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Influence of Environmental Parameters on *Trichoderma* Strains with Biocontrol Potential

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Summary

Several mycoparasitic strains belonging to the filamentous fungal genus *Trichoderma* are promising candidates for the biological control of plant pathogenic fungi. When planning the application of antagonistic *Trichoderma* strains for the purposes of biological control, it is very important to consider the environmental parameters affecting the biocontrol agents in the soil. A series of abiotic and biotic environmental parameters has an influence on the biocontrol efficacy of *Trichoderma*. Some important parameters to be considered are the effects of temperature, water potential and pH, and the presence of pesticides, metal ions and antagonistic bacteria in the soil.

Most of the *Trichoderma* strains are mesophilic. Low temperatures in winter may cause a problem during biological control by influencing the activity of the biocontrol agents. Another problem emerging during the application of *Trichoderma* strains as biocontrol agents is that they cannot tolerate dry conditions, however, we may need biocontrol agents against plant pathogenic fungi which are able to grow and cause disease even in dry soils. The pH characteristics of the soil also belong to the most important environmental parameters affecting the activities of mycoparasitic *Trichoderma* strains. Within the frames of a complex integrated plant protection strategy, we may have to combine *Trichoderma* strains with chemical pesticides or metal compounds, therefore it is important to collect information about the effects of pesticides and metal ions on the biocontrol strains. Antagonistic soil bacteria may also have negative effects on the biocontrol abilities of *Trichoderma* strains, therefore it may be advantageous if a biocontrol strain possesses bacterium-degrading abilities as well.

This review will discuss the literature about the influence of temperature, water potential, pH, pesticides, metal ions and antagonistic bacteria on mycoparasitic *Trichoderma* strains including the results of our work group in these fields.

Key words: Trichoderma, biocontrol, temperature, water potential, pH dependence, pesticides, metal ions, antagonistic bacteria

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Introduction

Trichoderma species are imperfect filamentous fungi with teleomorphs belonging to the Hypocreales order of the Ascomyceta division. The ecological role of this genus is that *Trichoderma* strains take part in the decomposition of plant residues in the soil *(1)*. Some *Trichoderma* species are very good cellulase producers and therefore they are important for the biotechnological industry *(2,3)*. The agricultural importance of the genus is that some *Trichoderma* species possess good antagonistic abilities against plant pathogenic fungi, *e.g. Fusarium (4)*, *Pythium (5)*, *Rhizoctonia (6)* and *Sclerotinia (7)* species. Antagonism is based on different mechanisms, like the production of antifungal metabolites by *Trichoderma (8–11)*, competition for space and nutrients *(12)* and mycoparasitism *(13)*. Mycoparasitic *Trichoderma* strains are able to recognise the host hyphae *(14)*, to coil around them, develop haustoria *(15)*, penetrate the cell wall of the host with cell-wall degrading enzymes like chitinases, glucanases and proteases, and utilise the contents of the host hyphae as nutrient source. *Trichoderma* strains with effective antagonistic abilities are potential candidates for the biological control of plant diseases *(16–18)*. Abiotic and biotic environmental parameters may have negative influence on the biocontrol efficacy of *Trichoderma* strains, therefore it is very important to collect information about the effects of environmental factors on the different activities of *Trichoderma* strains with biocontrol potential.

Effects of Temperature on *Trichoderma* Strains

Studies are available on the effects of temperature on the spore germination and germ-tube growth *(19)*, mycelial growth *(20,21)*, competitive saprophytic abilities *(12,22,23)* and on volatile and non-volatile metabolite production *(24)* of *Trichoderma* strains. The optimum temperature for growth differs among the *Trichoderma* species *(20,21)*. Most *Trichoderma* strains are mesophilic, and cannot protect germinating seeds from soilborne diseases caused by cold-tolerant strains of plant pathogenic fungi during cold autumn and spring conditions.

