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Pathogens for the Control of Weeds [and Discussion]

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Pathogens for the control of weeds

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The potential of pathogens for controlling plant populations has often been underestimated because of the subtle nature of their effects and the fact that only the final population equilibrium is observed. The potential exists for restoring such equilibria by classical biological control where they have become imbalanced, or for manipulating the host–pathogen system by the use of mycoherbicides, i.e. increasing the inoculum load. The use of exotic pathogens in classical control is often limited by considerations of sufficient host specificity for introduction into a new environment, whereas use of mycoherbicides is limited by the need to develop commercially viable systems of production, storage and application. Both approaches are subject to legislative restraints, classical control because of the inherent aim of establishing a new, freely dispersing organism throughout a region and mycoherbicides because they are subject to registration and patenting requirements. Neither the presence of a more variable genome in outbreeding plant species nor the high degree of specialization of obligate parasites are seen as significant restraints in re-establishing population equilibria in new environments. Sufficient effectiveness and safety have now been demonstrated in enough programmes to overcome initial hesitancy and considerable increase in activity in this field can be observed.

Introduction

Potato late blight, Dutch elm disease, chestnut blight and coffee rust are classic examples of the potential of plant pathogens to cause devastating diseases, yet the ability of pathogens in general to kill large numbers of plants and keep populations in check on a permanent basis is not always readily apparent or accepted. The above cases are examples of reintroductions on to hosts long separated in new areas or on to new hosts, and there is a tendency to consider them as rather exceptional. More commonly, pathogens are regularly observed on a plant or crop species, occasionally building up to significant levels, and most often in the artificial situation of crop monocultures which favour both pathogen increase and selection of new, more virulent strains. Fruit or seed production may be seriously affected, but the impression is seldom given of disease causing significant mortality of established plants.

This brief account will suggest that this impression is deceptive and it will try to demonstrate the potential and degree of progress achieved in the practical use of pathogens for weed control. At present only fungal pathogens and nematodes have been seriously considered, with the vast majority of the work concentrated on the fungi.

PRINCIPLES

The host–pathogen equilibrium

Natural systems represent the equilibrium phase of a population interaction between host and parasite, which may shift a little one way or the other according to the environment, the season or perhaps a genetic change in its components. The role of the pathogen may only be seen if it is removed or if for some other reason the plant population increases to a high level and an epidemic is initiated, which brings the population back down again. Crop plant populations are maintained at artificially high levels and are prone to such epidemics unless artificial preventive measures are taken. The relative roles of pathogens in natural and disturbed or agricultural situations has been well reviewed by Burdon & Shattock (1980), who point out the difficulties of observing the controlling effects of pathogens on plant populations, but produce considerable evidence as to the generality of their occurrence. Even when pathogens do cause important mortality, their effects can be cryptic and often only manifested when acting in combination with other stresses. The effect of flower and fruit loss, for example *Senecio vulgaris* infected by *Erysiphe fischeri* (Ben-Kalio & Clarke 1979), is not clear until the dynamics of seed production in the species is known. The effect of a foliar disease may be to reduce root growth or otherwise affect water uptake (Ayres & Paul 1986), which may not be very apparent until perhaps the plant is stressed, e.g. by a dry summer, whereupon it wilts and dies. A reduced vertical growth or leaf surface area, e.g. when *Dichanthium annulatum* is infected by *Sphacelotheca annulata* (Mall & Tugnawat 1973), may not seem very important until the plant is in competition with another species and succumbs because of reduced efficiency.

Thus it is not easy to appreciate the true role a pathogen plays in the population dynamics of a plant species. The best evidence often comes from disturbing the ecological equilibrium and some of the classic cases cited above are good examples of this. One of the best known examples of biological control is exactly similar in that the population density of form A of the European species *Chondrilla juncea*, introduced into Australia in the absence of its specific pathogens, increased to a level much higher than normal. The deliberate introduction of a strain of the rust *Puccinia chondrillina* in 1971 from Europe caused an epidemic (Cullen *et al.* 1973; Hasan 1974*a*), which has gradually reduced the density to approximately one hundredth of its previous value (Cullen 1988) i.e. the normal level in Europe (Wapshere 1971; Wapshere *et al.* 1974). Further, its effect is now not so obvious, and casual observers and some farmers have begun to doubt how it could be effective. These cases should not be thought of as exceptional reactions of host and pathogen, but rather as results of extreme disturbance of what is itself a normal course of events.

