intensive spraying, resistance in vector populations has developed. There is an urgent need for other methods of control. The most likely

alternatives appear to be microbial agents (Davidson, 1981; Roberts & Strand, 1977; Chapman, 1974; Laird, 1971a; 1971b; 1981; Jenkins, 1964).

In the fourth meeting of the Scientific Working Group of the United Nations on Biological Control of Vectors, special attention was given to the use of fungal agents (Anon., 1980b). Although fungi are not currently used in vector control, several species seem to have promise as mosquito larvicides (Federici, 1981; Davidson & Sweeney, 1983). These include Culicinomyces clavosporus Couch, Romney & Rao, Lagenidium giganteum Couch, several species of Coelomomyces, Metarhizium anisopliae, Tolypocladium cylindrosporum Gams, and a Leptolegnia sp.

Culicinomyces clavosporus (Deuteromycetes) was discovered independently in Australia (Sweeney et al., 1973) and in the United States (Couch et al., 1974). Taxonomic comparisons confirmed that the two isolates are of the same species (Sweeney et al., 1982). The fungus is highly pathogenic to Anopheles, Aedes and Culex mosquitoes in laboratory and field trials (Merriam & Axtell, 1982b; Sweeney & Panter, 1977; Sweeney, 1981a; Knight, 1980). Larval mortalities up to 100% within 5 days of fungal exposure have been reported. The concentration of inoculum used in these experiments was 10^5 conidia/ml or 10^{10} conidia/m^2.

Culicinomyces invades mosquito larvae through the gut wall following ingestion of conidia (Couch et al., 1974; Sweeney, 1975a). This mode of infection is particularly effective against

mosquitoes whose larvae are indiscriminate surface feeders (Sweeney et al., 1973). Infected larvae usually die 2-3 days after exposure to conidia (Couch et al., 1974). All instars are equally susceptible (Sweeney, 1981a).

Culicinomyces has a restricted host range which includes mosquitoes, midges, biting midges and black flies (Couch et al., 1974; Sweeney, 1975b; 1979; Knight, 1980). All mosquitoes tested to date have proven to be highly susceptible, whereas midges, biting midges and black flies tended to react rather weakly. Sweeney (1975b) speculated that mosquitoes are probably unusual hosts for the fungus and therefore possess no resistance to it.

Culicinomyces is safe to nontarget aquatic insect larvae, and it has no effect on the mosquito fish, Gambusia, or freshwater shrimps (Knight, 1980; Sweeney, 1975b). Fed daily for 4-6 weeks with conidia of Culicinomyces, laboratory and domestic animals, and two species of wild duck showed no ill effect (Egerton et al., 1978).

Culicinomyces is a facultative parasite and can be cultured on common artificial media. Sweeney (1981a) produced large quantities of conidia for field trials using a liquid medium containing 0.5% peptone and 0.3% beef extract. The culture was incubated at 24-26C with agitation for 4-5 days. The fungus can also be cultured in corn meal extract broth with equal satisfaction (Merriam & Axtell, 1982b). The fungus grew best at 25C and the optimum temperature for larval infection was 27.5C. At 30C, conidia germinated but did not grow further and no

infection of mosquito larvae was observed (Sweeney, 1978a; Knight, 1980).

Culicinomyces was reported to have little tolerance for high salinity (Sweeney, 1978b). Recently, however, Merriam and Axtell (1982b) obtained 100% larval mortality of Aedes taeniorhynchus (Wiedemann) in salt marsh pools with salinity in the range of 10.0-13.7 parts/thousand.

Conidia of Culicinomyces can be stored in distilled water for up to 2 weeks at 4C without loss of infectivity (Merriam & Axtell, 1982b) but they apparently cannot survive for several weeks at 25C (Sweeney, 1981b). Currently, conidia of Culicinomyces are maintained routinely for long periods at -70C or in liquid nitrogen. This is not satisfactory if the fungus is to be developed as a commercial product. Another drawback in developing Culicinomyces for mosquito control is the variable and unpredictable results that have characterized field trials in Australia (Service, 1983).

Lagenidium giganteum (Oomycetes: Lagenidiales) is another facultative parasite of mosquitoes with larvicidal potential. The fungus was first isolated by Couch (1935) who described it as a saprophyte with the capacity to function as a weak parasite of mosquito larvae, copepods and Daphnia. Interest in it as a possible biocontrol agent really began when an isolate discovered by Umphlett and Huang (1970) was found to be highly virulent for some culicines and to have a host range almost exclusively restricted to mosquito larvae (Umphlett & Huang,

1972; Umphlett, 1973; McCray et al., 1973a; 1973b). The fungus was rapidly lethal, usually killing its host within 72h of initial contact (Umphlett & Huang, 1972; McCray et al., 1973a; Domnas et al., 1974).

L. giganteum produces both zoospores (asexual) and oospores (sexual) (Couch & Romney, 1973; Bland et al., 1981). The thick-walled oospores enable the fungus to persist in the environment when unfavourable conditions prevail (Washino, 1981). The motile, biflagellate zoospores are the infective units which, on contact with mosquito larvae, encyst on the cuticle, usually on the head capsule (Domnas et al., 1974). Germ tubes are then sent into the haemocoel where the fungus proliferates. McCray et al. (1973a) found that, with the exception of the late fourth instar, all larval stages were vulnerable to attack.

Cultures of the fungus are routinely maintained on peptone, yeast extract and glucose agar or broth (Domnas et al., 1982). This is inadequate for zoospore production which requires a source of sterols such as soy or hemp seed extract (Domnas et al., 1977). To produce large numbers of zoospores for field applications, the fungus can be grown first in a mixture of peptone, yeast extract and glucose for 4-6 days, and then transferred to a defined nutrient broth called the z medium, containing wheat germ, hempseed extract, yeast extract, and glucose, for another 6 days (Domnas et al., 1982). This method is reported to produce 10-10 zoospores/liter at 25C. An

alternative method was proposed by Goettal et al.(1983) in which they used a simple soy flour medium for both fungal growth and sporulation.

There are a few impediments that may limit the usefulness of L. giganteum as a mosquito larvicide. Field trials conducted in California against Culex tarsalis Coquillet in rice fields and Aedes nigromaculis (Ludlow) in irrigated pastures yielded variable results (Washino et al., 1976; Christensen et al., 1977). The inconsistency in effectiveness is attributable to environmental factors of which water temperature, dissolved salts and organic pollution are the important ones (Fetter-Lasko & Washino, 1977).

L. giganteum is intolerant of low temperatures. Laboratory tests showed that it did not survive beyond 10 days at 10C (Jaronski et al., 1983). Below 18 and above 30C, the fungus produced very few or no infective zoospores (Domnas et al., 1982) although Jaronski et al. (1983) found that once zoospore production had been initiated, exposure to temperature at 35C for as long as 12h did not seem to affect it.

L. giganteum is very sensitive to dissolved salts. Goettal et al. (1983) found that zoospore production of a Fiji isolate was inhibited in 0.4% salt water. Merriam and Axtell (1982a) also showed that both zoosporogenesis and mosquito infection were arrested in two U.S. isolates at 1.5 parts/thousand NaCl; and mycelial growth was reduced at 7.5 parts/thousand NaCl. This puts a severe limitation on the use of the fungus as a mosquito

larvicide because salinities in salt marshes where mosquito larvae are found usually range between 0.6 and 20.2 parts/thousand NaCl (Peterson & Chapman, 1970). Merriam and Axtell (1982b) carried out field tests against salt marsh mosquito, Aedes taeniorhynchus, in pools containing 10.0 parts/thousand NaCl with L. giganteum without success. Glenn and Chapman (1978) reported, however, that over a period of 3 years, the average infection rate of L. giganteum in larval populations of Culex territans Wlk. in a black gum swamp in Louisiana was 61%. It was as high as 87% in 1975 and 93% in 1977. But the salinity of the water was not recorded.

It should be noted also that Domnas et al. (1982) found that NaCl had no effect on zoosporogenesis in their experiment, but that dilute aqueous solutions of magnesium sulfate, magnesium chloride, calcium chloride, manganese chloride, and some buffer solutions were greatly or completely inhibitive to zoospore production.