We screened 360 *Trichoderma* strains for cold-tolerance *(25)*. Fourteen – identified as *T. aureoviride*, *T. harzianum* and *T. viride* – grew well at 5 °C on both minimal and yeast extract agar media. The incidence of cold-tolerant isolates was the highest in species group *T. viride*. According to Widden and Abitbol *(26) T. viride* was the most abundant species in early spring and autumn in a spruce forest soil. The lower proportion of cold-tolerant strains in *T. harzianum* species aggregate (6 of 142) than in *T. viride* species aggregate (7 of 78) appears to be consistent with the higher optimum growth temperatures of the former group *(20)*. High level of variability in growth rates at lower temperatures among both species aggregates and strains within species aggregates suggests that a large number of strains need to be screened in order to select biocontrol candidate strains intended for use under cooler conditions.

In dual culture tests at 10 °C, all cold tolerant strains produced appressoria and antagonised plant pathogens *Rhizoctonia solani* and *Fusarium oxysporum* f. sp. *dianthi (25)*. Previous studies of cold-tolerant *Trichoderma* strains, which investigated the antagonistic abilities at different temperatures, found that temperature did not have an effect on hyphal interactions with the test fungi *(24,27)*. *T. aureoviride* and *T. viride* strains were more effective *in vitro* antagonists against *P. debaryanum* than *T. harzianum* strains. The effect of low temperatures on the production and activities of extracellular β-1,4-*N*-acetyl-glucosaminidase (NAGase), β-glucosidase and trypsin- and chymotrypsin-like proteases – all enzymes thought to be involved in the mycoparasitic process – were also examined and results showed that these enzymes were produced at 10 °C and remained highly active even at 5 °C in the cold-tolerant strains *(25)*.

Influence of Water Availability on *Trichoderma* Strains

One of the most important limitations of the use of *Trichoderma* strains as biofungicides is their low osmotolerance level. Water conditions in soils are limiting parameters affecting fungal activities. Dry conditions may occur even in normally less dry soils as a result of normal drying between rains. On the other hand, biocontrol agents may be needed against plant pathogens in dry soils.

Water conditions have been shown to strongly affect *Trichoderma* activities, most particularly spore germination and germ tube growth *(19)*, mycelial growth *(28,29)*, they have a critical effect on saprophytic ability *(23,30)*, on the interaction with other fungi *(22,31)* and on enzyme production *(32)*. Information about the influence of water conditions on metabolic activities of *Trichoderma* strains is essential for planning their application in biocontrol strategies.

We studied the influence of water potential on linear mycelial growth, secretion and *in vitro* activities of β-glucosidase, cellobiohydrolase, β-xylosidase, NAGase and chymotrypsin-like protease enzymes of the cold-tolerant *T. harzianum* strain T66 (ATCC MYA-1175) at different temperatures *(33)*. Nearly linear correlation was found between water potential and colony growth rate at both 25 and 10 °C with higher growth rates at higher temperature and water potential. Optimal water potential values for the secretion of β-glucosidase, cellobiohydrolase, β-xylosidase, NAGase and chymotrypsin-like protease enzymes were different. Cellobiohydrolase and NAGase enzymes showed optimal secretion at the highest examined water potential, while the maximum activities of secreted β-glucosidase, β-xylosidase and chymotrypsin-like protease enzymes occurred at lower water potential values than those optimal for growth. *In vitro* enzyme activities were affected by water potential, but significant enzyme activities were measured for most of the enzymes even at –14.8 MPa, which is below the water potential, where mycelial growth ceased. These results suggest the possibility of using mutants with improved xerotolerance for biocontrol purposes in soils with lower water potential.

pH-Dependence of *Trichoderma* Strains

Biocontrol *Trichoderma* strains are applied in agricultural soils with certain pH-characteristics. Therefore, it is important to collect information about the effects of pH on mycelial growth and on the *in vitro* activities of extracellular enzymes involved in nutrient competition and mycoparasitism of *Trichoderma* strains with biocontrol potential. pH can also play a role in the regulation of extracellular enzyme production, as it was demonstrated by Delgado-Jarana *et al. (34)* for β-1,6-glucanase of *Trichoderma harzianum*.