The potential for control

Given that actual or potential controlling effects of pathogens are not uncommon, it is their recognition and translation into effective action for the control of plants, when these are considered to be weeds, that is the challenge. Clearly, if presented with a plant system without the pathogen(s) normally associated with it, the opportunity exists to introduce the pathogen(s) to restore the appropriate equilibrium, with a reduced plant population as the expected result. Alternatively, if the pathogen is already present, or is introduced, but the resulting equilibrium still gives a higher plant population than desired, there is the possibility of displacing the equilibrium to the detriment of the plant e.g. by increasing the inoculum of the pathogen. These alternatives correspond to the two main forms of biological control of weeds: the classical approach, that of introducing exotic organisms, pathogens in this case, and the bioherbicide approach, involving treatment of the plants with artificially high levels of an organism, a mycoherbicide in the case of fungal pathogens.

The two approaches are obviously complementary, but involve different emphases and different sorts of problems. The classical approach is principally concerned with controlling exotic weeds, by finding the pathogens associated with them, or their close relatives, in their country of origin, or elsewhere, and importing them into the country where the weed is a problem so as to recreate a natural balance, both numerically and genetically. The bulk of the research is concerned with finding the pathogens, evaluating them for effectiveness and safety for introduction (a matter of specificity), establishing them and evaluating their effect. The mycoherbicide approach again involves finding a suitable pathogen, but often has endemic weeds as targets and therefore often uses indigenous pathogens. The problems associated with introducing an exotic organism are therefore rare, but production, storage and application problems are considerable. The two major requirements for any pathogen to be used in biological control are the same as for any prophylactic measure. It must be safe and effective, i.e. it damages or kills the weed without presenting any risk to other plant species. Problems arise when it is deficient in either of these requirements or when the demonstration of an adequate level in either proves difficult or impossible. In general, it is obligatory to demonstrate safety, i.e. specificity, before contemplating introduction or mass release, and it is highly desirable, from the point of view of research investment, if effectiveness is also demonstrated at an early stage.

Classical biological control

A pathogen normally associated with a weed species, and presumably reasonably frequently if it is to be of any promise, should not be too difficult to find if the correct regions are searched. In this, one is guided by a knowledge of the history of the distribution of the weed host. The original area of occurrence of a species, i.e. its evolutionary centre, is logically the area where the greatest variety of organisms will be found that are sufficiently specialized on the weed (Goeden 1971; Harris & Piper 1970; Wapshere 1974). However, if the plant has been present in other areas for a sufficiently long period, it is possible that there has been adaptation and evolution of other pathogen species or strains not present at the origin. Room (1981) has considered this point, but concluded that generally, the native range offers the best prospects. However, this author also admitted the possibility of effectiveness eventually declining with increasing evolutionary time, a possibility considered primarily by Pimentel (1961) in relation to biological control and considered again recently in detail by Hokkanen & Pimentel (1984) and Hokkanen (1985). These authors suggest that the area of origin may not be the best prospect and that new host–parasite associations have in fact been twice as effective in biological control of weeds. The example of chestnut blight, where the pathogen was introduced to a new, through closely related, host, would support this argument, but as pointed out by Moran *et al.* (1986), the data put forward by Hokkanen & Pimentel (1984) in support of their argument are considerably biased by one programme and although the basic principle should not be rejected, searching for new associations is not generally accepted as a guideline for practical programmes. The significance of the concept of co-evolution to a point of homeostasis is considered again later.

In practice, highly co-evolved and specialized pathogens, e.g. obligate parasites, have been damaging agents. A strain of *Phragmidium violaceum* has been extremely effective against at least one form of *Rubus fruticosus* in Chile (Oehrens & Gonzales 1974). In a similar situation, the use of *P. chondrillina* against *C. juncea* has shown the need for strains of the pathogen extremely specialized for their host. *C. juncea* is an apomict and exists as several distinct genetic clones or forms. Strains of *P. chondrillina* have specialized to the extent that one form will only be attacked by certain strains of *P. chondrillina* (Hasan 1972). To have any effect, a very high level of specialization and co-evolution is necessary. It is not known yet whether strain IT 32, which has been so virulent against form A of the weed did evolve with this form in Europe or whether, perhaps, it co-evolved with a closely related form and would thus constitute a 'new association' (*sensu* Hokkanen 1985), albeit at an extremely specialized level. Recent evidence does suggest that form A of *C. juncea* is very close or identical to the form occurring in the European locality where strain IT 32 was obtained (P. Chaboudez, personal communication).