Another factor that may render L. giganteum ineffective is organic pollution (Jaronski & Axtell, 1982). This is probably the greatest handicap the fungus has as a mosquito larvicide because many species of disease-transmitting mosquitoes flourish on organically polluted water.

It appears that L. giganteum has some serious constraints in its use. But, because of its proven pathogenicity to some important mosquitoes and its ability to persist in the environment, Davidson and Sweeney (1983) suggested that it might

be suited for use in unpolluted mosquito breeding sites subject to cyclical desiccation and flooding. It is also possible that isolates may exist which can tolerate high organic pollution and salt concentrations.

Coelomomyces (Chytridiomycetes: Blastocladiales) is a genus of about 40 species of water molds many of which are virulent, obligate parasites of mosquito larvae. The fungus has a worldwide distribution (Chapman, 1974; Laird et al., 1980; Popelkova, 1982; Shemanchuk, 1959; Umphlett, 1970). A list of some important species with hosts and references is presented in Bland et al. (1981).

The life history of six species of Coelomomyces is known (Federici, 1981). It appears that the genus is characterized by an alternation of generations between an intermediate crustacean host and a definitive larval mosquito host. Inside the mosquito host, the fungus produces sporangia. The sporangia germinate to yield meiospores which are infective only to copepods or ostracods. This explains the difficulty of previous attempts to culture the fungus in the laboratory using only mosquito larvae. Infected copepods or ostracods generate isogametes which fuse to give biflagellate zygotes, the infective stage to which mosquito larvae are susceptible.

Coelomomyces can be cultured in vivo (Federici & Chapman, 1977; Federici, 1980; 1981; Federici et al., 1982). In vitro culture has also been tried (Shapiro & Roberts, 1976; Castillo & Roberts, 1980), but with little success.

Species of Coelomomyces differ widely in host range and preference. C. indicus Iyengar, which infects 18 species of mosquitoes in 3 genera (Couch & Umphlett, 1963), is probably the one with the broadest host range. Infection mechanism and the basis of host specificity are being investigated (Travland, 1979a; 1979b; Zebold et al., 1979; Kerwin, 1983a; 1983b).

Records exist which document the ability of Coelomomyces to infect and kill mosquito larvae (Couch & Umphlett, 1963; Umphlett, 1969; Chapman & Glenn, 1972) and field inoculations have confirmed its potential as a mosquito larvicide (Muspratt, 1963; Laird, 1967; Couch, 1972). However, its usefulness is compromised by the impossibility of culturing the fungus in vitro, and even more importantly, by its need of an intermediate host which is an important food source for young fish. The ecological impact has to be fully assessed before any future field trials are undertaken.

Mosquitoes are not natural hosts of Metarhizium anisopliae (Roberts, 1967). The only case reported by Balaraman et al. (1979) of the fungus parasitizing mosquito larvae in nature is probably a misidentification (Hall & Papierok, 1982). Laboratory tests indicated, however, that the fungus was able to kill larvae of Anopheles, Culex, and Aedes species (Roberts, 1977). Daoust and Roberts (1982) screened 52 isolates of the fungus for pathogenicity and found that larval mortalities ranged from 0-100%. They also demonstrated that they could enhance the virulence of strains E6 and E9 by passing the fungus through

susceptible hosts.

The mode of infection of mosquito larvae by M. anisopliae is not completely understood (Al-Aidroos & Roberts, 1978). It was suggested that floating spores enter the perispiracular valves of the siphon where they germinate and kill the larva by impeding respiration as a result of mycelial proliferation (Roberts, 1970). A recent experiment showed, however, that toxins, not respiration blockage, were the cause of larval death (Al-Aidroos & Roberts, 1978).

Conidia of M. anisopliae are extremely hydrophobic. The method of formulation can greatly increase or decrease the virulence of the pathogen. Daoust et al. (1982) found that the virulence of M. anisopliae was lowered by 64% when they formulated the conidia with corn cob granules, diatomaceous earth, or either of two Kaolinite diluents. In contrast, conidial virulence against larvae of Culex pipiens L. was significantly increased above that of unformulated conidia when the fungus was mixed with Thixcin R, a diluent derived from castor oil. Ramoska et al. (1981) also suggested that fungal preparations must be formulated to match the feeding habits of target populations. They showed that unformulated conidia of M. anisopliae were effective against Anopheles albimanus Wildemann, a surface feeder; and by formulating the conidia with sand, they demonstrated that M. anisopliae could be equally effective against depth feeders such as the larvae of Aedes aegypti L. and Culex quinquefasciatus Say.

M. anisopliae is pathogenic to gyrinid beetles and dragonfly nymphs in the aquatic environment (Roberts, 1974; in Davidson & Sweeney, 1983). This is undesirable if the fungus is to be developed into a mosquito larvicide.

Tolypocladium cylindrosporum (Deuteromycetes: Moniliaceae) is a saprophyte and a facultative parasite of mosquito larvae. The fungus caused mortalities of larvae of Aedes australis Erickson in New Zealand and was also isolated from natural mosquito populations in California and Czechoslovakia (Soares et al., 1979; Weiser & Pillai, 1981). Laboratory experiments showed that infection of larvae was initiated by ingestion of conidia. The fungus required an incubation period of 5 days but most larvae exposed to it died within ten days (Weiser & Pillai, 1981).

T. cylindrosporum grows readily in artificial media, producing conidia on agar and blastospores in submerged culture. Both types of spores are infectious to adult and larval mosquitoes (Davidson & Sweeney, 1983).

A species of Leptolegnia (Oomycetes: Saprolegniales) isolated from an infected larva of Culex quinquefasciatus in South Carolina (McInnis & Zattau, 1982) is the newest addition to the list of fungi with larvicidal potential. The fungus was capable of killing 100% of Aedes aegypti larvae within 24h in laboratory tests. Several other species of culicine and anopheline mosquitoes were susceptible. Above 30C, however, it was found to be inactive. More study is needed to understand its

full potential.

There are many other species of fungi which have been reported to infect mosquitoes (Chapman, 1974; Laird, 1971a; 1971b) but they are generally not considered to be likely candidates for further studies at present.

As vectors of human and animal diseases, black flies (Diptera: Simuliidae) have to be ranked along with mosquitoes as amongst the world's worst. Capable of transmitting many disease organisms, black flies are particularly notorious for Onchocera volvulus Leuckart, the causal agent of onchocerciasis, or river-blindness. Control of black flies has depended mainly on DDT, temephos (Abate), malathion and methoxychlor. Recently, the potential of biological agents was reviewed (Laird, 1978; 1981). It was concluded that fungi on black flies are generally too benign to be effective control agents (Weiser & Undeen, 1981). However, several species are amenable to industrial production and these include Entomophthora culicis Fres., E. curvispora Nowakowski, Coelomycidium simulii Debaisieux, and Metarhizium anisopliae (Nolan, 1981). If only their pathogenicity and predictability could be enhanced, they would be prime candidates for commercial development.

IV. CONTROL OF PLANT DISEASES

Plant disease organisms are subject to parasitism, competition and antibiosis. The use of microorganisms such as bacteria and fungi to control plant diseases is therefore a very attractive idea (Baker & Cook, 1974), but experiments to exploit this method of pest control have not always been successful (Cook, 1981; Boosalis & Mankau, 1965; Snyder *et al.*, 1976; Leggett, 1983). However, there are enough cases in which control was spectacular and unequivocal to indicate that this area of research can be rewarding (Moore & Warren, 1979; Rishbeth, 1975; Aldrich & Baker, 1970; de Trogoff & Ricard, 1976). Several bacterial and fungal species are now in commercial use for control of the following diseases: crown gall on peach and related plants with *Agrobacterium radiobacter* strain 84; carnation stem rot in greenhouses with *Bacillus subtilis* (Ehr.) Cohn; dry bubble disease in mushrooms and silver leaf disease in fruit orchards with *T. viride*, *sensu* Bisby; and butt rot of pine trees with *Peniophora gigantea* (Fr.) Massee (Kommedahl & Windels, 1981; Ricard, 1981; Leggett, 1979; Corke, 1978). Although Baker and Cook (1974) rated fungi behind bacteria as potential antagonists in biological control, it is certain that in some situations, fungal pathogens can be very effective. To use fungi for plant disease control, at least three approaches are recognised: modification of the microenvironment to

stimulate resident mycoflora; introduction of antagonists (Papavizas & Lewis, 1981); and induction of resistance in host plants (Kuc, 1982).

