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TRICHODERMA SPP. – MECHANISMS OF ACTION IN THE CONTROL OF STORAGE PATHOGENS - REVIEW

Angela Cristina AMUZA[1, 2], **Roxana ZAHARIA**[1]

[1]Research and Development Institute for Plant Protection, 8 Ion Ionescu de la Brad Blvd,
District 1, Bucharest, Romania
[2]University of Agronomic Sciences and Veterinary Medicine of Bucharest,
59 Marasti Blvd, District 1, Bucharest, Romania

Corresponding author email: angela.amuza@yahoo.com

Abstract

Aim: The purpose of the paper is to revise the multiple methods of biological control of Trichoderma spp. The need to reduce the use of fungicides in phytosanitary control and makes it necessary to develop technologies that allow easy, economical and effective ways to obtain products from endogenous microorganisms with sufficient quality and quantity to their application in the crops areas. In addition to the industrial importance of the genus, certain Trichoderma species have the ability to antagonise plant pathogens. Trichoderma interacts with other microorganisms, but mainly with pathogenic fungi. These interactions include hyperparasitism, competition, and antibiosis. Hyperparasitism is connected with the direct contact of an antagonist with a pathogen and is composed of such stages as: pathogen recognition, attack, gradual penetration of the pathogen cells and death. Contamination of crops with phytopathogenic genera such as Fusarium, Aspergillus, Alternaria, and Penicillium usually results in mycotoxins in the stored crops and are designated as the most devastating species for small grain cereals.

Key words: biological control, phytopathogens, *Trichoderma spp.*

INTRODUCTION

Fungi in the genus *Trichoderma* have been known since at least the 1920s for their ability to act as biocontrol agents against plant pathogens. Phytopathogenic microorganisms and insects have been coexisting with plants since the very beginning of agricultural evolution. For about 70 years, *Trichoderma* spp. have been known to be able to attack other fungi, to produce antibiotics that affect other microbes, and to act as biocontrol microbes (Weindling, 1936; Weindling, 1934). Some landmarks along the way include the discoveries that these fungi frequently increase plant growth and productivity (Lindsey, 1967) either in the presence (Chang, 1986) or absence of other microorganisms and that they can induce disease suppression in soils (Chet, 1981). Further, strains differ remarkably in their abilities to colonize roots (to be rhizosphere competent) and the most effective strains will colonize roots and provide benefits for at least the life of annual crops (Harman, 2000). In addition, the complex mechanisms of mycoparasitism, which include directed growth of *Trichoderma* toward target fungi, attachment and coiling of *Trichoderma* on target fungi, and the production of a range of antifungal extracellular enzymes, were elucidated. These fungi were found to produce a wide range of other extracellular enzymes and some of these were implicated in the biological control of plant diseases (Harman, 2006).

Trichoderma spp. can be efficiently used as spores (especially, conidia), which are more tolerant to adverse environmental conditions during product formulation and field use, in contrast to their mycelial and chlamydospore forms as microbial propagules (Amsellem, 1999). Conidia and mycelia can be produced in either solid-state or liquid fermentation. In general, liquid fermentation is more suitable method over solid-state fermentation for large scale production, still special techniques are required for abundant conidia production (Mausam, 2007). *Trichoderma* fungi are well known for their antagonism against several soil-phytopathogens, involving fungi, invertebrates, and bacteria.

RESULTS AND DISCUSSIONS

Biocontrol genes of *Trichoderma*

The genome sequencing of Trichoderma species has provided exclusive data for phylogenetic and bioinformatic analyses toward understanding the roles of these opportunists in agroecosystems and forced the development of systems biological approaches, initiated and enhanced whole genome expression analysis (Singh et al., 2018). Many genomic studies reveal that Trichoderma spp. contains many valuable genes with great variety of expression patterns, which allows these fungi to use as biocontrol agents, plant growth promotional activities and their environmental adaptation (drought, salt, heavy metal tolerance etc.) At present the most important genome sequences of seven species are: *Trichoderma harzianum*, *Trichoderma asperellum*, *Trichoderma reesei*, *Trichoderma virens*, *Trichoderma atroviride*, *Trichoderma longibrachiatum* and *Trichoderma citrinoviride* (Sharma et al., 2011).

