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Humicola fuscoatra infects tomato roots, but is not pathogenic *

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Abstract

In 1993, a serious epidemic of a tomato root disease resembling corky root rot occurred in commercial greenhouses throughout Canada. *Pyrenochaeta lycopersici* could not be isolated from diseased roots, but *Humicola fuscoatra* was commonly isolated. The objectives of our work were to determine if *H. fuscoatra* is able to infect roots of tomato and cause corky root rot symptoms. *Humicola fuscoatra* was found to infect the roots of tomato seedlings and older plants. We concluded that *H. fuscoatra* is not a pathogen of tomato, however, because infection of tomato roots with the fungus did not necessarily lead to development of corky root rot or any other disease symptoms. Populations of *H. fuscoatra* increased greatly in sterile water or sterile nutrient solution, which would help to explain why commercial greenhouse growers can find this fungus in recirculating nutrient solutions.

Introduction

Since it was first described, corky root rot of tomato (*Lycopersicum esculentum* Mill) has been reported to be caused by *Pyrenochaeta lycopersici* Schneider and Gerlach (Schneider and Gerlach, 1966). This disease was last reported in Canada by Jarvis (1983) in Ontario, and earlier, by Richardson and Berkeley (1944), also in Ontario. It is commonly associated with plants grown in soil and has increasingly been seen in plants grown in rockwool soilless culture (W.R. Jarvis, pers. comm.).

In 1984, a root disease with symptoms closely resembling those of the *Pyrenochaeta* corky root rot of tomato was reported in the Netherlands (Gruyter et al., 1992). This disease did not appear to be associated with *P. lycopersici* and affected plants were grown in soilless culture. *Humicola fuscoatra* Traaen was always present in the cells of affected roots, but pathogenicity could not be proven. When tomato plants were grown on rockwool slabs which were inoculated by pressing rockwool slabs from a previous crop with corky root rot onto the new rockwool slabs, or on re-used rockwool slabs that had previously supported tomato plants with corky root rot symptoms, corky root rot symptoms developed on the roots. Aleurioconidia of *H. fuscoatra* were found in the roots of tomato plants and the fungus could be isolated consistently. Gruyter et al. suggested that artificial substrates such as rockwool might offer favourable conditions for the development of a complex root disease of tomato in which *H. fuscoatra* may play a role.

In 1993, serious outbreaks of a disease with symptoms similar to *Pyrenochaeta* corky root rot of tomato occurred in commercial greenhouses using soilless culture in Ontario, Québec and British Columbia, Canada, and in Colorado, U.S.A. In the Fraser Valley of British Columbia, all tomato greenhouse crops were affected, with almost all of the plants showing root symptoms in some greenhouses. Symptoms of the disease were similar to those reported by Gruyter et al. (1992), including the wilting of severely affected plants. Commercial greenhouse growers estimated that this disease caused a 20% decrease in yield in 1993 (Jim Portree, British Columbia Ministry of Agriculture, Food and Fisheries, Abbotsford, B.C.,

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Canada, pers. comm.). Similar to the Dutch situation in 1984, *P. lycopersici* could not be isolated from roots displaying symptoms of corky root rot collected across Canada, but *H. fuscoatra* was commonly isolated from these roots and from recirculating nutrient solutions.

The objectives of this study were to determine if *Humicola fuscoatra* could infect roots of tomato and cause symptoms of corky root rot. Experiments were conducted examining the potential infectivity and pathogenicity of *H. fuscoatra*. We also examined the potential for dissemination of *H. fuscoatra* in hydroponic nutrient solution.

Materials and methods

The Fusarium crown and root rot resistant tomato cv. Trust (DeRuiter Seeds Inc., Columbus, OH, USA) was used in all experiments.