1. Modification of microenvironment

The surfaces of plants provide habitats for epiphytic mycoflora as well as sites of infection for phytopathogens. Epiphytic mycoflora are saprophytic fungi which are commonly found on the surfaces of plants but do not harm the plants. Evidence suggests that these fungi, through competition for space and nutrients, and antagonistic activities such as parasitism and antibiosis, are capable of influencing the growth of phytopathogens and hence, their ability to infect plants (Blakeman & Fokkema, 1982; Baker & Cook, 1974; Papavizas & Lewis, 1981).

a. Aerial plant parts

Fungal antagonism on aerial plant parts has been discussed in several books and review papers (Preece & Dickinson, 1971; Dickinson & Preece, 1976; Fokkema, 1978; Blakeman, 1981; Blakeman & Fokkema, 1982). Most of the work is concerned with the phylloplane--the ecological niche of the leaf surface. The purpose of management is to encourage the activities of saprophytic species to the detriment of the pathogen. Several

critical parameters affecting the growth of microorganisms can be modified. The moisture on the plant surface, for example, can be altered by overhead irrigation. Indeed, Yarwood (1939) reported controlling powdery mildews on plants with water sprays alone. Jarvis and Slingsby (1977) also used water but in combination with a hyperparasitic fungus, Ampelomyces quisqualis Ces., to control powdery mildew on greenhouse cucumbers, caused by Sphaerotheca fuliginea (Schl.) Pollacei.

Another environmental parameter that can be changed is the availability of nutrients. The addition of nutrients to aerial plant parts for disease control is controversial because many unspecialized pathogens, such as Botrytis and Fusarium, require some exogenous nutrients for successful infection of host plants (Clark & Lorbeer, 1977; Fokkema, 1981). This is generally not true for the specialized pathogens like Colletotrichum, which tend to be inhibited by the presence of moderate quantities of exogenous nutrients (Blakeman & Parbery, 1977).

One of the best known examples of disease control with nutrient application is the spraying of urea onto apple trees before leaf fall to control Venturia inaequalis (Cke.) Wint., the causal organism of apple scab. The treatment is effective in preventing subsequent perithecial formation (Baker & Cook, 1974). Urea was also used in an attempt by Neely (1981) to control anthracnose of black walnut, caused by Gnomonia leptostyla (Fr.). Foliar sprays were found to be ineffective but soil treatments with urea, ammonium nitrate or ammonium sulfate

resulted in enhanced resistance of treated trees to the disease.

In order to make good use of foliar anatagonists for disease control, studies were made to elucidate their enviromental requirements (Bashi & Fokkema, 1977). It was found that nutrient deficiency is probably one of the main causes limiting the development of antagonistic yeasts on non-senescing leaves. By adding nutrients (2% sucrose + 1% yeast extract) to wheat leaves, Bashi and Fokkema demonstrated that a resident yeast species, Sporobolomyces roseus Kluyver & Van Niel, increased significantly in a few days and became antagonistic to the cereal rot pathogen, Cochliobolus sativus (Ito & Kuribayashi) Drechsler ex Dastur (=Helminthosporium sativum = Bipolaris sorokiniana). The growth of the pathogen was reduced, probably by competition for nutrients.

Taphrina deformans (Berk) Tul., causal agent of leaf curl, is present on the bark of peach trees as resident yeastlike cells. As part of the saprophytic flora, it is subject to antagonism. Baker and Cook (1974) suggested that this disease organism could be controlled by the application of selective nutrients or a combination of selective nutrients and antibiotics. The approach should be equally applicable against other plant pathogens with a resident, epiphytic phase in their life cycle.

The addition of pesticides represents another way in which the environment can be modified to favour one segment of the microflora over the rest. Sometimes, in our ignorance, pathogens

are promoted resulting in iatrogenic diseases (Griffiths, 1981). A specific example is the spraying of benomyl (Fokkema *et al.*, 1975) on rye leaves which resulted in a 60% increase in infection by *C. sativus* when compared with controls sprayed with water. Andrews and Kenerley (1978) also found evidence "that existing apple pesticide programs impede biological control" in that the chemicals suppressed resident saprophytes and reduced their antagonistic capacity. Control of plant diseases might be more effective if pesticides were screened to ensure that they do not harm resident antagonists.

b. Subterranean plant parts

The subterranean environment is more amenable to management than the phylloplane. Cultural practices such as clean tillage and crop rotations are sigificant ways of reducing pathogenic inocula. In effect, propagules of pathogens are subjected to prolonged antagonism from resident microflora while being denied parasitism on susceptible hosts. Continued monoculture, however, is not always detrimental to crops. For example, take-all, caused by *Gaeumannomyces graminis* var. *tritici*, has been shown to decline in severity when plots were sown continuously to wheat or barley. Evidence suggests, however, that bacterial rather than fungal antagonists are responsible for the decline (Baker & Cook, 1974).

Microorganisms are intensely competitive in the soil environment. A dynamic equilibrium normally prevails. Adding nutrients to the soil increase the activity of the microorganisms, resulting in a shift of the equilibrium hopefully detrimental to plant pathogens. Examples of the successful use of organic and inorganic amendments to control soilborne pathogens are numerous (Baker & Cook, 1974; Cook, 1977; Papavizas & Lumsden, 1980), but the role of fungal antagonists in disease control is often not clear. Generally, it is believed that nutrients may cause propagules to germinate (Lockwood, 1977). Endolysis follows in the absence of a susceptible host. Nutrients may also increase soil fungistasis, and hence the dormancy of some propagules. Digestion of soil microorganisms by mycoparasites may also be enhanced (Baker & Cook, 1974).

Culturing plants in containers presents a situation in which the soil environment is largely under control. Soilborne diseases in potted media can be eliminated by sterilization of the culture media or proper use of fungicides. Recently, it has been discovered that these physical and chemical treatments are unnecessary if composted tree bark is incorporated in the container media (Hoitink, 1980). Either pine bark or hardwood bark can be used although hardwood bark appears to be superior (Spencer & Benson, 1982; Chef et al., 1983). Plant diseases that can be controlled by tree bark compost include Fusarium wilt (Chef et al., 1983), Phytophthora root rots (Hoitink et al.,

1977; Sivasithamparam, 1981; Spencer & Benson, 1982), and Rhizoctonia damping-off (Stephens et al., 1981; Nelson & Hoitink, 1982; 1983). The level of control is satisfactory. In one experiment, disease supression was equivalent to that obtained by treating the soil with aerated steam and then drenching it twice with 60 g/hectoliter of Dexon 35% WP or 30 g/hectoliter of Terraclor 75% WP (Hoitink, 1980). In Japan, Sekiguchi (in Hoitink, 1980) incorporated 30 tons of pine bark/ha into field soil to control Fusarium wilt of Chinese yam. Results were similar to those obtained with methyl bromide fumigation.

The mechanisms of the suppression have been investigated (Hoitink, 1980; Nelson & Hoitink, 1983). It appears that the suppression is probably biological in origin because heating for 5 days at 60C negates the suppressive effect (Chef et al., 1983) but it can be reestablished by introducing 10^7 colony-forming units (CFU) of Trichoderma/g of container medium (Nelson & Hoitink, 1983). Trichoderma species are hyperparasitic fungi known to be antagonistic to Rhizoctonia, Pythium, and Sclerotium spp. (Chet et al., 1981; Elad et al., 1980).

Suppressive and conducive soils have been known for a long time (Baker & Cook, 1974; Toussoun, 1975). The mechanisms involved are complex (Papavizas & Lumsden, 1980) but the evidence is strong that there is a biological component involving soil antagonists (Broadbent & Baker, 1975; Lin & Cook, 1979; Liu & Baker, 1980; Sher & Baker, 1980; Baker, 1982).