Plant-Trichoderma interaction

The release of various compounds into the rhizosphere by plant roots generates a carbon rich environment and also contributes towards establishing a dynamic molecular communication between roots and soil-inhabiting microbes (Bais et al., 2006). One of the main carbohydrates secreted by plant roots is sucrose, which has been detected in high concentrations near root tips (Kraffczyk et al., 1984; Jaeger et al., 1999; Mahmood et al., 2002). Studies have revealed that this secreted disaccharide plays important roles in the uptake of minerals and in the association of plants with microbial communities (Kraffczyk et al., 1984; Jaeger et al., 1999; Mahmood et al., 2002; Baudoin et al., 2003). Plants, generat sucrose that have several fundamental roles involved in the control of various plant developmental processes. Sucrose coordinates the carbohydrate distribution network in the whole plant and is involved in carbohydrate-mediated signalling pathways. The degradation of sucrose inside the plant cells also yields important sources of carbon and energy for microbes during plant–microbe associations (Dennis and Blakeley, 2000; Koch, 2004). Many fungal species express extracellular invertases that influence sink activity in host tissues and are likely to attract greater amounts of carbohydrates to the infection site (Doidy et al., 2012; Vargas and Kenerley, 2012). Similarly to mycorrhizal fungi, *Trichoderma* spp. can also use monosaccharides produced in the plant root; however, a distinctive feature between *Trichoderma* spp. and mycorrhizal fungi is that most *Trichoderma* spp. are also able to use sucrose as a substrate. In contrast to mycorrhizal fungi, these species of *Trichoderma* gained the ability to use the sucrose released into the rhizosphere with no dependence on the plant metabolism (Vargas et al., 2013). In the presence of plant roots or when growing saprophytically in the presence of sucrose, *T. virens* expresses a highly active intracellular invertase (Vargas et al., 2009). Photosynthesis and carbohydrate metabolism establish the basis for the control of plant growth and productivity. Among carbohydrates, sucrose is the main photosynthetic product that is transported from the source to the sink tissues (Dennis and Blakeley, 2000). The basis of the results reported, sucrose may play two important functions in *T. virens:* (i) as a signal molecule to control plant root colonization; and (ii) as a source of carbon and energy in the rhizosphere.

The endophytic *Trichoderma*

The mechanisms by which *Trichoderma* contributes to disease management are divergent and isolate/species dependent (Harman et al., 2004). Antimicrobial activities, such as mycoparasitism, antibiosis and induced resistance, along with factors contributing to plant growth promotion, such as improved photosynthesis efficiency, nutrient uptake, production of antioxidants and solubilization of nutrients, are some of the most studied of these biological attributes (Howell, 2003; Harman et al., 2004; Vinale et al., 2008; Hermosa et al., 2012). For mycoparasitism to occur, Trichoderma must at least be in the proximity of the target organism to take advantage of metabolites released through enzymatic/toxin activities. In the best described interactions, Trichoderma comes in direct contact with the target organism's cell walls. In some interactions, *Trichoderma* coils around its target, forms appresoria-like structures and directly penetrates (Rocha-Ramirez et al., 2002; Howell, 2003; Harman et al., 2004). The ability of *Trichoderma* to parasitize other hyphae-forming microbes can be both *Trichoderma* specific and target microbe specific (Bailey et al., 2006). During penetration, *Trichoderma* produces many different hydrolytic enzymes capable of degrading the targeted hyphae cell wall. Production of these enzymes can be a direct response to signals coming from the target hyphae (Vinale et al., 2008; Druzhinina et al., 2011). *Trichoderma* species produce a vast array of secondary metabolites, many of which are selectively toxic against microbes rather than to plants, resulting in the process that is called antibiosis (Howell, 1998). Notable examples include gliotoxin and its related metabolites. Gliotoxin has limited toxicity to plants compared with its inhibitory activity against microbes such as *Phytophthora cactorum* (Smith et al., 1990), *Botrytis cinerea* (Di Pietro et al., 1993), *Rhizontonia solani* (Howell et al.,1993) and *Pythium* spp. (Chet et al., 1997). In comparison, viridiol shows poor selectivity, having significant toxicity towards plants (Jones et al., 1988). It is here that endophytic associations, at least at some level, have been implicated in contributing to plant disease and stress management. The best characterized systems indicate that when *Trichoderma* colonizes plant root systems, it penetrates the roots, going a few cells in, where it induces both local and systemic defence reactions that limit further colonization (Harman et al., 2004). Root colonization, which as described includes penetration, may be essential for induced resistance and plant growth promotion (Hermosa et al., 2012). In terms of protection in the field, induced resistance provides protection against disease that is spatially and temporally separated from the application of *Trichoderma* (Harman et al., 2004). *Trichoderma* has been shown to promote growth in a range of crop plants through increased root development, increased secondary root formation (Samolski et al., 2012) and increased shoot size (Hermosa et al., 2012). *T. harzianum* T22 increased maize root growth for the entire cropping season while increasing efficiency of nitrogen use and elemental uptake (Harman et al., 2004). An increase in micronutrient concentrations was implicated in the increased growth of cucumber colonized with *T. harzianum* (later on identified as *T. asperellum* and subsequently as *Trichoderma asperelloides*) T-203 (Yedidia et al., 2001). As mentioned above, root colonization includes the formation of penetration structures (Viterbo and Chet, 2006), expression of enzymes (Yedidia et al., 1999, 2000; Viterbo et al., 2004; Brotman et al., 2008; Moran-Diez et al., 2009), and penetration between cells to a depth of a few cells into the root cortex where plant recognition and defence in the form of enzymes and callose deposition stop growth of the fungus (Yedidia et al., 1999; Harman et al., 2004).