Four isolates of *Humicola fuscoatra* (CR1, CR2, CR3 and CR4) were obtained from plants displaying severe corky root rot in commercial greenhouses in the Fraser Valley of British Columbia. The isolates were stored separately on potato dextrose agar (PDA) in petri dishes at 5C. One week before plant inoculation, PDA petri dishes were streaked with conidia from the appropriate stock culture and incubated at room temperature under natural light conditions. The inoculum was collected by flooding each petri dish with sterile distilled water and scraping the surface of the colony with a sterile glass slide to dislodge the spores. The suspensions were filtered through 4 layers of sterile cheesecloth and diluted to obtain the required spore concentration as determined using a haemocytometer. Unless otherwise stated, the inoculum used in these experiments consisted of a mixture of equal amounts of each of the four *H. fuscoatra* isolates.

Seedling inoculation

Experiment 1. Infection of young seedlings under aseptic conditions

Experiment 1 was conducted using sterilized growth pouches (Dispo Growth Pouch, Baxter Canlab, Vancouver, B.C.) as described by Menzies (1993). The treatments consisted of shaking tomato seeds in sterile distilled water or a spore suspension of 10^6, 10^5, 10^4, 10^3, 10^2 or 10^1 conidia of *H. fuscoatra* ml^{-1} for 30 min. Three seeds of the same treatment were then placed in a growth pouch; there were 6 pouches per treatment. The pouches were placed upright in a completely random design in a pre-sterilized plastic tray covered with a presterilized plastic bag. Five cm slits were cut in the plastic bags near the bottom of the plastic tray to allow for air exchange with a minimum of contamination by air-borne microorganisms. The pouches were incubated for four weeks at 22 $\pm$ 2C, at which time the roots from the seedlings were harvested. The seedling roots were surface sterilized by immersion for 5 min in 0.5% NaOCl and rinsed twice with sterile water before being placed separately onto aPDA. The number of plant roots supporting growth of *H. fuscoatra* was recorded and the data were analysed using ANOVA, followed by a Ryan-Einot-Gabriel-Welsch multiple F test (SAS 1989). The experiment was repeated once with 4 pouches per treatment.

Mature plant studies

Experiment 2. Seed and fertilizer dripper inoculation

Eight untreated and eight inoculated seeds (10^6 conidia ml^{-1} as in Experiment 1) were seeded into rockwool cubes and 8 weeks later transplanted onto rockwool slabs with two seedlings of the same treatment per slab. The rockwool slabs were arranged in a completely randomized design in a greenhouse and grown using standard commercial greenhouse practices (Anon., 1993). The plants were inoculated twice each week from the time of transplanting until final plant harvest by applying 10 ml of sterile distilled water to plants arising from uninoculated seed and 10 ml of a 10^5 spores ml^{-1} water suspension of conidia to plants arising from inoculated seed at the point of insertion of the fertilizer dripper into the rockwool cubes. The plants were all harvested at 8 weeks after transplanting. The roots were also assessed for corky root symptoms and random pieces of root from each plant were surface-sterilized and placed onto aPDA. Corky root rot severity was rated on a 0-5 scale as follows: 0 = healthy roots, 1=few lesions, slight browning of roots, 2=few lesions, definite browning of roots, 3=moderate number of lesions, definite browning of roots, 4=numerous lesions, moderate browning, 5=numerous lesions, severe browning of the roots.

This experiment was repeated once. In this case, there were 5 rockwool slabs (10 plants) per treatment arranged in a randomized complete block design in the greenhouse. One plant from each slab was harvested and assessed for corky root rot symptoms and infection by the fungus at 16 weeks after transplanting. The rest of the plants were harvested and assessed

for symptoms and fungal infection at 24 weeks after transplanting.

Experiment 3. Root dip inoculation

One month old seedlings started in rockwool cubes were inoculated using a root dip technique. The cubes containing the young seedlings were immersed in trays containing either sterile distilled water or a suspension of 10^6 conidia of *H. fuscoatra* ml^{-1} for 30 min. There were 30 plants per treatment, and after treatment, the seedlings were transplanted onto rockwool slabs with two plants of the same treatment per slab. One hundred ml of the conidial suspension used for the root dip were applied between the rockwool slab and the rockwool cube at the time of transplanting. Eight weeks after transplanting, one plant per slab was harvested, examined for corky root symptoms and sections of the roots surface sterilized and placed onto aPDA. The remainder of the plants were harvested 12 weeks after transplanting.

