

RHIZOSPHERE EFFECT OF HORTICULTURAL PLANTS LETTUCE (*LACTUCA SATIVA* L.) AND TOMATO (*SOLANUM LYCOPERSICUM* L.) ON NEMATOPHAGOUS SPECIES FROM FUNGAL COENOSES

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Abstract

*The presence of nematophagous fungi in microbial communities from horticultural plants grown in greenhouses is considered beneficial because they are possible biological control agents of plant-parasitic nematodes. Previous studies performed to elucidate the rhizosphere effect on nematode-trapping fungi are scarce and therefore is important to investigate the ecology of nematophagous fungi in the rhizosphere of different plants. The aim of this paper is to present the results of research carried out in greenhouse conditions to compare the rhizosphere effect of two horticultural plants, represented by lettuce (*Lactuca sativa* L.) and tomato (*Solanum lycopersicum* L.) on naturally occurring nematophagous fungi with special focus on nematode-trapping fungi and endoparasitic fungi, as well as ecological aspects in fungal community structure and functions. Nematophagous fungi from lettuce rhizosphere belong to nematode-trapping species (*Arthrobotrys oligospora*, *Dactylaria candida*, *Monacrosporium cionopagum*) and endoparasitic species (*Harposporium anquillulae*). Excepting *Dactylaria candida*, the same nematophagous species were identified in the rhizosphere of tomato plants. In both plant rhizospheres, different adhesive or non-adhesive hyphal structures to capture nematodes and non-adhesive infection conidia detected were photographed and presented.*

Key words: *nematode-trapping fungi, rhizosphere effect, microbial communities, endoparasitic fungi, biological control agents.*

INTRODUCTION

Rhizosphere is defined as the zone in soil which is influenced by the physical, chemical and biological processes of plant roots (Jeffery et al., 2010).

The composition of plant exudates depends on cultivar and is influenced by growth stage or plant exposure to stress.

Plants' exudates, also determine microbial species richness and their abundance in the rhizosphere (Singh et al., 2007; Verma et al., 2018; Alawyie & Babalola, 2019).

Plants are able to fix the carbon in the photosynthates, partly being transported into the root and excreted from root tissues in rhizosphere. Various metabolites secreted by the roots such as organic acids (aliphatic and aromatic acids - lactic, malic, oxalic, pyruvic, succinic, and amino acids), amides, carbohydrates (glucose, xylose, fructose), play chemotactic role. They are also plants growth promoting bioactive factors (Babalola, 2010).

Literature reported the antagonistic capacity of various fungi from rhizosphere of wheat (Matarese et al., 2012) or tomato against specific plant myco-pathogens (Mogle & Mane, 2010; Sharma & Singh, 2014; Jaiswal et al., 2017).

Nematophagous fungi, especially from rhizosphere of horticultural plants grown in greenhouses, play a beneficial role in biological control of plant-parasitic nematodes (Chen et al., 2020). Nematophagous fungi can be divided into four categories: nematode-trapping fungi, endoparasitic fungi, fungi which parasitise eggs and females, and toxin-producing fungi (Dackman et al., 1992).

Research has been carried out in greenhouse conditions to compare the rhizosphere effect of two horticultural plants, represented by lettuce (*Lactuca sativa* L.) and tomato (*Solanum lycopersicum* L.) on naturally occurring nematophagous fungi with special focus on nematode-trapping fungi and endoparasitic fungi, as well as ecological aspects in fungal community structure and functions.

MATERIALS AND METHODS

Rhizosphere samples (consisting in roots with closely adhering soil) were collected (Persmark & Jansson, 1997) by gently shaking for removing the most of the soil from the roots of 18 weeks old tomato plants (*Solanum lycopersicum* L.) cultivar Cindrel and lettuce (*Lactuca sativa* L.) cultivar Lolobionda cultivated in experiment under controlled conditions.

Research has been conducted in greenhouse of HORTINVEST-Research Center for Studies of Food Quality and Agricultural Products, from University of Agronomic Sciences and Veterinary Medicine – Bucharest, Faculty of Horticulture, during summer 2020.

Microbiological analyses were performed by soil dilution method on specific solid culture media for fungi (PDA and water-agar).

After 7 days incubation at 25°C in the dark, colonies were counted and results expressed as colony forming units (c.f.u. x 10⁻³), each reported to gram of dry soil (Matei, 2011).