Various ways of exploiting this phenomenon have been proposed including the seeding of conducive soil with a small amount of suppressive soil (Baker & Cook, 1974; Baker, 1980), and the use of organic amendments (Cook, 1977).

It is also possible to enhance antagonists with sublethal chemical and physical treatments which reduce but do not eradicate microorganisms from the soil (Papavizas & Lewis, 1981; Rodriguez-Kabana & Curl, 1980). A good example was the control of Armillaria mellea Vahl ex Fr. by treating citrus orchard soils with carbon disulfide. Bliss (1951) postulated that the pathogen was controlled not by direct toxicity of the chemical but by the quick proliferation and antagonism of Trichoderma spp.

Another practice aimed at modifying the microenvironment and thus changing the microflora in our favour was suggested by Leach (1939). He advocated the removal of a strip of bark around the stem of an infected tree some time before felling. By so doing, the carbohydrate reserves in the roots would be reduced, permitting rapid colonization by saprophytic fungi and restricting the growth of pathogens.

2. Introduction of fungal pathogens

Theoretically, it has been argued that "the population is a reflection of the habitat" (Garrett, 1956) and that any introduction of organisms without change of the habitat must be

a transient one. But the habitat is heterogeneous and ecological refuges do exist. Hosts often escape parasitism or predation because of the inadequate searching or dispersal ability of the antagonists. This phenomenon exists in the vertebrate and insect worlds, and there is no reason why it should not also exist in the microbial world. Indeed, it has been proven practical in certain situations to control plant diseases with direct, purposeful introductions of fungal antagonists.

a. Dutch elm disease

This disease, caused by Ceratocystis ulmi (Buisman) C. Moreau, is responsible for the death of millions of much valued ornamental elms in North America and Europe. Control by chemical treatments or the removal of diseased trees is unsatisfactory. In Britain, a fungal preparation made up of Trichoderma viride and a Scytalidium sp. was used to inject thousands of elms to combat the disease in 1981. The treatment, costing about US$6.5/tree, is expected to give protection for at least ten years (Anon., 1982).

b. Silver leaf of fruit trees

Caused by Chondrostereum (Stereum) purpureum (Pers. ex Fr.) Pouz., silver leaf is mainly a problem of temperate zone fruit

trees such as apples, pears, peaches and plums. Diseased trees are weakened, show silvering of the leaves and are often killed. Studies at the Long Ashton Research Station of the University of Bristol, Great Britain, indicated that the disease can be controlled biologically with T. viride (Corke, 1980). Experiments in Italy (D'Ercole & Lugaresi, 1981) also showed that four years after treatment with T. viride, at least 90% of previously infected peach trees were nearly free of the disease.

T. viride is now registered in Great Britain and is obtainable commercially in the form of pellets from Stokes Bomford (Chemical) Ltd. Quality control is conducted with routine tests for viable spore counts and for bacterial and fungal contaminants (Ricard, 1981). The pellets are implanted into diseased trees for therapeutic treatments (Corke, 1980). Because C. purpureum usually invades trees through pruning wounds, an effective way to protect the trees is by using specially designed pruning shears which introduce the antagonist while the branches are being cut (Grosclaude et al., 1973). It has been observed that the chance of successful control with antagonists is much enhanced if the antagonists gain possession of the substrate before the arrival of the disease causing organisms (Baker & Cook, 1974).

T. viride is a species aggregate with great differences amongst isolates. The strains selected for the control of silver leaf do not produce antibiotics although some others do (Corke, 1978). No restriction is placed on the sale of fruit from

treated trees (Corke, 1980).

c. Dry bubble disease of mushrooms

Verticillium malthousei Ware, the causal agent of dry bubble disease, is very destructive to cultivated mushrooms. The disease can be controlled by Trichoderma viride (de Trogoff & Ricard, 1976). The mycoparasite gives excellent results when applied to casing soils at the rate of 10^8 propagules/litre/m^2.

T. viride is easily cultured on artificial media. Commercial production is on solid substrates using cracked barley kernels. The infective spores can be stored for up to 2 years (Corke & Rishbeth, 1981). A wettable powder formulation is sold in France under the trade name BINAB T SEPPIC (Papavizas & Lewis, 1981). The price and field efficacy of the fungus are comparable to those of benomyl (de Trogoff & Ricard, 1976; Leggett, 1979).

d. Butt rot of pines

This disease, also known as heart rot, is the first practical example of biological control of a plant disease with introductions of a fungal antagonist. Heterobasidion annosum (Fr.) Bref. (=Fomes annosus), the disease organism, and Peniophora gigantea, the antagonist, are natural competitors in

the colonization of freshly cut stumps of pine trees. The use of the antagonist began in 1962 and the British Forestry Commission found it effective enough to extend its usage to all suitable pine forests under its jurisdiction (Webb, 1973).

P. gigantea produces both sexual (basidiospores) and asexual (oidia) spores. Oidia are used as inoculum and are mass-produced on malt-agar plates. Stored in a sucrose solution, these spores can be kept for up to 3 months at temperatures below 20C (Greig, 1976a). Ecological Laboratories Ltd. in Great Britain is producing the fungus and is selling it in sachets each containing a minimum of 5×10^6 viable oidia (Greig, 1976a). For stump inoculation, the contents of each satchet are mixed with 5 liters of water and 5 grams of dye and poured onto freshly cut surfaces, brushed to cover the whole area. A more innovative way to apply the inoculum is to mix oidia with chainsaw motor oil so that stumps are inoculated while being cut. The method has been investigated but more work is necessary before it becomes practical (Artman, 1972; Greig, 1976b).

Control of butt rot is better with P. gigantea than with fungicides because P. gigantea is one of the wood-rotting basiodiomyces and it hastens the decay of the stump (Kommedahl & Windels, 1981). In sites with very severe infestations, the antagonist may fail and stump removal is recommended (Greig, 1976a).

e. Diseases of row and field crops

Several mycoparasites are being studied as potential controls of plant diseases in row and field crops. Coniothyrium minitans Campbell is one of these. The fungus apparently is an obligate parasite of the sclerotia of many Sclerotinia spp., Botrytis spp., and Sclerotium cepivorum Berk. (Turner & Tribe, 1976). It has a wide geographical distribution and it has been isolated in 9 countries over 3 continents (Ayers & Adams, 1981). The fungus degrades sclerotia with the aid of lytic enzymes (Jones et al., 1974).

C. minitans is a primary parasite of Sclerotinia sclerotiorum (Lib.) de Bary (=Whetzelinia sclerotiorum), a causal agent of rots and wilts of sunflower (Huang, 1980) and nearly all vegetables (Jones & Watson, 1969). Huang (1977) studied the parasitism of sclerotia by the fungal antagonist and concluded that under natural conditions in Manitoba, control provided by C. minitans was inadequate but massive introductions of the control agent may be beneficial. In greenhouse and field plot trials over a period of 3 years, Huang (1980) showed that it was possible to increase seed yield of sunflower by 100 kg/ha. To obtain that result, he incorporated inoculum into field soil at 225g/m of row, 8cm wide and 5cm deep.

S. sclerotiorum causes white mold of beans and lettuce drop. In Australia, chemical control of the diseases was found

to be unsatisfactory (Merriman et al., 1979) and biological control with C. minitans was investigated (Trutmann et al., 1980). Results of field experiments indicated that soil treatments with the antagonist were effective in reducing the survival structures of the phytopathogen to negligible levels (Trutmann et al., 1980) but aerial applications to protect bean plants from white mold failed (Trutmann et al., 1982). They believed that antifungal inhibitors on the leaf surface were responsible for the reduced effectiveness of C. minitans on the phylloplane.