This experiment was repeated twice with the following modifications. The inoculum for the seedlings contained 10^5 conidia ml^{-1} and the plants harvested at 20 weeks after inoculation in run 2 and 23 weeks after inoculation in run 3. Run 2 was conducted with 30 plants per treatment and run 3 with 8 plants per treatment. The roots of each plant were graded for severity of corky root rot at final plant harvest. The results were analysed using an F test (SAS 1989).

Experiment 4. Root dip and fertilizer dripper inoculation

There were two treatments in this experiment; uninoculated tomato seedlings, and seedlings inoculated with *H. fuscoatra* by a 30 min root dip in a water suspension containing 10^6 conidia ml^{-1}, followed by a inoculation with 10 ml of a similar conidial suspension at the point of fertilizer dripper placement (on the rockwool cube) at the time of transplant and every two weeks thereafter until the plants had been inoculated for a total of 10 times. At final harvest, at 30 weeks after transplanting, the plants were rated for the presence and severity of corky root rot lesions and samples of root surface sterilized for 10 min in 10% NaOCl, rinsed and placed onto aPDA. The presence or absence of *H. fuscoatra* was noted and the relationship between the presence or absence of corky root rot symptoms and the isolation of *H. fuscoatra* from the lesions was examined using a 2-tailed Fisher's Exact test (SAS 1989). This experiment was repeated once without modifications.

The experiment was repeated a second time with the following modifications. There were 8 rockwool slabs (16 plants) per treatment arranged in a randomized design in the greenhouse. The plants were harvested 23 weeks after transplanting.

Experiment 5. Growth of H. fuscoatra *in water and nutrient solution*

Flasks containing 100 ml of either sterile distilled water or sterile nutrient solution recommended for growth of tomato (Anon., 1993) were inoculated with approximately 100 spores of isolate CR1 of *H. fuscoatra* and incubated on a rotary shaker at 25C. A control treatment of sterile distilled water was also included in the experiments. There were 3 flasks for each treatment. At 0, 1, 3, 6, and 14 days, two 0.1 ml aliquots were taken from each flask and the population of the fungus in the flask determined by conducting a dilution plating onto aPDA.

This experiment was repeated with the following modifications. The spores of the fungus were washed by centrifuging the spore suspension at 2500 rpm for five min, and re-suspending the pellet in sterile distilled water. The spores were washed twice more in sterile distilled water before use. There were 4 flasks for each of the fungus-inoculated treatments and 2 flasks for the uninoculated control treatment. The flasks were sampled as above at 0, 1, 2, 3, 8 and 15 days after inoculation.

Results

Seedling studies

Experiment 1. Infection of young seedlings under aseptic conditions

Most of the seedlings in the growth pouches were infected when the seeds were treated with spore suspensions of 10^6, 10^5 and 10^4 conidia ml^{-1} in both runs of the experiment (Table 1). Numbers of seedlings infected decreased significantly as the inoculum concentration decreased from 10^4 conidia $ml^{-1.}$ Some seedlings in the water inoculated control treatments were also infected by *H. fuscoatra*.

In these experiments, the plants were infected at the crown and/or on the roots. It was common to see black growth within the roots (Figure 1). When the roots were surface sterilized and placed onto aPDA, black fungal colonies identified as *Humicola fuscoatra* developed from these areas (Figure 2).