Taxonomic identification was carried out using morphologic criteria, according to Domsch & Gams (1970) and Watanabe (2002) determinative manuals for fungi. Nematophagous fungi were identified using specific keys (Cooke & Godfrey, 1964; Schenck et al., 1977; De Hoog & Oorschot, 1985; Liu et al., 1992; Philip, 2001; Meyer & Carta, 2005; Kendrick, 2020; Zhang et al., 2021).

All morphological characteristics were measured under a MC 5.A optic microscope and photographs of different adhesive or non-adhesive hyphal structures to capture nematodes and non-adhesive infection conidia were taken by attached ToupCam.

The total number of species in community (S) was recorded for lettuce and tomato rhizosphere.

The ratio between the number of species in community and microbial effectives expressed species richness index (SR₂).

Comparative composition analysis in harvested, culturable fungal species from lettuce and tomato rhizosphere was performed to interpret the relationships between the two sets of species identified (Gentleman & Ihaka, 1996) by using a Venny 2.1 program to create Venn diagrams.

Similarity index (SI) between lettuce and tomato rhizosphere communities of fungi was calculated (Tiwari et al., 1994).

The Shannon index (*H'*), evenness (ϵ) were used to evaluate the fungal diversity (Mohan & Ardelean, 1993).

The index of Brillouin (1956) and Simpson (D) index (Stugren, 1982) were also used to calculate the diversity and “equitability” component of fungal species diversity.

The constancy, referring to the presence of the species in samples, was expressed by the value of frequency (F%) and species were grouped in: accidental species (F value by 25%), accessory species (F = 25-50%), constant species (F = 50-75%), euconstant species (F = 75-100%) (Mohan & Ardelean, 1993).

All assays were carried out in triplicate and results represent the average mean of 3 replicates.

RESULTS AND DISCUSSIONS

The results of microbiological analyses evidenced that composition of fungal cenosis and the relative abundance values of the species were influenced by rhizosphere environment, with higher number of species and lower abundance values in lettuce rhizosphere (Figure 1) and lower number of species with higher abundances in tomato rhizosphere (Figure 2).

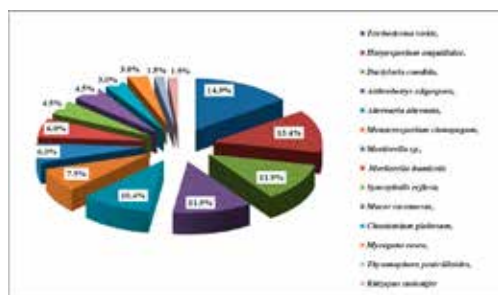


Figure 1. Percent mean relative abundance of fungal microflora composition in rhizosphere of lettuce

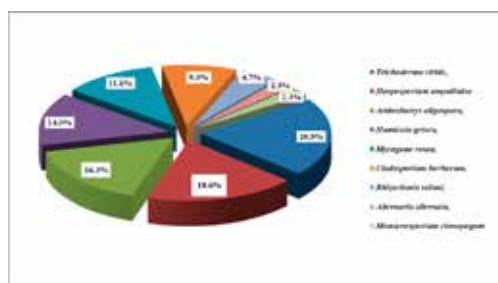


Figure 2. Percent mean relative abundance of fungal microflora composition in rhizosphere of tomato

There were clear differences in the relative abundances of the nematophagous fungal species between the crop plants. The data analysis showed that there was higher relative abundance of *Harposporium anguillulae* in rhizosphere of tomato plants (18.6%) than in rhizosphere of lettuce (14.6%). The nematode-trapping species *Arthrobotrys oligospora* was also found with higher abundance in rhizosphere of tomato (16.3%) than in rhizosphere of lettuce (11.9%, the same relative abundance as for differential species *Dactylaria candida*). Conversely, *Monacrosporium cionopagum* was most abundant in rhizosphere of lettuce (7.5%) as compared with rhizosphere of tomato (2.3%).

Examination of Petri plates by optic microscopy revealed morphological characteristics and specific fungal structures (Figure 3) developed by nematophagous species on water agar medium.