In terms of Room's (1981) concept of a peak in effectiveness of an agent at some intermediate point in evolutionary time, present experience suggests that this peak is well towards the later end of the evolutionary time scale.

Leaving aside the above issues, judging the effectiveness of a pathogen is often more important and difficult than simply finding a promising species. Assessments of effectiveness in terms of infection type in the laboratory are often used, but they do not always translate to effectiveness under field conditions, as witnessed by the discrepancy between the number of species regarded as promising on the basis of laboratory data and the number of eventually successful effective species. Searching for biological control agents in those regions of the original range of pathogens that are ecologically and climatically similar to the regions where the weed is a problem and examining their effectiveness in the field (Hasan & Wapshere 1973), has given extra insight into the eventual field effectiveness following introduction (Cullen & Groves 1977).

The major problem for classical biological control using pathogens is that of demonstrating satisfactory specificity before introducing a new exotic pathogen. At times it seems that such a radical change from the philosophy of protection against pathogens has been too difficult to accept, and occasionally there have been problems in finding a course of experimentation and approval that might allow a proposal to be considered. Concerns have been expressed about the stability of specificity, and the interpretation and extrapolation of test results, while the complexity of life cycles and ignorance of mechanisms of specificity and their genetic bases have tended to foster a climate of extreme caution. However, guidelines for testing and introduction have now been in use in Australia and the U.S.A. for several years (Charudattan 1982). Watson (1985) has comprehensively reviewed current procedures and problems. In general, the emphasis is on defining the host range as carefully as possible, with extensive testing of species closely related to the host, examination and interpretation of degrees of susceptible and resistant reactions and consideration of alternate hosts and different spore types. Efforts are essentially limited to those groups of fungi with records of well-developed and stable host specificity, including many obligate pathogens. Many potentially useful species are currently not seriously considered because of a lack of knowledge of the mechanisms of host specificity. Biological control is making significant contributions to the level of knowledge in this area (Clement & Watson 1985; Hasan 1974*b*; Mortensen 1985; Politis *et al.* 1984; Watson 1985; Watson & Alkhoury 1981).

A final concern about classical biological control, which is not unique to the use of pathogens, is related to the inherent aim of establishing a new self-perpetuating organism, capable of causing damage throughout the distribution of a weed species. Serious conflicts of interest can arise if the weed is considered desirable in some situations. Cullen & Delfosse (1985) have recently described a classic example of such a case and the legislation it has given rise to in order to resolve such disputes.

MYCOHERBICIDES

The development of mycoherbicides is the current growth area in the biological control of weeds. With the current increased sensitivity to the effects of chemicals in the environment, the realization that plant resistance to herbicides is already a problem and likely to increase, and the demonstration that successful, commercially viable products can be developed, several major agricultural chemical companies are now investing considerable resources in this development.

The importance of specificity for a mycoherbicide, particularly when developed from an indigenous pathogen, is different from that for an exotic pathogen imported for classical biological control. The pathogen already exists in the environment and would not be considered if it were already known to cause a disease of any crop in the area. However, the amount of inoculum is enormously increased and is applied in the manner of a chemical product. Registration is necessary and, although sufficient specificity still needs to be demonstrated with regard to species likely to be exposed to infection, assurance is also necessary that the large quantity present will not be harmful in any way to other forms of life (Charudattan 1982). However, the fact that the distribution of the pathogen at artificially high densities is under the control of man, allows a little more flexibility than when using an exotic species intended to spread and establish itself in areas where it was unknown before. Thus, it is possible to use particular host specific strains of a pathogen, the host range of which at the species level could be quite broad (Hasan 1987), or pathogens with a relatively broad range, which will not come into contact with susceptible hosts under the conditions of intended use (Watson 1985). The use of mycoherbicides is also less likely to run into the problems of conflict of interest.

The problems of developing mycoherbicides are essentially related to having an effective, marketable product. To some extent, problems of insufficient virulence or sporulation or both of the pathogen for example, can be overcome by increasing the inoculum. However, commercial mass production, maintenance of viability in storage and environmental requirements for infection, can pose severe problems. These are essentially technical and economic, but demand sophisticated research on the biology and epidemiology of the pathogen concerned, and considerable cooperation between the research scientist and industry (Templeton *et al.* 1980).

The commercial and economic nature of the development of mycoherbicides also poses legislative problems, though of a different nature from those in classical biological control. Related to the development of registration requirements for formulation of mycoherbicides is the right of patent of a commercial product, although it is based on a naturally occurring organism. Patents for formulations related to techniques of storage and application already exist for two products, and are justifiable and necessary to encourage commercial development.