Table 1. The effect of different spore concentrations of *Humicola fuscoatra* on the rate of infection of germinating tomato seedlings (Experiment 1)

Inoculum: spores ml^{-1} of *Humicola fuscoatra*	Mean infected seedlings per pouch[a]	
	Run 1	Run 2
10^6	3 a	3 a
10^5	2.5 a	3 a
10^4	3 a	3 a
10^3	1.3 b	2 b
10^2	0.5 b	2 b
10^1	0.3 b	0 c
0	0.5 b	0.75 c

[a] There were 3 seedlings per pouch and 6 pouches per treatment in run 1 and 4 pouches per treatment in run 2. The pouches were incubated for four weeks at 22 ± 2 C, at which time the seedling roots were harvested. The roots were surface sterilized by immersion for 5 min in 0.5% NaOCl and rinsed twice with sterile water before incubation on aPDA. The number of plant roots supporting growth of *H. fuscoatra* was recorded and the data were analysed using ANOVA, followed by a Ryan-Einot-Gabriel-Welsch multiple F test (SAS 1989). The means are significantly different at $P<0.05$.

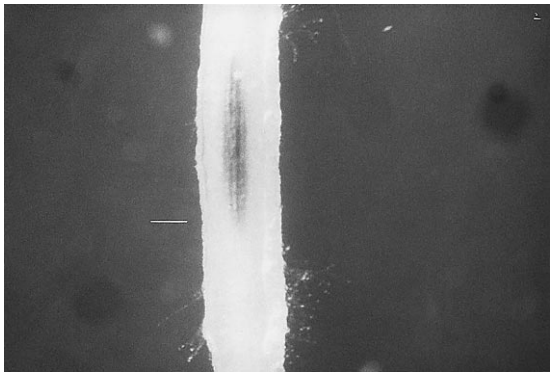

Figure 1. Root of a four week old tomato seedling showing symptoms of infection with *Humicola fuscoatra*. The seeds were treated by immersion in a water suspension of spores of *H. fuscoatra* and grown in growth pouches. (bar = 0.8 mm).

Mature plant studies

Experiment 2. Seed and fertilizer dripper inoculation

Run 1 resulted in no corky root rot symptoms visible on the roots of any of the tomato plants. All the plants (8 plants on 4 rockwool slabs) inoculated with *H. fuscoatra* were infected, whereas only one set of uninoculated control plants (two plants on one rockwool slab) were infected.

At the end of run 2, there were no corky root rot lesions on any of the plants. At 16 weeks after inoculation, *H. fuscoatra* was recovered from the roots of 4 of 5 of the inoculated plants, and 0 of 5 of the control plants. At 24 weeks after inoculation, despite surface sterilizing some of the root pieces for 10 min in 0.5% NaOCl, growth of other fungi made it difficult to assess root infection by *H. fuscoatra*. The fungus was isolated from root pieces at the final harvest date, but because of heavy overgrowth of other fungi, we were not confident of the results so they are not reported.

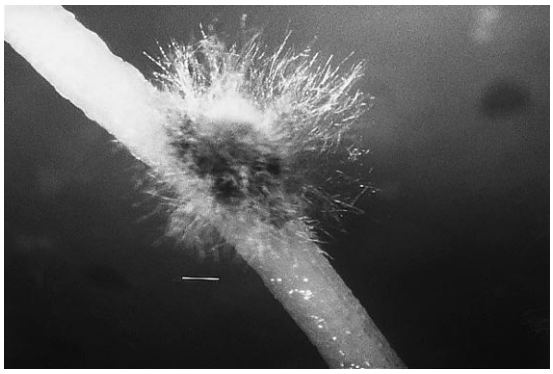

Figure 2. Colony of *Humicola fuscoatra* growing out of a root showing symptoms of infection similar to the root in Figure 1 (bar = 0.8 mm).

Experiment 3. Root dip inoculation

Corky root rot symptoms were not observed on the roots of any of the tomato plants in run 1 and run 3. However, in run 1, at eight weeks after inoculation, all the inoculated plants and 4 of the 15 of the first set of control plants were infected with *H. fuscoatra*. At 12 weeks after inoculation, all of the inoculated plants and 1 of 15 control plants of the second set were infected. In run 3, two of eight of the inoculated plant roots and none of the control plant roots were infected with *H. fuscoatra.*

Corky root symptoms were observed on the roots of the tomato plants in run 2 and the differences between treatments for the number of infected plants and the severity of the symptoms were significant ($P<0.05$). All plants inoculated with *H. fuscoatra* were infected and had symptoms with a mean severity rating of 1.00. Half the control plants were infected and all infected plants showed symptoms of corky root rot; the other half of the control plants were not infected and did not show disease symptoms. The uninoculated control plants had a mean severity rating of 0.44.