Figure 3. Conidia and adhesive reticulate traps of *Arthrobotrys oligospora* - tomato rhizosphere (300x)

Images illustrate aspects of the specific morphology of conidia with apical cell twice larger than the basal cell (Figure 4) and three dimensional adhesive nets formed by *Arthrobotrys oligospora* to capture nematodes (Figure 5). Nordbring-Hertz & Stålhammar-Carlemalm (1978) found a lectin in the fungal net matching with a carbohydrate in the cuticle of the nematode. Tunlid & Jansson (1991) described the proteases involved in the infection and immobilization of nematodes by the nematophagous fungus *Arthrobotrys oligospora*.



Figure 4. *Arthrobotrys oligospora* conidia with apical cell twice larger than the basal cell - lettuce rhizosphere (600x)



Figure 5. Digestion of nematode trapped in adhesive reticulate net by predaceous fungus *Arthrobotrys oligospora* - lettuce rhizosphere (300x)

The endoparasites belonging to genus *Harposporium* are obligate parasites, nutritionally dependent exclusively on nematodes, which they infect with non-adhesive spores, respectively.

The nematode-trapping fungi (*Arthrobotrys oligospora*, *Dactylaria candida*, *Monacrosporium cionopagum*) may also feed saprophytically in soil and are less dependent on their ability to consume nematodes. In order to capture nematodes, they develop different traps: adhesive hyphae, three-dimensional networks, as previously presented for *Arthrobotrys oligospora*, adhesive branches to *Monacrosporium cionopagum*, or non-constricting rings and two branches joined to form a loop for *Dactylaria candida* (Figure 6).



Figure 6. *Dactylaria candida* - nematode-trapping devices - lettuce rhizosphere (300x)

The fungi in both groups completely destroy the nematode host by enzymatic lysis followed by consumption of the body content (Figure 7).

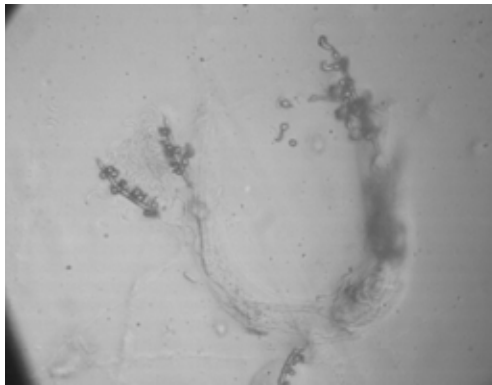


Figure 7. *Harposporium anquillulae* fungal structures emerged from digested body of the nematode (600x)

The image illustrates the conidiophores of *Harposporium anquillulae* emerged outside the destructed content of nematode body and sickle-shaped infecting conidia spread on the culture medium. After their ingestion by another nematode, the new infection appears even from the pharynx where the conidia stick. The hyphal system developed inside the host dissolute its content and after this, penetrates the cuticle and develops its own structures outside, to continue the cycle of infections.

Further analysis of the other fungal components of rhizospheres revealed that, in both fungal communities, the most abundant species was antagonistic fungus *Trichoderma viride* (Figure 8) but with higher relative abundance value re-

corded for rhizosphere of tomato plants (20.9%) than for rhizosphere of lettuce (14.9%).

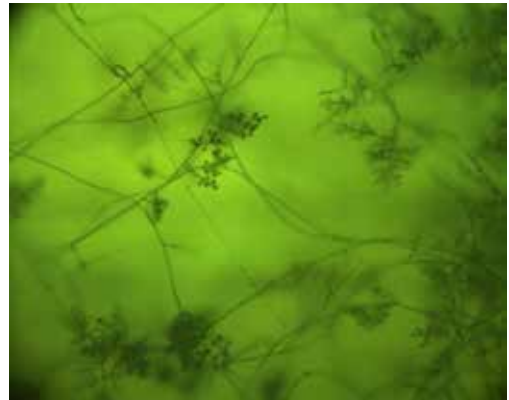


Figure 8. *Trichoderma viride* from the tomato rhizosphere(150x)

Recent studies (Yan et al., 2021) reported the role of *Trichoderma* spp. in improving plant defences against plant pathogenic nematodes by increasing the synthesis of secondary metabolites and defences-related enzyme activity in plant.

Apart of the relative abundance of species, their frequency in samples was helpful for establishing their constancy and the status of a certain species in the structure of myco-cenosis from rhizosphere of lettuce or tomato plants.