Promotion of plant growth and induction of systemic defence

Plant growth and development are greatly affected by environmental stresses such as drought, salinity, nutrient deficiency, and adverse temperatures. Pathogens can also have a severe impact on plant health, decreasing agricultural production. For the past 50 years, the major challenge of providing sufficient food for the increasing human population has been facilitated by the application of high inputs of chemical fertilizers containing nitrogen (N), phosphorus (P) and potassium (K), which, together with advances in crop and agricultural techniques focusing on shoot biomass and seed yield, has resulted in increasing productivity (Gonzaxszlez et al., 2009; Xing and Zhang, 2010). Current production methods based on high amounts of nutrients are not only costly but also lead to several environmental and health problems (Conway and Pretty, 1988). Additionally, in crops such as wheat and maize, intensive arable cultivation is no longer sustainable because it often leads to soil degradation. Several fungi are known to proliferate in the rhizosphere, the part of the soil that receives the influence of plant roots, or even penetrate plant tissues without causing disease. These include endo- and ecto-mycorrhizas, binucleate *Rhizoctonia spp., Piriformospora indica* and *Trichoderma spp.* (Waller et al., 2005; Shoresh et al., 2010; Harman et al., 2011). Some of these organisms were initially appreciated because of their biocontrol properties antagonizing root pathogens and protecting plants from diseases, but recent studies have demonstrated that they may possess additional attributes for application in agriculture. Many complex interactions between plants