pH-optima of the linear mycelial growth of five cold -tolerant *Trichoderma* strains belonging to three different species groups and of some plant pathogenic fungi were determined on yeast extract medium *(35)*. The examined *Trichoderma* strains were able to grow in a wide range of pH from 2.0 – 6.0 with an optimum at 4.0. However, the mycelial growth of some of the examined plant pathogenic fungi had pH-optima at alkalic values. Jackson *et al. (36)* have found that optimum biomass production of three *Trichoderma* isolates occurred at pH ranges between 4.6 and 6.8. We examined the effect of pH on the *in vitro* activities of *Trichoderma* extracellular enzymes. Optimal pH values were pH=5.0 for β-glucosidase, cellobiohydrolase and NAGase, pH=3.0 for β-xylosidase, pH=6.0 for trypsin-like protease and pH=6.0–7.0 for chymotrypsin-like protease activities *(35)*. Extracellular enzymes of the examined mycoparasitic *Trichoderma* strains were found to be able to display activities under a wider range of pH values than those allowing mycelial growth. Data about the effects of pH on mycelial growth and on extracellular enzyme activities of mycoparasitic *Trichoderma* strains reveal useful information about the applicability of biocontrol strains in agricultural soils with certain pH-relations.

Effects of Pesticides on *Trichoderma* Strain

One of the most promising possibilities for the application of biocontrol *Trichoderma* strains is within the frames of a complex integrated plant protection, which is based on the combined application of physical, chemical and biological means of control. In the case of the application of a complex integrated strategy we may have to combine *Trichoderma* strains with chemical pesticides, therefore it is important to collect information about the effects of pesticides on the biocontrol agent. The effects of the herbicide propyzamide and five fungicides (benomyl, quintozene, vinclozolin, thiram and prothiocarb) on the colonisation of substrates by *T. harzianum* were investigated by Davet, and discussed with a view to practical applications *(37)*. *In vitro* action of 5 mixtures of fungicides and 11 insecto-fungicides to different antagonistic fungi, among them to *T. viride*, was tested by Sesan and Oprea *(38)*, and a restricted group of the examined pesticides with low inhibitory action was suggested to be applicable in the integrated protection of different crops. The influence of mancozeb, benomyl and vinclozolin on the antagonistic effect of four *Trichoderma* strains against *Sclerotinia minor* was investigated by Naár and Kecskés *(39)*, and vinclozolin and mancozeb were proposed for combined application with *Trichoderma* against *Sclerotinia*. The sensitivity of the fungal antagonists (*Chaetomium globosum* and *Trichoderma* species) of onion white rot, caused by *Sclerotium cepivorum*, to captan, mancozeb, thiram, benomyl and two dicarboximides was also evaluated, and dicarboximide-resistant biotypes were selected *(40)*.

The effects of three fungicides (benomyl, carbendazim and dicloran) and four herbicides (fenuron, fluometuron, monuron and diuron) on the growth of *T. aureoviride* T122, *T. harzianum* T66 and T334, and *T. viride* T124 and T228 strains *(41)* were examined. In the case of diuron, 50 % inhibition could not be reached. For the other herbicides and dicloran the IC_{50} concentrations were found to be so high that their values cannot be present in the soil during their application. However, the susceptibility of the strains to benomyl and carbendazim may cause problems during their combined application with benzimidazole compounds. For such purposes fungicide resistant mutants should be applied. UV-mutagenesis was found to be a useful method for the isolation of benomyl-resistant *Trichoderma* strains *(42)*. Some of the benomyl-resistant *Trichoderma* strains, *e.g. T. harzianum* T95 (ATCC 60850) isolated by Ahmad and Baker *(43)* are undergoing detailed investigations *(44–46)*.