Sclerotinia trifoliorum Erickson, the causal agent of clover rot, is also susceptible to C. minitans. In pot experiments at the Cambridge University Farm, Tribe (1957) discovered that a cornmeal-sand culture of C. minitans, well-mixed with soil, killed 85-99% of the sclerotia of S. trifoliorum within 11 weeks. The artificial inoculum also persisted in the soil for up to 14 months with little reduction in virulence. In field trials, Turner and Tribe (1975) reported 88-98% infection with 37-65% of the sclerotia completely destroyed.

Another plant disease that has been studied with the intention of control, using C. minitans as the control agent, is the white rot disease of onions (Ahmed & Tribe, 1977; Leggett, 1983). In glasshouse experiments, Ahmed and Tribe compared biological control with chemical treatment using calomel; they concluded that C. minitans was the superior agent. Leggett,

using a different strain of C. minitans, performed her experiment in the field. Her results were disappointing although antagonism was confirmed in dual culture tests.

C. minitans can be cultured readily on milled rice (Ahmed & Tribe, 1977), rye, barley and sunflower seeds (Leggett, 1983), cornmeal and sand mixture (Tribe, 1957) or bran (Ahmed & Tribe, 1977). The pycnidiospore is believed to be the infective unit but Turner and Tribe (1976) found that a pycnidial dust, consisting of relatively large conglomerates of spores protected within whole or broken pycnidia, was effective in controlling plant disease but not pycnidiospores applied with an atomizer to the soil. No explanations were given for the difference.

C. minitans is not pathogenic to plants. Turner and Tribe (1976) tested the mycoparasite against 17 species of plants, most of which are hosts to Sclerotinia spp., Botrytis spp., and Sclerotium cepivorum. None showed any symptoms of infection.

Sporidesmium sclerotivorum is another obligate mycoparasite of fungal sclerotia. Isolated and identified in 1978 by Uecker, Ayers and Adams, the fungus has since been tested in laboratory and field experiments and found to be effective against lettuce drop (Ayers & Adams, 1979a; 1979b; 1981; Adams & Ayers, 1982). With artificial introductions, Ayers and Adams (1979a) obtained more than 95% infection and destruction of sclerotia of Sclerotinia minor in 10 weeks or less at 25C. They also reported (1982) that a single application of the mycoparasite at 10^2-10^3 macroconidia/g of soil achieved 40-83% reduction in disease

incidence in 4 successive crops of lettuce over 2 years. In 1981, the use of S. sclerotivorum for biological control was patented in the United States (Adams & Ayers, 1982).

Besides Sclerotinia minor which is its chief host, Sporidesmium sclerotivorum also attacks Sclerotinia trifoliorum, Sclerotinia sclerotiorum, Sclerotium cepivorum and Botrytis cinerea (Ayers & Adams, 1981). Coniothyrium and Sporidesmium share some common hosts. But unlike Coniothyrium which invades both sclerotia and hyphae of susceptible species, Sporidesmium has been observed to infect only sclerotia (Ayers & Adams, 1979a).

The activity and infectivity of Sporidesmium are sensitive to environmental factors (Ayers & Adams, 1979b; Adams & Ayers, 1980). The fungus is active in soils with a temperature range of 10-30C and a pH range of 5-8, but it is most infectious to sclerotia at 20-25C, pH 5.5-7.5 and a soil water potential of -8 bars or higher.

Sporidesmium can be cultured on nonsterile moist quartz sand containing live sclerotia of Sclerotinia minor (Adams & Ayers, 1980). Incubated at room temperature (20-25C) for 6-12 weeks, the culture can produce approximately 10^5 macroconidia/g of sand and sclerotia mixture. The pH range of the culture medium is critical and must be maintained between 4.0 and 5.5 for maximum growth (Ayers & Adams, 1981). Trials have been made to grow the mycoparasite on artificial media. It appears that the fungus needs mineral salts, glucose or mannitol as a source

of carbon, and hydrolyzed casein as a source of nitrogen. Thiamine and biotin are also required (Ayers & Adams, 1981).

The infective propagules of Sporidesmium can survive in the soil for up to 15 months (Ayers & Adams, 1979b). They are induced to germinate by the presence of susceptible hosts. After being established, the fungus can spread through the soil by hyphal extensions. These hyphal extensions often produce abundant conidia which serve as secondary inoculum (Ayers & Adams, 1979a). Laboratory observations (Ayers & Adams, 1983) showed that conidia of Sporidesmium increased almost 100-fold in 12 weeks in soils containing sclerotia of Sclerotinia minor. This ability to increase with time in response to the presence of a host is a very desirable feature in a pest control agent.

Rots and damping-off are serious diseases of many cultivated plants. These diseases are often caused by Rhizoctonia solani Kuehn, Sclerotium rolfsii Sacc. or Pythium spp., which can sometimes be effectively controlled by introductions of Trichoderma (Wells et al., 1872; Liu & Vaughan, 1965; Backman & Rodriguez-Kabana, 1975; Henis et al., 1978; Elad et al., 1980; 1981; Hadar et al., 1979; Harman et al., 1980; Lewis & Papavizas, 1980).

Species of Trichoderma are not well-defined. The revision by Rifai (1969) is the most recent taxonomic work on the genus. Several aggregates of species are recognized. Of these, T. harzianum Rifai and T. hamatum (Bon.) Bain, seem to receive the most attention as potential biocontrol agents for rots and

damping-off.

Isolates of T. harzianum differ greatly in host specificity. For example, isolate 1970-3A (Wells et al., 1972) was highly pathogenic to Sclerotium rolfsii, Sclerotinia trifoliorum and Botrytis cinerea, but was innocuous to R. solani, Pythium aphanidermatum (Edson) Fitz. and P. myriotylum Drechs. Another isolate (Hadar et al., 1979) attacked only R. solani and P. aphanidermatum but not Sclerotium rolfsii, Fusarium oxysporum f. sp. lycopersici Sacc. Snyd. & Hans. or Sclerotinia sclerotiorum. Yet another isolate (Elad et al. 1980) was equally pathogenic to both Sclerotium rolfsii and R. solani. It is possible that the three isolates are separate species with very similar morphological characteristics.

T. harzianum has been shown by a modification of Koch's postulates, to be the cause of suppression of R. solani in soil (Liu & Baker, 1980). Suppression in soil can sometimes be induced by monoculture or by artificial introduction of the causal agent to a conducive soil. In the case of artificial introduction, an adequate food base for the causal agent can be an important factor in determining the success of disease control. Wells et al. (1972) grew T. harzianum on a mixture of ground ryegrass seeds and soil. Applying the culture with an equal amount of fresh food base 3 times, 10 days apart, they obtained 99.5% healthy plants as opposed to 21.9% in the control. The method was rather cumbersome because a rate of 4200kg/ha of the mixture was required. A more convenient way was

developed by Backman and Rodriguez-Kabana (1975) who impregnated diatomaceous earth granules with 10% molasses. Kelly (1976) also used nutrient-enriched clay granules as a medium for growth and as a carrier for delivery of T. harzianum. But in his attempt to control damping-off of pine seedlings caused by Phytophthora cinnamomi Rands, the preparation actually increased the severity of the disease instead of reducing it. He reasoned that the leakage of nutrient from the granules probably provided an added food source for the plant pathogen.

Wheat bran is another food base that has been used for T. harzianum. Henis et al. (1978) found that in sterilized sandy loam infested with R. solani, a preparation of T. harzianum in wheat bran culture protected radish seedlings from damping-off better than chemical treatments with pentachloronitrobenzene (PCNB). Similar preparations were used with success against diseases in beans, cotton, tomatoes and carnation, caused by Sclerotium rolfsii or R. solani (Elad et al., 1980; 1981; Hadar et al., 1979).

Dressing seeds with an antagonist before planting, is theoretically, more efficient than applying the antagonist to the soil. In seed treatment, the antagonist gains possession of the infection court before the pathogen appears on the scene. This is a distinct advantage to the antagonist in its fight against plant pahogens (Baker & Cook, 1974). Also, in seed treatment, the immediate purpose is to protect the plant from disease organisms. This is different from soil treatment which

aims at reducing pathogen inoculum in the soil.