and microorganisms occur at the rhizosphere, the soil zone in close contact with roots. The root system performs the essential activities of providing water, nutrients and physical support to the plant (Contreras-Cornejo et al., 2013). The primary root originates in the embryo and produces many lateral roots during vegetative growth, and each of these will produce more lateral roots. A further adaptation to take in water and nutrients is performed by root hairs. These are long tubular-shaped outgrowths from root epidermal cells. Root hairs play an important role in the uptake of sparingly soluble nutrients that have low diffusion in the soil, such as phosphate. Because they have a small radius, root hairs explore a larger volume of soil per unit of surface area than thicker lateral roots. Root hairs also play a role in modulating the properties and composition of the rhizosphere because they exude high quantities of organic compounds, including organic acids, aminoacids, sugars, proteins, mucilage, phenolics and secondary metabolites (Contreras-Cornejo et al., 2011). Root exudates perform diverse functions in the rhizosphere including mineral weathering, mobilization of nutrients, metal detoxification and growth inhibition of pathogenic bacteria, invertebrate herbivores, or neighbouring plants (Badri and Vivanco, 2009). Some compounds such as organic acids can act as chemotactic signals to attract symbiotic fungi and bacteria (Rudrappa et al., 2008), whereas sugar plays a fundamental role in interactions with mycorrhizal fungi and *Trichoderma* (Vargas et al., 2009, 2011). Microorganisms and plants emit signalling molecules for communication. Plants are able to recognize microbe-derived compounds and adjust their defence and growth responses according to the type of microorganism encountered. This molecular dialogue will determine the final outcome of the relationship, ranging from pathogenesis to symbiosis, usually through highly coordinated cellular processes (Ortiz-Castro et al., 2009). Plant-growth-promoting rhizobacteria (PGPR) are natural rhizosphere inhabiting bacteria that belong to diverse genera such as *Pseudomonas* and *Bacillus* species (Soleimani et al., 2005). The general effect of PGPR is an increased growth and productivity of plants. Their contribution can be exerted through different mechanisms including modulation of root system architecture and increased biomass production through the release of phytohormones such as auxins or cytokinins (Lugtenberg et al., 2002; Lopez-Bucio et al., 2007; Ortiz-Castro et al., 2009). Besides, several fungi such as mycorrhizas, *Trichoderma spp.* can interact with plants in many beneficial ways, some of which resemble those of PGPR. *Trichoderma spp.* are free-living fungi that are common in soil and root ecosystems. They have been widely studied for their capacity to produce antibiotics, parasitize other fungi and compete with deleterious plant microorganisms (Harman et al., 2004). Until recently, these traits were considered to be the basis for how *Trichoderma* exert beneficial effects on plant growth and development. It is clear, however, that certain strains also have substantial direct influence on plant development and crop productivity (Harman, 2006, 2011). It was reported that cucumber seedlings grown in soil amended with *Trichoderma harzianum* propagules sustain a 30% increase in seedling emergence 8 days after sowing. Three weeks later, these plants exhibited a 95% and 75% increase in root area and cumulative root length, respectively, and substantial increases in dry weight (80%), shoot length (45%) and leaf area (80%) were registered (Yedidia et al., 2001).

The use of high quantities of chemical fertilizers in agriculture causes pollution of soils and water bodies. Thus, a major goal of biotechnology is to develop novel strategies to optimize fertilizer use. With this aim, Molla et al. (2012) tested the ability of *Trichoderma spp.* to increase growth of tomato plants when supplied together with fertilizer. It was found that supplementation of fertilizer with Trichoderma enhanced plant production by 50% compared with a standard dose of NPK macronutrients, minimizing the use of fertilizers and their potential negative effects in the environment. A recent application in the field came from manipulation by genetic means of the *T. harzianum,* which encodes a cysteinerich cell-wall protein (Samolski et al., 2012). It is generally believed that plants activate defence responses upon pathogen or insect attack. This means that plants save energy under enemy-free conditions and could invest photosynthetically fixed carbon in growth and reproduction. Interestingly, some types of soil can suppress the symptoms of plant diseases. Research has shown that the observed increased resistance in these plants is the result of the presence of rhizosphere microorganisms, including bacterial and fungal species, which exert their protective effect by directly inhibiting the growth of pathogens or by means of the activation of a part of the plant's immune system (Pieterse et al., 2009).

Trichoderma: mechanisms for controlling pathogens

Trichoderma spp. are the most widely studied mycoparasitic fungi. However, their mycoparasitism is difficult to demonstrate *in situ* until very recently due to technical difficulties in making *in situ* microscopic observations (*e.g.*, fluorescence imaging and differential staining), such as at the soil–root interface. Moreover, techniques involving antibodies, such as combined baiting-ELISA (enzyme linked immunosorbant assay) techniques to detect *Trichoderma* spp. in composts, would certainly increase our understanding of the mycoparasitic interaction of these fungi (Thornton, 2002).