In Table 1 are also presented the values of the most utilized indices of characterization of biodiversity and evenness in microbial communities.

Thus, the values of Shannon index (H') and evenness (ϵ) were higher in rhizosphere of lettuce plants as compared with those from rhizosphere of tomato plants. The value of this diversity index increases with the increased number of fungal species (14 species in rhizosphere of lettuce as compared to 9 species in rhizosphere of tomato) and is also higher when the species are evenly distributed ($\epsilon=0.749$ in rhizosphere of lettuce as compared to $\epsilon=0.708$ in rhizosphere of tomato), as confirmed by other results from literature (Morris et al., 2014).

The values of index of Brillouin and D index of Simpson calculated confirmed the higher diversity and “equitability” component of fungal species diversity in rhizosphere of lettuce than in rhizosphere of tomato plants.

Thus, according to index of Simpson that takes values between 0 and 1, depending on the number of species and their proportion of representation, the diversity index value $D=0.901$ in myco-cenosis from lettuce

rhizosphere is higher than the value $D=0.850$ in myco-cenosis from tomato rhizosphere, and the values of “equitability” (Brillouin) $E=0.735$, respectively $E=0.698$, too.

Table 1. Taxonomic composition, species status and biodiversity indices of fungal rhizosphere communities of lettuce and tomato, in greenhouse experiment

Lettuce rhizosphere (Fungal species constancy)	Tomato rhizosphere (Fungal species constancy)
¹ <i>Trichoderma viride</i> , ¹ <i>Harposporium anquillulae</i> , ² <i>Dactylaria candida</i> , ² <i>Arthrobotrys oligospora</i> , ² <i>Alternaria alternata</i> ³ <i>Mortierella humicola</i> , ³ <i>Mortierella sp.</i> , ³ <i>Monacrosporium cionopagum</i> , ³ <i>Syncephalis reflexa</i> , ³ <i>Mucor racemosus</i> , ³ <i>Chaetomium globosum</i> , ³ <i>Mycogone rosea</i> , ³ <i>Thysanophora penicillioides</i> , ³ <i>Rhizopus stolonifer</i>	¹ <i>Trichoderma viride</i> , ¹ <i>Harposporium anquillulae</i> , ² <i>Arthrobotrys oligospora</i> , ² <i>Humicola grisea</i> , ² <i>Mycogone rosea</i> , ³ <i>Cladosporium herbarum</i> , ³ <i>Rhizoctonia solani</i> , ³ <i>Alternaria alternata</i> , ³ <i>Monacrosporium cionopagum</i>
$S=14$ $SR_2=0.208$ Shannon $H'=2.441$ $H'_{max}=2.639$ $\epsilon=0.749$ Brillouin $H=0.933$ $B=62.531$ $H_{max}=1.269$ $E=0.735$ Simpson Index $D=0.901$	$S=9$ $SR_2=0.209$ Shannon $H'=1.999$ $H'_{max}=2.197$ $\epsilon=0.708$ Brillouin $H=0.751$ $B=32.296$ $H_{max}=1.085$ $E=0.698$ Simpson Index $D=0.850$ ¹ euconstant species ($F=75-100\%$) ² constant species ($F=50-75\%$) ³ accessory species ($F=25-50\%$) ⁴ accidentally species ($F=by\ 25\%$)

Comparative analysis of fungal microbiomes composition from lettuce and tomato rhizosphere revealed that the exudates from plant roots influenced the composition of rhizosphere myco-cenoses, with only 6 shared (common) species ($SI=52.17\%$), half of them being represented by nematophagous species *Arthrobotrys oligospora*, *Harposporium anquillulae* and *Monacrosporium cionopagum*.

Other 3 shared species were represented by antagonistic and cellulolytic *Trichoderma viride*, as dominant species in both rhizospheres, *Alternaria alternata*, potential pathogen for lettuce and tomato plants and *Mycogone rosea*. The last species is rarely isolated from soil, being more often reported as parasite on Basidiomycetes (Baron, 1968).

Humicola grisea, *Cladosporium herbarum*, and *Rhizoctonia solani* were differential species, isolated only from tomato rhizosphere. Differential species, isolated only from lettuce rhizosphere were nematode-trapping fungus

Dactylaria candida and other 7 species from genera *Mortierella*, *Syncephalis*, *Mucor*, *Chaetomium*, *Thysanophora* and *Rhizopus*. Venn diagram (Figure 9) represents the number and proportion of shared (common) and differential species.