The method of treating seeds with an antagonist was used with some success by Liu and Vaughan (1965) against preemergence damping-off in table beets. They coated beet seeds with spores of T. viride or Penicillium frequentans Westling before planting. The treatment was effective in protecting seeds and young seedlings but not old seedlings from attack by Pythium ultimum Trow or P. debaryanum Hess.

Harman et al. (1980) used the same approach to protect radish and peas from Pythium spp. and R. solani. The seeds were treated with conidia of Trichoderma hamatum in a Methocel slurry. Methocel is a sticker and spreader. At 3-8 X 10^8 conidia/ml, the treatment protected seeds of radish and peas against preemergence damping-off as effectively as treatments with captan, PCNB, or fenaminosulf. Methocel alone or T. harzianum did not protect seeds against Pythium.

T. hamatum also appears to be effective as a soil treatment. Chet and Baker (1981) added T. hamatum to conducive soil and the soil became suppressive to R. solani, Sclerotium rolfsii and Pythium spp. Lewis and Papavizas (1980) also discovered that T. hamatum (isolate WT-6) can be used effectively in integrated management of cucumber fruit rot with other control methods. Cucumber fruit rot is caused by R. solani.

Trichoderma, Sporidesmium, and Coniothyrium are the most promising mycoparasites at the present stage of knowledge and

development. Other fungal antagonists that have been studied as potential biocontrol agents in row and field crops include: Chaetomium globosum Kze. (Tveit & Moore, 1954; Chang & Kommedahl, 1968; Mew & Kommedahl, 1972; Kommedahl & Mew, 1975); Gliocladium roseum Bain (Moody & Gindrat, 1977); G. catenulatum Gilman & Abbott (Huang, 1978; 1980); Penicillium oxalicum Currie & Thom (Kommedahl & Windels, 1978); P. nigricans (Bain) Thom (Ghaffar, 1969); Corticium sp. (Hoch & Abawi, 1979; Lewis & Papavizas, 1980; Odvody et al., 1980); and Phialophora radicicola Cain var. radicicola, sensu Deacon (Wong & Southwell, 1980). C. globosum is also seen as a possible control agent for apple scab caused by Venturia inaequalis (Heye & Andrews, 1983; Andrews et al., 1983).

f. Other diseases of plant and wood

Eutypa armeniacae Hansf. & Carter is a vascular pathogen which causes gummosis or dieback of apricot trees. It enters trees through pruning wounds. Fusarium lateritium Nees is a strong antagonist of the pathogen (Carter & Price, 1974). F. lateritium has an incubation period of about 7 days but it is 10 times more tolerant of benomyl than E. armeniacae. Carter and Price (1975) found that protection of apricot trees could best be provided by the use of a sublethal dose of benomyl in combination with the antagonist.

Douglas-fir utility poles are often attacked by a decay fungus, Poria carbonica Overh. A Scytalidium sp. isolated by Ricard and Bollen (1968) is highly antagonistic to P. carbonica (Ricard et al., 1969). Although it would be a significant improvement over the toxic chemicals used to preserve utility poles at the present time (Leggett, 1979), no widespread use of the fungus is anticipated.

3. Induction of hypovirulence or host resistance

Breeding plants for resistance, the use of chemical pesticides, and the practice of various cultural methods are the traditional ways of protecting plants against disease. We have reviewed the use and attempted use of antagonists either by deliberate introduction or by modification of the microenvironment to encourage the antagonistic activity of resident microflora against pathogenic organisms. To protect desirable plants, we can also make pathogens less virulent or we can induce systemic resistance in host plants by limited infections with fungi.

The recognition of different isolates or strains is important in the study of fungi. Previously, we have been concerned with seeking the most virulent strains because they would do the most damage to target pest populations. When the fungus is a disease-causing organism of desirable plants, hypovirulent or avirulent strains are preferred. It has been

demonstrated that a virulent strain can sometimes be rendered less virulent by hyphal anastomosis with a hypovirulent strain (Anagnostakis & Jaynes, 1973; Van Alfen et al., 1975; Day et al., 1977; Elliston, 1979; Elliston et al., 1979).

Endothia parasitica (Murr.) Anderson is an introduced fungus that causes blight in American chestnut, Castanea dentata Borkh. Because it is a ravaging disease, mature stands of the American chestnut were virtually wiped out during the last century. The disease organism has many strains. Virulent (V) strains kill trees. Hypovirulent (H) strains, however, are unable to produce large lesions and the trees survive. Hypovirulence is caused by a cytoplasmic determinant that is transmissible by hyphal anastomosis (Van Alfen et al., 1975). Introduction of H strains into canker tissue of the host leads to formation of callus and healing of lesions formed by V strains (Anagnostakis & Jaynes, 1973). Although not yet proven, there is strong evidence that the cytoplasmic determinant is a piece of double-stranded RNA (Day et al., 1977; Elliston, 1979). Double-stranded RNA had been found in all H strains but not in V strains. It is transmissible by hyphal anastomosis.

The ability of H strains to reduce the size of cankers and thus to save the chestnut tree was first discovered in Europe. But attempts to use the European H strains against the American V strains failed (Anagnostakis & Jaynes, 1973). It was found that the strains were vegetatively incompatible. No anastomoses were formed and therefore there was no reduction in virulence

(Elliston, 1979). A search in the United States recently turned up several H strains in Michigan and Tennessee (Elliston et al., 1979). The problem of incompatibility is resolved by inoculating cankers with a mixture of H strains that includes several compatibility groups (Elliston, 1979).

Induced host resistance in plants is an intriguing idea because of its practical implications in disease management. The phenomenon has been widely reported (Matta, 1971; Kuc, 1981; 1982). It has been demonstrated against take-all of wheat (Deacon, 1973; 1974; 1976; Wong, 1975; 1980; 1983; Wong & Southwell, 1980), against Gaeumannomyces (Ophiobolus) in bentgrass turf (Gould et al., 1961; Wong & Siviour, 1979), against anthracnose in bean (Rahe et al., 1969b), against blue mold in tobacco (Cohen & Kuc, 1981), and against a range of fungal, viral, and bacterial diseases in cucurbits (Kuc, 1982). The phenomenon was evident in both greenhouse and field experiments (Caruso & Kuc, 1977a; 1977b). Effective inducing agents include viruses, bacteria, and fungi (Bergstrom et al., 1982) but most experiments so far have been conducted with fungi using nonpathogens (Rahe et al., 1969b; Yarwood, 1956; Elliston et al., 1976), or cultivar nonpathogenic races of pathogens (Rahe et al., 1969b; Elliston et al., 1971), or heat-killed pathogens (Bell & Presley, 1969; Sequeira & Hill, 1974), or the pathogens themselves (Kuc et al., 1975; Kuc & Richmond, 1977; Hammerschmidt et al., 1976; Staub & Kuc, 1980; Guedes et al., 1980). Induction experiments are performed by preinoculating

plants with an inducing agent, which is followed in a few weeks by the challenge inoculation. Resistance is expressed by the reduced number and size of lesions and increased survival rates. It has been found almost without exception that inoculated plants respond to infections more quickly and in greater magnitude than noninoculated plants, but the infection does not become systemic and remains localized. Kuc (1982) argued that all plants possess genetic potential for resistance to most diseases and that the key to resistance is the speed and magnitude with which this potential is expressed when the plants are challenged.

There is a fair understanding of the immune response of animals and the knowlege is used very effectively against some serious diseases. Our understanding of the immune response in plants, however, is still rudimentary. We know that plants do not produce antibodies but that they produce phytoalexins and lignin. Evidence suggests that these nonspecific chemicals may play a role in host defence (Cruickshank, 1963; Cruickshank & Perrin, 1963; Rahe et al., 1969a; Elliston et al., 1977; Kuc, 1972; 1981; 1982; Hammerschmidt et al., 1982; Vance et al., 1980; Henderson & Friend, 1979; Pearce & Ride, 1978; 1980; Ride, 1980).

Phytoalexins are fungitoxic substances such as pisatin and phaseollin which accumulate in damaged or hypersensitive plant tissue in response to an infection or mechanical injury. The phtoalexin theory was proposed by Muller (1961, in Cruickshank,

1963) to explain the mechanism of disease resistance in plants.