Experiment 4. Root dip and fertilizer dripper inoculation

Corky root rot symptoms were observed in all three runs of the experiment, with no significant differences among treatments in runs 1 and 2. The mean corky root rot severity values for the uninoculated control treatment were 2.3 and 0.8 for runs 1 and 2, respectively.

Humicola fuscoatra was commonly isolated from surface-sterilized roots in run 1. *Humicola fuscoatra* was isolated from 5 and 12 of 18 plants in the uninoculated and inoculated treatments, respectively. There were significant differences between treatments for the number of slabs that contained plants infected by *H. fuscoatra* ($P<0.04$). The uninoculated control treatment had significantly fewer slabs containing infected plants (4 of 9 rockwool slabs) than the inoculated treatment (8 of 9 rockwool slabs). There was no relationship between the presence of corky root rot symptoms and the isolation of *H. fuscoatra* from infected plant roots.

In run 2, *H. fuscoatra* was not isolated from plants of the uninoculated control treatment 1 and was isolated from only 4 of 18 plants in treatment 2. There were no significant differences between treatments for the number of slabs that contained plants infected by *H. fuscoatra*. As in run 1, there was no relationship between the presence of corky root rot symptoms and the isolation of *H. fuscoatra* from infected plant roots.

Corky root rot lesions were found on the roots of the plants in run 3, although the incidence and extent of symptoms were very low. There were no significant differences between treatments for either the number of plants displaying symptoms of corky root rot, or the severity of corky root rot. Six of 16 plants inoculated with *H. fuscoatra* had symptoms of corky root rot, and 4 of 16 uninoculated plants had symptoms. The mean severity of the corky root rot on control plants was 0.5 and on the inoculated plants was 0.3. *Humicola fuscoatra* was isolated from the roots of all plants inoculated with the fungus. *Humicola fuscoatra* was not isolated from any of the control uninoculated plants, including those showing symptoms of corky root rot.

Experiment 5. Growth of H. fuscoatra *in water and nutrient solution*

Humicola fuscoatra grew very rapidly in sterile water and sterile nutrient solutions, despite the lack of an added carbon source (Figure 3). In run 1, colony counts averaged 5.6×10^4 and 5.9×10^4 in the *H. fuscoatra* water and nutrient solution cultures, respectively, and in run 2 where washed spores were used as inoculum, colony counts averaged 1.4×10^5 and 5.9×10^5 in the *H. fuscoatra* water and nutrient solution cultures, respectively.