The biocontrol mechanisms attributed to *Trichoderma* spp. are: competition for nutrients, parasitism, antibiosis, secretion of enzymes, and the production of inhibitor compounds (Guédez et al., 2009; Zimand et al., 1996; González-Estrada et al., 2019). This biocontrol agent attacks and penetrates fungal cells, causing an alteration with the consequent degradation of the cell wall, causing retraction of the plasma membrane and disorganization of the cytoplasm (Tronsmo et al., 1977). These mechanisms are favored by the ability of *Trichoderma* to colonize the rhizosphere of plants. Competition is defined as the unequal behavior of two or more organisms before the same requirement (substrate, nutrients), if the use of this substrate by one of the organisms reduces the amount or space available to others. This type of antago- nism is favored by the characteristics of the biological control agent as ecological plasticity, growth rate primarily as chlamydospores (Hjeljord et al., 1998) speed of development, and external factors such as soil type, pH, temperature, and humidity (Ahmad, 1987). Nutrient competition can occur for nitrogen nonstructural carbohydrates (sugars and polysaccharides such as starch, cellulose, chitin, laminarin, and pectin, among others) and microelements (González-Estrada et al., 2019). Mycoparasitism is defined as an antagonistic symbiosis between organisms, generally involving extracellular enzymes such as chitinases, cellulases, and which correspond to the composition and structure of the cell walls of parasitized fungi (Lorito et al., 1990). Degradation of the cell walls of the host is observed in the late stages of the parasitic process (Carsolio et al., 1999), which leads to almost total phytopathogen weakening. *Trichoderma* can excrete metabolites like cellulases, glucanases, lipases, prote- ases, and chitinases in order to facilitate the insertion of hyphae for nutrient uptake of the pathogen, ending with the loss of cytoplasmic contents of the host cell (Demain et al., 2008). Antibiosis is the inhibition of pathogen development by metabolized products and small toxic molecules, volatile and lytic enzymes, which operate structural polymers, such as chitin and β-1-3-glucans of the cell wall in most pathogenic fungi, producing an adverse effect on development and differentiation (Goldman at al., 1994). Given the above, it is said that the greater the amount of metabolic products, the antagonistic power increases; additionally, some authors mention that this mechanism is not the principle, due to the risk of emergence of the antibiotic-resistant pathogens (Goldman at al., 1994). The production of enzymes such as chitinase and/or glucanases produced by the fungus of *Trichoderma* is involved in the control of pathogenic fungi. These hydrolytic enzymes can degrade the cell wall polysaccharides (chitin and β glucans) affecting its stability and integrity (Howell et al., 2003; González-Estrada et al., 2019).

For example, *Trichoderma* has been applied as postharvest biocontrol agent in different crops such as strawberries, tomatoes, apples and pears. Existing different species of *Trichoderma* with high antagonistic capacity are *T. asperellum*, *T. viride*, and *T. harzianum.* Several authors have investigated different species of *Trichoderma* with the objective to find the most effective biocontrol agent for each crop and pathogen. At present, *Trichoderma* is produced at industrial level as active component of biological products “biopesticides”; other ingredients that conform the biopesticides are the edible polymers, which can form coating for easy adhesion to the fruit and give to the product protection and stability dur- ing its shelf life. The application of biopesticides is widely used in agriculture and can be applied by immersion or spraying during the industrialization of agricultural products (Marín et al., 2017). The incorporation of *T. harzianum* into edible coatings as biopesticide produced higher inhibition of the pathogens *Botrytis cinerea* and *Penicillium expansum* compared to the application as simple conidial suspension of the antagonist on the fruits (Batta et al., 2015). The same author previously reported the same effect on other fruits such as pears, grapes, apples, strawberries and peaches [Batta et al., 2004, 2007; González-Estrada et al., 2019). Yasmeen et al. (2017), demonstrated that shoot and root length of maize significantly declined with the increase in salinity concentration in the soil. However, seed of maize treated with *Trichoderma harzianum* (has shown substantial increase in plant mM NaCl treatments as compared to those plants that were not treated with *Trichoderma.* Anothert study (Zhang et al., 2019) also showed that *Trichoderma* species played a critical role in host plant metabolic processes in response to NaCl stress. The use of *T. longibrachiatum* TL-6 strain increased proline content in wheat seedlings under NaCl stress, which helped maintain the cell osmo regulation (Rasool et al., 2013) and energy storage (Aggarwal et al., 2012).