Patenting of organisms as such has not been generally recognized as acceptable or possible, but novel uses for them have been patented, at least in the U.S.A., where patenting of novel forms of microorganisms has also been ruled permissible (Templeton *et al.* 1980). It seems that patenting of specially developed strains will certainly occur, but the definition of 'novel' or 'specially developed' is not yet clear for mycoherbicides. To what extent a change in genetic structure from the wild type has to be deliberately induced as against selected, is not yet well defined. The question of secrecy becomes important when considering commercial development in this field, and the state of research on any weed–pathogen interaction may only be known when public knowledge of it is commercially acceptable. Given the assurances of Templeton *et al.* (1980) that patenting can proceed without undue delay in the dissemination of information, it is to be hoped that the publication and availability of mycoherbicide research and application will be encouraged by commercial interest rather than hindered in any way.

Resistance, variability and coevolution

Variation in susceptibility to a pathogen or to a particular strain is normal. Apart from the potential for the selection of resistant populations, the presence of a mixture of susceptible and non-susceptible host forms may hinder the development of disease in the population (Burdon & Chilvers 1976, 1977). Burdon & Marshall (1981) took this point further to suggest that outcrossing plant species, which thus possess a more variable genome, would be less suitable targets for biological control by pathogens or insects, and demonstrated the existence of a positive correlation between inbreeding and level of success of classical biological control programmes. This suggestion has not been generally accepted by entomologists, who find most insect agents slightly less finely tuned to their hosts and more capable of coping with a broader range of genetic variation within the host. It might be considered more applicable to pathogens. It does not however, take into account the evolutionary potential of the agent, and pathogens in particular, turn over their generations several times faster than the plant. The equilibrium between the host and pathogen in the original environment may be complex, as suggested by Harlan (1976), involving differing susceptibilities on the part of the plant to different strains of a pathogen and the presence of more than one strain of the pathogen, but there is no reason why a similar balance should not be obtained in the new environment, i.e. the equilibrium is both ecological and genetic, and the basic principle of classical biological control should still operate. If not, one would expect to see far more native outbreeding species escaping any control by pathogens and becoming important new weeds. From a practical point of view, in at least one important project, it is the variation between forms of an apomict, *C. juncea*, that is causing more problems, the extremely specialized strains of the pathogen associated with these 'stable' forms also showing considerable stability and requiring considerable searching.

Thus the tendency is to suppose that the evolution of resistant populations will not be a major problem in classical control, particularly if efforts are made to broaden the genetic base of the pathogen population when imported, e.g. by using a selection of several strains of *Phragmidium violacaeum* for control of *Rubus fruticosus* (Bruzzese & Hasan 1986). However, in the case of mycoherbicides, the operative strain is that produced and applied by man and, if unchanged, will exert considerable directed selection pressure on the weed to favour the production of one or more resistant forms. Commercial use of mycoherbicides will therefore have to consider the use of mixtures of strains or be prepared to change strains as required. In fact many of the pathogen–host interactions, which from a practical point of view are likely to be used in mycoherbicide programmes, i.e. non-obligate pathogens, seem to involve variable pathogen populations that can produce a range of new virulence types. They should thus be able to overcome the variation in resistance of the host population rapidly, and where this is characterized by partial resistance genes, the increased inoculum load would also help overcome this potential problem (J. J. Burdon & R. H. Groves, personal communication). Obligate pathogens, showing perhaps less variation, are in any case, unlikely to be used in mycoherbicide programmes, at least at present, because of the difficulties of mass production.

Reference has already been made to the possibility of decreased virulence of a pathogen in a highly co-evolved host–pathogen relation and the consequences this could have for the sources and choice of biological control agents. Although the recommendation of Hokkanen & Pimentel (1984) that priority should be given to seeking new parasite–host associations is not accepted, the potential inherent in the suggestion probably merits further attention. However, this line of reasoning has been taken further, to the extent of suggesting that the use of obligate pathogens in any form of biological control is unlikely to be successful. Harper (1977) has described such pathogens as 'trapped in the co-evolutionary rut of host specialization and cause little damage to the host', and objections were raised to the utility of introducing *P. chondrillina* for control of *C. juncea* on these grounds. Co-evolution to favour decreased virulence might be possible in some circumstances, e.g. where group selection does not need to be invoked, but the relation between host and pathogen populations is still a dynamic equilibrium. An increase in density of the host will produce a numerical response by the pathogen such as to increase its rate of infection and therefore the damage inflicted. This is one of the basic conditions for starting an epidemic and is readily observed in monocultures. Although the level of the population equilibrium may be influenced by the history of co-evolution of the system, control is still being exerted by the pathogen. If that host population density at equilibrium is acceptable as a level of control in a new environment, where the host plant has increased to a much higher density in the absence of its obligate, co-evolved pathogen, there is every possibility that biological control would be successful. The effectiveness of introducing *P. chondrillina* into Australia should not be seen as exceptional but to be expected. Such an outcome has been achieved several times in insect parasite systems.