Rahe et al. (1969b) reasoned that if phytoalexins could be induced in plants with nonpathogens or cultivar-nonpathogenic races of pathogens, then the plants would be protected against subsequent infections by pathogens intolerant of the levels of phytoalexins encountered. They succeeded in demonstrating induced resistance in bean (Phaseolus vulgaris L.) to bean anthracnose caused by Colletotrichum lindemuthianum (Sacc. & Magn.) Scribner but they concluded that "phaseollin and the other phenolic substances associated with visible cell collapse are not the primary sources of protection" because subsequent protection was uniformly high irrespective of phaseollin levels. After numerous studies, it is still uncertain how important phytoalexins are in host plant resistance (Rahe, 1973; Fraile et al., 1982). It appears that some fungal pathogens are capable of metabolizing phytoalexins and that an inducible enzyme system is probably involved (Heuvel & Glazener, 1975; VanEtten & Stein, 1978; Fraile et al., 1982).

Kuc (1981) observed that disease resistance in plants probably involves multiple mechanisms. There is strong evidence that lignification is one of these (Vance et al., 1980; Ride, 1980; Pearce & Ride, 1978; 1980; Henderson & Friend, 1979; Kuc, 1982). Ride (1978) suggested that lignification might function in the following ways to protect plants from pathogens: by increasing the mechanical resistance of plant cell walls; by reducing the susceptibility of cell walls to degradation through

extracellular enzymes; by restricting the diffusion of enzymes and toxins from the pathogen to plant cells, and of nutrients and water from plant cells to the pathogen; by inhibiting growth of the pathogen through the action of toxic lignin precursors; and by lignification of the pathogen. Evidence of how lignification can function as a mechanism for inducing systemic resistance in cucumber plants was presented by Hammerschmidt, Nuckles and Kuc (1982).

Most recent studies on induction of resistance involve the use of pathogens to control subsequent infections by the same organisms. If such an approach is to be successful, the host plant has to survive the induction inoculation. That plants can survive the initial inoculation has been repeatedly demonstrated by Kuc and his colleagues. They also showed that the yield of cucumbers was not reduced by the inoculation. But the danger of inadvertantly causing disease is ever present. It can be anticipated that the idea of preinoculation with a pathogen to control damage by the same pathogen is bound to come up against grower resistance.

The evidence is strong that immunization in plants is triggered by chemical inducers (Jenns & Kuc, 1979; 1980; Caruso & Kuc, 1979; Kuc & Richmond, 1977). Efforts are being made to isolate and identify the inducers (Iwata et al., 1982; Kuc, 1982). If successful, the inducers can be used as sprays or dipping solutions to activate the immune system in plants much as is the case of immunizing shots in animals.

V. CONTROL OF NEMATODES

It is estimated that nematodes, sometimes called nemas or eelworms, cause yearly damage of $4.5 billions to crops in the United States (Maggenti, 1981). Control of nematodes is mainly by soil fumigation with toxic chemicals. This is very costly and in many crops, the profit margin is simply not high enough to cover the cost of repeated treatments. Added to the problem is the withdrawal from the market of effective and hitherto widely used chemical nematicides, such as dibromochloropropane (DBCP), because of health hazards associated with their production or use (Kerry 1981). Alternative or supplementary methods of control are available and these include quarantine, sterilizing soils with heat, crop rotation, flooding, fallow, planting trap crops, planting companion crops (e.g. Tagetes spp.), sanitation, breeding plants for resistance, and using biological control agents (Jenkins & Taylor, 1967). Of the various biological control agents, many workers believe that "fungal parasites and fungal predators of nematodes are potentially the most useful" (Webster, 1972) against plant-parasitic nematodes.

Predatory nematode-destroying fungi capture their prey with traps. These are either adhesive structures or mechanical rings which may be constricting or non-constricting (Barron, 1977). These fungi are not host-specific and will catch rotifers and free-living nematodes, as well as plant-parasitic nematodes.

Furthermore, they do not rely on trapping prey as their chief source of food (Stirling et al., 1979). Indeed, they do not always produce traps (Webster, 1972). Trap morphogenesis is triggered by a substance conveniently called nemin (Pramer & Kuyama, 1963). The identity of nemin is still unclear. Several studies (Balan & Lechevalier, 1972; Nordbring-Hertz, 1968; 1973; 1977; Nordbring-Hertz & Brinck, 1974) demonstrated that trap formation can be induced by nematodes, nematode extracts, animal sera, certain peptides, other soil organisms, or suitable environmental conditions. It is further indicated (Cooke, 1968) that a readily available carbon source is critical for the fungi to engage in predacious activity. Theoretically, the energy source can be supplied easily with organic amendments. But attempts to enhance trapping activity by adding organic matter to soils have not been very successful. Cooke (1968) showed that the effects of organic amendments were short-lived and that trapping activity sometimes declined even when nematode populations in the soil were increasing.

To exploit predacious fungi for biological control, another approach is to introduce them into soils where none existed before. This approach was studied seriously in France by Cayrol and coworkers (in Tribe, 1980; Mankau, 1980a) and their work of 15 years resulted recently in the trial use of two isolates of Arthrobotrys to control mycophagous nematodes in mushrooms and root-knot nematodes in tomatoes. Arthrobotrys spp. are easily cultured on a rye medium. To control root-knot nematodes in

tomato fields, the fungus, together with the culture medium, is incorporated into the soil at the rate of 140g/m^2 one month before planting. Protection of crops has been reported as satisfactory. A separate isolate of Arthrobotrys is used in mushroom culture. The predatory fungus protects mushrooms and is capable of increasing yields by more than 20%.

Parasitic nematode-destroying fungi exist in the soil as spores. The spores adhere to passing nematodes, then germinate, grow, and destroy the hosts. Several of these fungi have received considerable attention recently. These include: Nematophthora gynophila Kerry & Crump; Verticillium chlamydosporium Goddard; and Dactylella oviparasitica Stirling & Mankau.

N. gynophila attacks many species of cyst-nematodes including: the cereal cyst-nematode, Heterodera avenae Woll. (Kerry, 1974; Kerry & Crump, 1980); the soybean cyst-nematode, H. glycines Ichinohe (Crump et al., 1983); the sugar beet cyst-nematode, H. schachtii Schmidt; and four other species (Kerry & Crump, 1977). The potato cyst-nematode, Globodera (Heterodera) rostochiensis Woll., however, is not a host (Kerry & Crump, 1977). The fungus is specific on the females, killing them before they can form cysts. Field samples showed that about 50% of the nematodes were parasitized and destroyed. This is probably an under-estimation because infected nematodes disintegrate, which makes it difficult to extract them from the soil (Crump & Kerry, 1977).

N. gynophila is diplanetic. This ability to encyst and later give rise to secondary zoospores extends the period during which the host can be infected (Kerry, 1980). Infected nematodes are killed in less than 7 days at 13C (Kerry, 1981). Each infected female can give rise to more than 24,000 zoospores and 3,000 resting spores (Kerry, 1980). But the natural dispersal of the fungus in the soil is limited. To ensure adequate protection of crops, mass introductions of the fungus in the field may sometimes be necessary. This is not possible at present because the fungus has not been successfully cultured on artificial media (Kerry & Crump, 1980).

V. chlamydosporium is a parasite of nematode eggs (Tribe, 1977; Kerry & Crump, 1977; Kerry *et al.*, 1980). Together with *N. gynophila* and *Catenaria auxiliaris* (Kuhn) Tribe, *V. chlamydosporium* is considered to be chiefly responsible for the effective, long-term control of the cereal cyst-nematode in England (Kerry, 1980).

V. chlamydosporium has a wide geographical distribution: it has been isolated from nematode cysts in England, Holland, Germany, Belgium, Poland, Italy, Sweden, and Czechoslovakia (Tribe, 1977). Isolates of the fungus with different characteristics exist (Bursnall & Tribe, 1974). One isolate tested by Willcox and Tribe (1974) was only weakly pathogenic to nematode eggs. The fungus can be grown on cornmeal agar (CMA) or potato-dextrose agar (PDA).