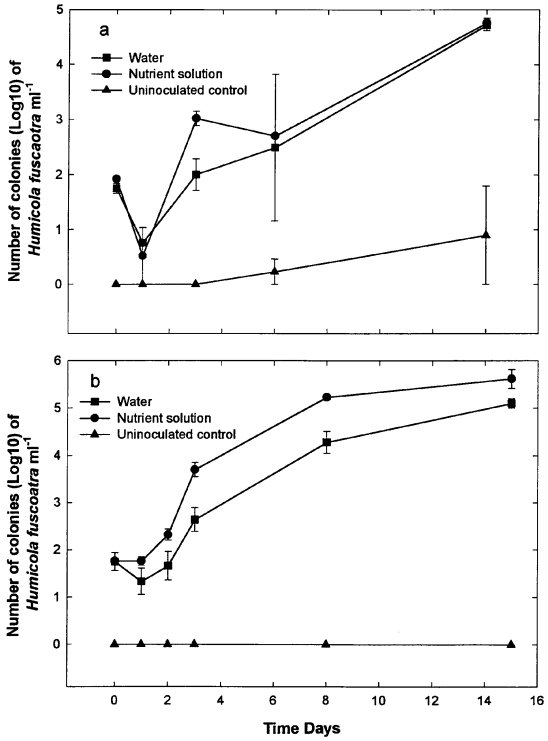

Figure 3. Growth at 25C of *Humicola fuscoatra* in sterile distilled water or sterile nutrient solution. Control treatments consisted of uninoculated sterile distilled water. a = run 1. b = run 2. Run 1 was conducted using unwashed conidia of the fungus as the initial inoculum, while run 2 was conducted using conidia washed twice in sterile distilled water.

Discussion

Gruyter et al. (1992) were unable to demonstrate that *H. fuscoatra* could infect the roots of tomato plants. In our studies, *H. fuscoatra* was readily able to infect roots and crowns of tomato seedlings and roots of older plants. With tomato seedlings, it was common to see black discolouration within the roots (Figure 1) out of which colonies of the fungus grew (Figure 2) when the roots were surface sterilized and placed onto aPDA. These black spots, indicating infection by the fungus, were not visible within older plant roots. However, *H. fuscoatra* was readily isolated from surface sterilized root pieces of older plants. As noted by Gruyter et al. (1992), *H. fuscoatra* can be extremely

difficult to isolate. At times, the presence of other fungi arising from lesions of corky root rot made it difficult to isolate the slower growing *H. fuscoatra* (i.e. Experiment 2 run 2 at 24 weeks after inoculation). The other fungi were generally species of *Fusarium* or *Pythium*. We did not isolate *Pyrenochaeta lycopersici*. However, with more stringent sterilization procedures such as increasing the time of immersion in 0.5% NaOCl to 10 min, and at times, re-surface sterilizing root pieces that had already been incubated on aPDA for 2 or 3 days, it was possible to isolate *H. fuscoatra* from these root pieces. In other cases, especially when isolating the fungus from apparently healthy, symptomless roots, immersion of the root pieces in 0.5% NaOCl for 5 min was sufficient to get good recovery from root pieces.

We conclude that *Humicola fuscoatra* is not a pathogen of tomato or a causal agent of corky root rot. Despite the infection of tomato roots by the fungus, root infection did not necessarily lead to development of corky root rot or any other disease symptoms and the presence of corky root rot lesions did not indicate that *H. fuscoatra* would be isolated from the tissue. The seedling tests were not of much help in this respect because the incubation period was short and corky root rot appears to take much longer to develop than just a few weeks. To the best of our knowledge, corky root rot has not been observed on young seedlings. In experiments using older plants, corky root rot symptoms were observed on plants harvested at 20, 23 and 30 weeks after inoculation in some experiments, but not on plants harvested at 8, 12, 16, 23 and 24 weeks in other experiments. Apparently, the disease has a lengthy latent period of approximately 20 weeks, but given the nature and objectives of our experiments and the inability to achieve corky root rot lesions consistently, no conclusions can be drawn. Nevertheless, given the duration of our experiments and the fact that corky root rot symptoms were observed on plants grown for 20 weeks after inoculation, our experiments should have been of sufficient duration to determine if *H. fuscoatra* causes corky root rot. In our experiments, we could not consistently get symptoms of corky root rot following inoculation with *Humicola fuscoatra*. Koch's third postulate remained unsatisfied. In experiment 2, run 2 at 24 weeks after inoculation, and in experiment 3 run 3 at 23 weeks after inoculation, no symptoms were observed on mature plant roots even though *H. fuscoatra* could be isolated from some roots. In experiment 3, run 2 at 20 weeks after inoculation, all plant roots displaying corky root rot symptoms were infected with the fungus, while none of the symptomless roots were infected. However, in experiment 4, runs 1 and 2 at 30 weeks after inoculation, there was no relationship between the presence of corky root rot symptoms and the isolation of *H. fuscoatra* from infected plant roots, and in run 3 at 23 weeks after inoculation, there was no significant differences between inoculated and uninoculated plant roots for symptoms or severity of corky root rot, but *H. fuscoatra* was not isolated from any roots of uninoculated plants. Therefore we concluded that there was no relationship between infection with *H. fuscoatra* and the development of corky root rot symptoms.