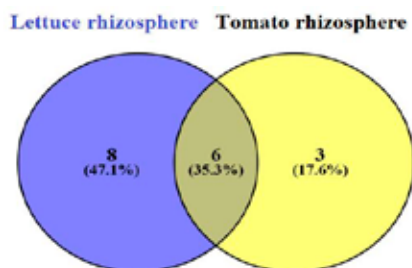


Figure 9. Venn diagram of unique and shared number and proportion of fungal species from lettuce and tomato rhizospheres

Microbial communities were dominated by antagonistic fungi *Trichoderma viride* and endoparasitic *Harposporium anquillulae*,

present in all samples (frequency F=100%) as euconstant species from both rhizospheres, accompanied by species with role in organic matter decomposition, plant growth promoting, improvement of soil structure, humification (*Humicola grisea*, *Cladosporium herbarum*), and less frequent phytopathogenic species (*Rhizoctonia solani*).

Our previous research evidenced the presence of *Harposporium anquillulae* as constant species in rhizosphere of soybean plants, cultivar PR91M10, grown in greenhouse (Matei & Matei, 2010).

Results from the present research are in concordance with other data from literature evidencing the importance of root–soil–microbe interactions in rhizosphere for crop production (Verma et al., 2011; Zhang et al., 2017).

Preece & Penuelas (2016) studied the role of rhizodeposition under drought and underlined the beneficial effect for biodiversity of soil microbial communities and ecosystem resilience.

Other research revealed the rhizosphere effect of three agricultural plants (barley, pea and white mustard) on naturally occurring nematophagous fungi and nematodes in both field and pot experiments and discussed various types of traps found, underlining that nematophagous species forming adhesive networks have a high saprophytic ability and a complex relationship with nematodes (Persmark & Jansson, 1997). The greatest number of species of nematophagous fungi (average of 2.4 species recovered from 0.1 g material) was detected in pea rhizosphere, as compared with white mustard and barley rhizospheres and root-free soil (less than 1.7 species).

The most common species in both soil and rhizosphere was *Arthrobotrys oligospora*. Liang et al. (2017) reported that the Woronin body in *Arthrobotrys oligospora* is essential for formation of fungal traps and the efficiency of pathogenesis process.

In the present experiment, four nematophagous species were identified in fungal communities of lettuce and tomato rhizospheres, with capacity to develop various typical infection structures ranging from adhesive nets, branches, non-constricting rings and ingested conidia.

The genetic reservoir of nematophagous fungal species could be utilised for reducing the populations of nematodes that detrimentally impact a wide variety of economically important horticultural plant species, especially in greenhouse conditions.

Further experiments with isolates of these fungi will need to be followed up to test them as inoculum added to soil in nematode population suppression assays.

CONCLUSIONS

Nematophagous fungi identified in lettuce rhizosphere belong to nematode-trapping species (*Arthrobotrys oligospora*, *Dactylaria candida*, *Monacrosporium cionopagum*) and endoparasitic species (*Harposporium anquillulae*).

Nematophagous fungi from tomato rhizosphere belong to nematode-trapping species (*Arthrobotrys oligospora*, *Monacrosporium cionopagum*) and endoparasitic species (*Harposporium anquillulae*).

Different adhesive or non-adhesive hyphal structures to capture nematodes and non-adhesive infection conidia were detected in rhizospheres of both plants.

There were differences in the relative abundances of the nematophagous fungal species between the crop plants.

The fungal community from rhizosphere of lettuce plants presented a higher biodiversity and homogeneity as compared to rhizosphere of tomato plants.

Plants' exudates influenced the composition of rhizosphere myco-coenoses, with only 52.17% shared species, half of them being represented by nematophagous species *Arthrobotrys oligospora*, *Harposporium anquillulae* and *Monacrosporium cionopagum*.

Microbial communities were dominated by antagonistic fungi *Trichoderma viride* and endoparasitic *Harposporium anquillulae*, (euconstant species), accompanied by constant and accessory species with role in organic matter decomposition, plant growth promoting, improvement of soil structure, humification and, less frequent, by potential phytopathogenic species.

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