Current status

It is appropriate to summarize what has been achieved in practical terms before considering, finally, the current direction of development and prospects.

Classical programmes

The introduction of *P. chondrillina* has already been cited as an illustration of several points raised in this discussion. The outstanding success of the introduction of strain IT32 against form A of *C. juncea* has been adequately reported and quantified, and the significance of the status of the other two forms has been described (Cullen 1978, 1985). The successful introduction of *P. violacaeum* to Chile has also been reported (Oehrens & Gonzales 1974), and the introduction of *Cercosporella* sp. into Hawaii has been successful in controlling *Ageratina riparia* (Trujillo 1985). Currently, there are programmes in various stages of development on *Uromyces heliotropii* for control of *Heliotropium europaeum* (Hasan 1985), *Puccinia jaceae* for *Centaurea diffusa* and *Puccinia carduorum* for *Carduus nutans*.

Mycoherbicides

Two products are currently registered for commercial use, in the U.S.A.: *Colletotrichum gloeosporioides* f. sp. *aeschynomene* for control of *Aeschynomene virginica*, and *Phytophthora palmivora* for control of *Morrenia odorata* (TeBeest & Templeton 1985). A third pathogen, *Cercospora rodmanii*, is also a candidate for use and is likely to be registered soon for the control of *Eichornia crassipes* (Charudattan 1986). In addition, Hasan (1987) reports 35 other projects in both areas currently in course of investigation.

POTENTIAL AND PROSPECTS

Apart from a steady increase in the number of pathogens put into practical use and a refining of techniques, particularly in the commercial production of mycoherbicides, what else can be expected?

A field that has been slow to develop has been integrated control or weed management, where biological control techniques are integrated with other systems, including use of chemicals, to produce the level of control desired. There is a relatively long history of development in this field for insect control, but for weeds it is still in its infancy. Although of interest, the reasons are not relevant here, being mainly historical. The fact is that integrated control is long overdue for development and its basic requirements are at last beginning to be realized by biological control workers, weed scientists and by the agrochemical industry. The interaction between herbicide effects and pathogens seems a fertile area for research. It has been found for instance, that the destructive action of the fungus *Cochliobolus lunatus* on *Echinochloa crus-galli*, normally quite limited, is increased considerably when used with 10% of the normal dose of a chemical herbicide (Scheepens & van Zon 1982).

Weed management implies the ability to manage the whole weed environment, i.e. the local agroecosystem and therefore a knowledge of the ecology of the weed, the ecology of the biological control agents, the interaction of these and the weed with the agricultural system, and the level of control desired. The necessary ecological knowledge has often been lacking in weed control programmes, but quantitative, population-orientated approaches are becoming more common so that management of weed populations incorporating the use of pathogens and other methods now seems to be an achievable aim.

Finally, it is virtually certain that the expanding field of biotechnology and genetic engineering will be called on to improve the pathogens. Induction and screening of mutants for finding more virulent strains of pathogens is routine procedure in plant breeding for resistance and studies on the genetics of host–pathogen relations (McIntosh & Watson 1982; Simons 1979) but as yet untried in any serious manner in the use of pathogens for weed control. For insect control, it is now possible to use transformation techniques to construct new strains of entomopathogens without the need for sexual reproduction (Faull 1986). For weed pathogens, the identification of key features for improvement by genetic engineering is still difficult except possibly for resistance to fungicides that can be incorporated into integrated crop protection schemes. A comprehensive knowledge of the genetics of resistance–virulence will be necessary.

There is currently no shortage of projects or interest, and an impression that the potential is enormous. Despite some acceleration in the pace of technical development with increasing investment from private industry, progress towards effective control will continue to be slow and steady, because of the time involved in host specificity testing and, in the case of mycoherbicides, the development of economic production and storage techniques. The potential will therefore only be slowly realized, but there is every confidence that pathogens will become a commonplace component of weed management systems.