Gruyter et al. (1992) reported that in experiments in which there were differences among treatments for the number of plants displaying symptoms of corky root rot, there were no significant differences among treatments for yield. Yield data were taken in experiment 3 run 2 in which we found differences between treatments for the incidence and severity of corky root rot on tomato. In agreement with Gruyter et al. (1992), we found no significant differences in yield as measured by individual and total fruit weight, number of fruit and fruit grade (Menzies, Ehret, Koch and Bogdanoff, unpubl.). These findings would appear to be contrary to the estimated 20% yield loss to crops in commercial greenhouses in the Fraser Valley of B.C. in 1993 (Jim Portree, pers. comm.). However, it is important to note that commercial greenhouse growers would have their tomato crops growing for longer periods of time than in the present experiments, giving a greater period of time for yield losses to occur, and in experiment 3 run 2, corky root rot lesions as severe as those experienced by the commercial industry did not develop.

We also examined a possible means of dissemination of *H. fuscoatra* within the greenhouse. This was in response to growers' fear that they may be spreading this fungus and possibly the disease through recirculation of their nutrient solutions. Gruyter et al. (1992) reported that *Humicola fuscoatra* can be spread in a recirculating water system and growers in B.C. who have had their nutrient solutions tested for the presence of this organism (in a manner similar to that in Experiment 5) have detected it at various concentrations. Growth experiments in sterile water or sterile nutrient solution demonstrated the ability of this fungus to greatly increase its population in these two media. Such an ability for rapid population growth in water or nutrient solution suggests that the fungus would be able to spread rapidly and efficiently in recirculating

water systems. However, from the results of our experiments in which recirculating of nutrient solutions was not practised, the fungus appears to be able to spread rapidly from plant to plant even in the absence of recirculating systems.

Pyrenochaeta lycopersici was not isolated from tomato roots in these experiments. We did not inoculate with *P. lycopersici* in these experiments because our objective was to examine the role of *H. fuscoatra* in this disease and including *P. lycopersici* may have caused confusion in determining which fungus is causing corky root rot if the different treatments became cross-contaminated. However, our failure to demonstrate that *H. fuscoatra* causes corky root rot leads us to reconsider the role of *P. lycopersici* in this disease. Jarvis (pers. comm.) has frequently found *Colletotrichum coccodes* in *P. lycopersici*-incited corky roots. The *C. coccodes* is generally regarded as a secondary opportunist, parasitising the roots after *P. lycopersici* has initiated disease. This situation is exacerbated by the difficulty in isolating the slow growing *P. lycopersici* from corky roots. It may be that *H. fuscoatra* has a similar relationship with *P. lycopersici*. Also, *H. fuscoatra* has been reported to parasitize the oospores of *Phytophthora cactorum* (Sneh et al., 1977). Perhaps *H. fuscoatra* parasitizes *P. lycopersici* in corky roots, which could explain the isolation of *H. fuscoatra* and the inability to isolate *P. lycopersici* from these roots, but we have not examined this hypothesis.

It is important to note that our results and those of Gruyter et al. (1992) have not established if the disease is abiotic or biotic in origin. Gruyter et al. (1992) were able to get corky roots only when they grew tomato plants on previously used rockwool slabs with a history of corky root rot. Similar experiments with previously used rockwool slabs in our greenhouses (Menzies, Ehret, Koch and Bogdanoff, unpubl.) and greenhouses belonging to the British Columbia Ministry of Agriculture, Food and Fisheries (Jim Portree, pers. comm.) have also demonstrated that corky root rot of tomato can be reproduced in this way. It may be that the development of corky roots on tomato plants is a physiological reaction to an environmental stress such as poor aeration, rather than stress caused by biological agents.

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