D. oviparasitica is another parasite of nematode eggs. The fungus was first isolated in 1978 by Stirling and Mankau from root-knot nematode (*Meloidogyne* sp.) egg masses in California. Although they put the fungus in the genus *Dactylella*, which contains many predacious species, *D. oviparasitica* has not been observed to form traps.

Experiments (Stirling *et al.*, 1979) showed that *D. oviparasitica* is very effective against *Meloidogyne incognita* (Kofoid & White) Chitwood on peach roots but is not as effective against the nematode on the roots of tomato or grape. Peach is not an optimum host of *M. incognita*. The nematode produces on the average 300-400 eggs on peach roots instead of the 1000-1500 eggs it is capable of producing on the roots of tomato or grape. On peach, infection rate of eggs reached 96% but it was only 57% on tomato or grape (Stirling *et al.*, 1979). Infection and mortality of eggs is also affected by temperature (Stirling, 1979).

D. oviparasitica is easily cultured on artificial media (Stirling & Mankau, 1978). It appears to be an excellent candidate for further development as a biological control agent for root-knot nematodes. The search for a highly virulent isolate is urged (Mankau, 1980a).

Fungal control of nematodes is still in the experimental stage. No fungi have yet been found that can compete with chemical nematicides. The few species mentioned in this paper are the more promising ones amongst the many that have been

studied (Barron, 1977; Tribe, 1977; 1980; Mankau, 1980a; 1980b; Kerry, 1980; 1981).

VI. CONTROL OF PLANT PESTS WITH MYCORRHIZAL FUNGI

Mycorrhizae are structures formed on feeder roots by symbiotic fungi (Cooke, 1977). Found in most plants (Trappe, 1977), these structures are significant in improving nutrient and water uptake, particularly in semiarid soils low in phosphorus (Gerdemann, 1968; Mosse, 1973; Safir et al., 1971; Ruehle & Marx, 1979; Krikun & Levy, 1980). They have also been reported to lower the incidence and severity of plant diseases (Zak, 1964).

Mycorrhizal fungi and plant pathogens compete for the same host and it is not surprising that they can profoundly affect one another's survival and growth. Zak (1964) postulated that these fungi inhibit pathogens : by using surplus carbohydrates on root surfaces, thus denying pathogens a food base to initiate their parasitic attack; by serving as a mechanical barrier to infection; by secreting antibiotics; and by supporting a population of microorganisms antagonistic to pathogens in the rhizosphere. Marx (1973) noted that the host plant may also react to mycorrhizal fungi by producing nonspecific inhibitors.

Mycorrhizae are taxonomically separated into ectomycorrhizae and endomycorrhizae on a morphological basis. An intermediate group, the ectendomycorrhizae, are often collected under ectomycorrhizae (Marks & Kozlowski, 1973).

Ectomycorrhizae are common in forest trees such as pine, hemlock, spruce, fir, oak, birch, eucalytus, willow, and poplar (Ruehle & Marx, 1979). The distinguishing features of ectomycorrhizae are the fungus mantle on the surface of roots and the Hartig net in the root cortex. Both structures are said to contribute to host defence against disease organisms.

Some ectomycorrhizal fungi have been successfully cultured on artificial media. One species, Pisolithus tinctorius (Per.) Coker & Couch, has been prepared commercially by Abbott Laboratories, North Chicago, Illinois (Schenck, 1981). This preparation can form ectomycorrhizae on several species of pine, oak, spruce, Douglas fir, and hemlock (Ruehle & Marx, 1979). Being able to suppress Phytophthora cinnamomi (Schenck, 1981), this mycorrhizal fungus should enhance survival and growth of seedlings in nurseries.

Endomycorrhizae occur more frequently in plants than ectomycorrhizae. They are especially important in orchard and agricultural crops (Sanders et al., 1975). The predominant group amongst the endomycorrhizae are the vesicular-arbuscular (=VA) mycorrhizae. Ruehle and Marx (1979) reported that in phosphorus-deficient soils, VA mycorrhizae have the potential to increase plant growth by several hundred-fold. Recent research efforts indicate that these fungi may be also potentially useful as biocontrol agents (Hussey & Roncadori, 1982; Schenck, 1981; Dehne, 1982).

The phytopathogenic fungus, Thielaviopsis basicola (Berk. & Br.) Ferraris, causes black root rot in tobacco and in cotton. Baltruschat and Schonbeck (1972) showed that the pathogen was inhibited by a VA mycorrhizal fungus on tobacco roots. On cotton, damage caused by T. basicola was the same on mycorrhizal and nonmycorrhizal roots (Schonbeck & Dehne, 1977), but mycorrhizal seedlings grew better.

Davis and Menge (1980) tested the effectiveness of mycorrhizal fungi to control Phytophthora root rot in citrus seedlings. They noted that in soils with a low phosphorus content, VA mycorrhizae enhanced the performance of sweet orange, Citrus sinensis (L.) Osbeck. However, they suggested that the enhanced tolerance was due to improved nutrition as a result of mycorrhizal formation and not because of any induced resistance in the host.

Plant-parasitic nematodes are also affected by mycorrhizae. Kellam and Schenck (1980) showed that the root-knot nematode, Meloidognye incognita was inhibited by Glomus macrocarpus var. macrocarpus on Pickett soybeans. Sometimes, mycorrhizal roots may support a higher population of nematodes than do nonmycorrhizal roots with no apparent increase in damage (Roncadori & Hussey, 1977). It is also possible that both the nematode and the fungus are adversely affected by the interaction (Fox & Spasoff, 1972).

It must be pointed out that the effects of mycorrhizae are not always beneficial. In fact, according to the list made by

Dehne (1982), there are 28 papers which indicate that mycorrhizal plants suffered less disease damage than nonmycorrhizal plants; but there are also 7 papers which indicate that the opposite was the case. Schenck et al. (1975) noted that interactions between plant-parasitic nematodes and VA mycorrhizae depend on the level of inoculum, on the species of the fungus involved, and on the susceptibility of the plant cultivar to infection.

Control of plant diseases and nematodes with mycorrhizal fungi is controversial. But, in view of the high costs of fertilizers and chemical pesticides, it is imperative that alternatives are made available to growers. The manipulation of mycorrhizae, should it be realized, would particularly benefit developing countries with large areas of marginal lands which are poor in nutrients.

VII. CONCLUSIONS

Fungi are increasingly being recognized as viable pest controls. This is so, not only because of the recent advancements in the study of these agents, but also because of the need for alternatives, resulting from real and perceived deficiencies of chemical pesticides.

The greatest potential use of fungal pathogens is in the form of mycopesticides. The application technology is easily transferrable from chemical pesticides. Repeated, massive introductions of fungal agents have made it feasible to develop some fungal pathogens for commercial use. This inundative approach is also most effective because it compensates for the inefficient, natural spread of many fungal pathogens in pest populations. With this strategy, fungal epiphytotics or epizootics can now be induced earlier than they occur in nature, thus reducing the possibility of economic damage to crops.

The development of a fungal product undergoes many stages which include : 1. detection, isolation, and identification of the fungal agent; 2. laboratory experiments to determine its virulence, host range, safety, culturability, and its compatibility with other control agents; 3. field experiments to evaluate its field efficacy; 4. market research to evaluate financial feasibility; 5. development of formulation and storage techniques; 6. development of quality control procedures; 7.

mass productions; and 8. marketing. To share the financial risks with private companies in developing fungi as pest controls, governments and universities can assist by doing primary research in stages 1, 2, and possibly 3.

For fungal products to be competitive with chemical pesticides, they must have good quality control. This should include : a viable spore count; a test for the level and the nature of contaminants; and an index of virulence. To assign an index of virulence would probably require the development of a bioassay for each fungal product. And for the index of virulence to be meaningful, the target pests, plus the environmental conditions under which the fungal agent is to be applied, must be specified.

The present use of fungi as pest controls is rather limited. Many problems are waiting to be solved. However, it is anticipated that increased use of these control agents will be made, particularly as a component of integrated pest management systems.

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