Effects of Metal Ions on *Trichoderma* Strains

Several pesticides used in agriculture contain metal ions. On the other hand, metals may be present in the soil as result of contamination. Although several heavy metal ions (*e.g.* copper, zinc, nickel, cobalt, *etc.*) are necessary trace elements for the growth of fungi, they are toxic at high concentrations. The sorption of toxic metals by fungi (*Rhizopus arrhizus* and *T. viride*) and clay minerals was examined by Morley and Gadd *(47)*. Accumulation of zinc, cadmium and mercury by *T. harzianum (48)*, and the effect of some heavy metals on the growth, sporulation *(49,50)*, and differentiation *(51)* of *Trichoderma* strains were also examined.

We investigated the effects of ten metals (aluminium, copper, nickel, cobalt, cadmium, zinc, manganese, lead, mercury and iron) on mycelial growth and on the *in vitro* activities of trypsin-like protease, chymotrypsin-like protease, NAGase, β-1,3-glucanase, β-glucosidase, cellobiohydrolase, β-xylosidase and endoxylanase enzymes in the case of strains *T. aureoviride* T122, *T. harzianum* T66 and T334, and *T. viride* T124 and T228 *(52–54)*. Mycelial growth was influenced significantly by the metals. The lowest IC_{50} values were found for copper, while the highest were for aluminium. In a concentration of 1 mmol only mercury inhibited the examined extracellular enzymes significantly, in the case of the other metals the enzymes of *Trichoderma* could remain active even at concentrations inhibiting mycelial growth, suggesting that breeding for metal resistant *Trichoderma* strains could result in biocontrol agents effective against plant pathogenic fungi even under metal stress.

A total number of 177 metal resistant mutants were isolated by UV-mutagenesis and tested for possible cross-resistances *(53,54)*. Significant cross-resistance was found in the case of aluminium- and nickel-resistant mutants to copper and in the case of copper resistant ones to nickel. The emergence of cross-resistance indi-

cates that similar or identical mechanisms may reveal the background of resistance to different metal ions, however, there is still a lack of knowledge about the metal-resistance mechanisms in *Trichoderma*. Some of our mutants were effective antagonists of plant pathogenic *F. culmorum*, *F. oxysporum* f. sp. *dianthi*, *P. debaryanum* and *R. solani* strains even on media containing the respective metals. Such mutants might be the preferred choice for combined application with metal-containing pesticides in the frame of a complex integrated plant protection.

Effects of Antagonistic Bacteria on *Trichoderma* Strains

One of the limiting factors of the application of mycoparasitic *Trichoderma* strains as biofungicides in agricultural soils is that many strains of soil bacteria suppress the activity of *Trichoderma (55)*. Therefore, this is advantageous if a biocontrol *Trichoderma* strain is able to antagonise and degrade bacteria present in compost or in the rhizosphere of plants. Interestingly, there are many publications on the enzymological background of the mycoparasitic processes of *Trichoderma* strains, but there are few investigations aimed at bacteria adversely affecting their biocontrol abilities. The influence of bacteria on the competitive saprophytic ability of *Trichoderma* species has been investigated by Naár and Kecskés *(12)*, and the competitive success of *Trichoderma* has been suggested to be attributable mainly to its sensitivity to the inhibitory effect of bacteria.

Eighteen *Trichoderma* strains were screened for their ability to degrade bacterial cells *(56)*. The specificity spectrum and the intensity of degradation were highly variable. In the case of five strains showing outstanding degrading abilities towards *Bacillus subtilis*, the NAGase, trypsin-like and chymotrypsin-like protease activities were determined under inductive and non-inductive circumstances. All strains were able to produce NAGase and proteases constitutively at a moderate level, which could be elevated by induction with *B. subtilis* cells. In inductive media, 3 – 6 times more NAGase and proteases were produced.