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Discussion

W. D. Hamilton, F.R.S. (*Department of Zoology, University of Oxford, U.K.*). Dr Hasan indicated that his main examples of weeds controlled by fungi, skeleton weed and *Rubus*, were apomicts. Although conceding the evidence of apomixis most of the time, I have always found it surprising that plants claimed to be long-established apomicts still have large showy flowers and are still very attractive to insects. I have wondered whether occasional successful crosses may not be quite important to them, and indeed the very success of his control programme might suggest why it should be important from their point of view as hosts. I wanted to ask whether his work threw any light on how completely apomicitic your plants are. For example, did any unexpected and resistant strains appear that might be the result of sexual recombination?

S. Hasan. *Chondrilla juncea* was accidentally introduced into Australia towards 1910 and, since then, it has gradually spread in the southeastern parts, infesting mainly the cereal crops. Studies on the reproduction of the weed have shown that it is an apomicitic triploid ($3n = 15$) and there is no exchange of genetic material in seed formation. Later on, it was demonstrated that in Australia, *C. juncea* occurs in three distinct morphological forms (narrow-, intermediate- and broad-leaved). These three clones have been further confirmed by the modern techniques of electrophoresis.

A strain of the rust fungus *Puccinia chondrillina* was found to be aggressive against the most common narrow leaf form and was released in the field in Australia in 1971. Shortly after the rust became well established and widespread, progressively reducing populations of the weed. The pathogen has continued its destructive action and skeleton weed is no longer a problem. However, during the past 15 years the introduced strain of the rust has attacked only the narrow-leaf form whereas the intermediate and broad leaf forms have remained unaffected and have been increasing in some places. More strains of the rust virulent to these other forms are being discovered in Europe and studies on the efficacy as biological control agents are currently underway.

These results show again how distinct and stable are the three skeleton weed clones. Also, so far, there is no evidence of change in the pathogenicity of the rust or of the presence of other forms of the weed in Australia. However, Burdon *et al.* (1980) have raised doubts about obligate apomyxis in the three Australian forms and suggest the possible formation of new variants through occasional sexual recombination, autosegregation and or random mutation. Thus, studies are currently underway, using electrophoretic techniques, on clonal variation in skeleton weed in Europe and Australia and on the possible existence of a genetic pool close to the weed's centre of distribution giving rise to new forms.

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A. E. Akingbohungbe (*Department of Plant Science, University of Ife, Nigeria*). (1) I noted that some well-established crop pathogens such as *Phytophthora palmivora* have been mentioned as part of D. Hasan's agents released in control programmes. What steps are taken to ensure that these do not re-establish on other crops?

(2) Is there any possibility of utilizing toxins of known plant pathogens for herbicide formulations?

S. Hasan. (1) The particular isolate of *P. palmivora* from milkweed vine (*Morrenia odorata*) was tested for specificity against 58 plant species from 12 families. A few plants other than milkweed vine were found to be infected, but only with a very high dose of the fungus. Although *P. palmivora* was pathogenic to several citrus rootstocks in pre-emergence tests, no pathogenicity of the isolate from milkweed vine could be demonstrated in the field. Also, isolates from roots of citrus trees treated with *P. palmivora* in the field did not reveal infection by this pathogen.

(2) It may be possible to use host-selective toxins produced by plant pathogens in biological control of weeds. However, their action will be short term, limited to each application, whereas mycoherbicide formulations based on mycelia or spores of pathogens may continue to infect the host, and thus have a prolonged effect in the field.

J. W. Deacon (*Department of Microbiology, Edinburgh University, U.K.*). Are there any programmes to investigate the potential use of mycoherbicides against parasitic higher plants such as *Striga* and *Orobanche* spp.?

S. Hasan. Attempts are being made to control parasitic weeds with plant pathogens. Thus, among fungal pathogens of *Orobanche* spp. (broomrape), *Fusarium oxysporum* var. *orthoceras* destroys 70% of the seed. It has been formulated for field use in the U.S.S.R. as 'Product F', which remains effective for 80 d, and has been applied to infested water melon and tobacco with encouraging results. Also in the U.S.S.R., *Alternaria cuscutacidae* is reported to have been successfully used against dodder (*Cuscuta* spp.).

Considerable interest has been shown in the use of plant pathogens for biological control of dwarf mistletoe, *Arceuthobium* spp. in the U.S.A. Among several pathogens, the anthracnose fungus *Glomerella cingulata* has been shown to be most effective.

There has not yet been any practical application of biological control to witchweeds (*Striga* spp.).