Shoresh and Harman observed that tomato plants inoculated with *T. harzianum* expressed genes that encode antioxidant enzymes (Shoresh and Harman, 2008). Mastouri et al. (2010) proved that under conditions of osmotic saline stress or extreme temperatures, tomato seeds treated with *T. harzianum* T22 germinated earlier and more evenly than did non-inoculated seeds. Similarly, soil application of *T. viride* along with farm yield manyre (FYM) and NPK increased the plant growth parameters, grain yield, and biomass of wheat crop (Mahato et al. ,2018). Hajieghrari (2010) found that maize crop treatment with T. *hamatum* T614 isolate increased the leaf area, shoot weight, and fresh roots of seedling compared to the non-inoculated seedling. Similarly, bulb treatment with *T. harzianum* enhanced the plant growth of tuberose and resulted in increased flower production and quality (Nosir, 2016). The application of *Trichoderma* strains TH1 and T4 increased root weight, shoot weight, and dry root weight against Pythium. In addition, lateral root development and nodule formation were also found to be enhanced. Application of *Trichoderma* strains TH1, T4, and T12 significantly increased the soil fungal population and significantly reduced the cell-wall- degrading enzyme activities of *Pythium* (Naseby et al., 2000). A typical interaction of *Tricoderma* with *Fusarium* involves attraction, attachment, coiling, and lysis by hydrolytic enzymes or secondary metabolites (Mukherjee et al., 2012).

Many previous studies have established a beneficial effect of *Trichoderma* on several pathogens that affect this crop, especially the most representative, *Fusarium oxysporum, Phytophthora capsici*, and *Rhizoctonia solani*, so its application is common as part of integrated management programs of these diseases. It was observed that the greatest effect on root length was *T. asperellum* with the lowest concentration of conidia (1.0 x 10^6 conidia/ml), which draws attention to the issue of doses that are recommended for field applications (Bal and Altintas, 2006).

CONCLUSIONS

Trichoderma species establish complex and dynamic interactions with inhabitants of the rhizosphere, such as plant roots and microbes.

The metabolic activity of the fungal cells mainly depends on the uptake and degradation of different carbohydrate sources. Because of the metabolic complexity of carbon metabolism in fungal cells, intricate regulatory pathways control the carbon flux from the rhizosphere to the fungal cells that is vital for root colonization and the fungal life cycle.

Peptaibols, linear oligopeptides produced by *Trichoderma spp*., inhibit beta-glucan synthase which prevents the pathogen from reconstructing its cell wall. Culture filtrates of a *T. harzianum* isolate changed the colony color of *A. flavus* and had a clear effect on the growth. *T. viride* showed a potent antagonisms of *F. verticillioides* in an in vitro assay which was proven by the suppression of radial extension of the fungus by 46% after 6 days and by 90% after 14 days. Like biocontrol agent is a safer and the cheapest method to control these severe diseases and to facilitate better plant growth, yield, and production. The pathogenic fungi *Fusarium spp*. generally cause wilt nearly in all the crop plants from various groups and cause a severe threat to food demand. Among the various biocontrol agents, *Trichoderma spp*. are considered to be the most beneficial, and they assure increased level of safety with minimum environmental impacts.

Trichoderma spp. are well-known fungi that enhance plant growth by nutrient solubilization in the soil, growth hormones production in plants, and defense against pathogens. Due to these characteristics, *Trichoderma* protect the plants against various biotic as well as abiotic stresses. To defend against pathogenic fungi, various mycotoxins have been reported to be produced in this fungus. In the interaction of *Trichoderma* with *Fusarium* a mechanism involves in a series from attraction to cell lysis via attachment and coiling of hyphae through different hydrolytic enzymes and second- ary metabolites.

Trichoderma-based bioinoculants are increasingly used in agriculture, with several hundred formulations available as registered products worldwide. Several strategies have been applied to identify the genes and signals involved in the interactions of *Trichoderma* with plants. Biological control is applicable and many novel methods are being discovered, mostly based on microbiological research and the application of microorganisms that can suppress fungal growth and detoxify mycotoxins. *Trichoderm*a reduce the damage and suppress the fungal growth, it is common to add antifungal substances during growth in the field or storage.

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