The inductive fermentation broth of an outstanding strain, *T. harzianum* T19, was fractionated on a Sephadex G 150 column. The strain produced at least 3 trypsin-like proteases, 6 chymotrypsin-like proteases, and 4 NAGases upon induction with *B. subtilis* cells. Muramidase-like activities were also present in the fermentation broth of this *T. harzianum* strain *(56)*.

These results indicate that bacterium-degrading ability is common, but highly variable among *Trichoderma* strains. Proteases, NAGases and muramidases seem to have great importance in the degradation of bacterial cells.

In addition to testing their ability to antagonise plant pathogenic fungi, the determination of their bacterium-degrading capabilities may also be useful in the evaluation of biofungicide *Trichoderma* strains, as this property can perhaps help the strains to be dominant microorganisms in the habitats where they are applied.

Conclusions

The number of studies about the effects of different environmental factors on mycoparasitic *Trichoderma* strains is increasing from year to year, indicating, that in order to reach effective biological control, it is necessary to broaden our knowledge about the ecophysiology of this genus.

Based on our results, the extracellular enzyme systems of *Trichoderma* important for competition and mycoparasitism can remain active even under environmental conditions unfavorable for mycelial growth, which suggests the possibility of strain improvement for better stress tolerance. Effective tools for strain improvement involve mutagenesis *(53,54,57)*, protoplast fusion *(58,59)* and genetic transformation *(60–62)*. Progresses in the field of *Trichoderma* strain improvement are discussed by Manczinger *et al. (11)*. The application of mycoparasitic *Trichoderma* strains with improved tolerance of unfavorable environmental conditions could increase the efficacy of biological control. The breeding of *Trichoderma* for cold-tolerance, osmotolerance, bacterium-tolerance, pesticide- or metal-resistance may result in effective mycoparasitic strains for biocontrol application against fungal plant pathogens under a wider range of environmental conditions.

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Utjecaj parametara okoliša na sojeve *Trichoderma* sposobne za biološku kontrolu

Sažetak

Mnogi mikoparazitski sojevi, koji pripadaju filamentoznim gljivama genusa *Trichoderma*, potencijalni su kandidati za biološku kontrolu patogenih funga biljaka. Planirajući primjenu antagonističkih sojeva *Trichoderma* radi biološke kontrole, važno je uzeti u obzir parametre okoliša koji utječu na agense biokontrole u tlu. Niz abiotičkih i biotičkih parametara okoliša utječe na učinkovitost biokontrole soja *Trichoderma*. Od važnijih parametara treba razmotriti utjecaj temperature, potencijala vode i pH, te prisutnost pesticida, iona metala i antagonističkih bakterija u tlu.

Najveći broj sojeva *Trichoderma* jesu mezofili. Niske zimske temperature mogu biti problem jer pri biološkoj kontroli utječu na aktivnost biokontrolnih agensa. Daljnji je problem tijekom primjene sojeva *Trichoderma* kao biokontrolnih agensa što ne podnose suhe uvjete. Nama su potrebni biokontrolni agensi protiv patogenih funga biljaka što mogu rasti i uzrokovati bolesti, čak i u suhim tlima. Karakteristike pH tla najvažniji su parametri koji utječu na aktivnost mikoparazitskih sojeva *Trichoderma*. Unutar kompleksa postupaka

zaštite biljke mogu se povezati sojevi *Trichoderma* s kemijskim pesticidima ili metalnim spojevima. Stoga je važno da se prikupe informacije o utjecaju pesticida i metalnih iona na sojeve koji služe za biokontrolu. Antagonističke bakterije tla mogu također negativno utjecati na sposobnost biokontrole sojeva *Trichoderma*, pa je korisno ako biokontrolni soj ima sposobnost razgradnje bakterija. U radu su razmotreni literaturni podaci o utjecaju temperature, potencijala vode, pH, pesticida, metalnih iona i antagonističkih bakterija na mikoparazitske sojeve *Trichoderma*, kao i rezultati našeg tima na tom području.