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Review

Diversity in plant systemic resistance induced by *Trichoderma*

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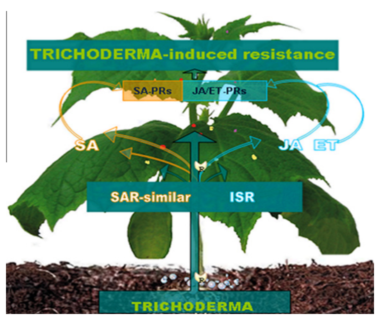
HIGHLIGHTS

- *Trichoderma* may be biological control agent able to induce systemic resistance in plants.
- Elicitors released by *Trichoderma* are involved in induction of defense mechanisms.
- Defense induction leads to changes on physiological, biochemical and molecular level.
- *Trichoderma*-induced resistance may include both ISR and SAR pathways in plants.

GRAPHICAL ABSTRACT



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ABSTRACT

Trichoderma species includes many important in agriculture strains, known as effective biological control agents (BCAs). While their capability of mycoparasitism and strong position as antagonists of pathogenic microorganisms are quite well understood, there are still many questions about the process of systemic resistance induced in plants by these fungi. During plant – *Trichoderma* interaction, numerous elicitors released by the *Trichoderma* hyphae may induce different types of signals transmitted within the plant e.g. by salicylic acid (SA), jasmonic acid (JA) or reactive oxygen species (ROS), triggering expression of defense proteins. As a result of gene activation, the plant produces enzymes involved in direct supression of pathogens and enhancing the biochemical and structural barriers in plant organism. Depending on the *Trichoderma* strain, plant species as well as biotic and abiotic conditions, the defensive reactions activated by fungi may oscillate between the two types of systemic resistance: induced systemic resistance (ISR) and systemic acquired resistance (SAR). Different pathways of ISR are investigated both at the biochemical and molecular level, however there are still many issues that need clarification. The main objective of this paper is to present an overview of information about the influence of *Trichoderma* on the diversity of systemic resistance induction in plants and the possible development of this process.

1. A wide range of resistance responses induced in plants by fungi of the *Trichoderma* species

Nowadays, a lot of attention is paid to physiological and biochemical reprogramming of plants, triggered by dynamic interaction with their microflora, and by abiotic environmental influence which activates immunity called induced resistance (Baker et al., 2012; Mathys et al., 2012; López-Mondéjar et al., 2011; Contreras-Cornejo et al., 2011; Salas-Marina et al., 2011; Perazzolli et al., 2008). Induction of immunity in plants is the consequence of interactions between different elicitors released by microorganism and plant receptors, leading to the activation of signalling pathways, triggering physiological and biochemical changes in plants (Harman et al., 2012; Contreras-Cornejo et al., 2011; Mastouri et al., 2010). This leads to earlier and stronger reactions to pathogen and parasite attack, which significantly reduce the possibility of disease spread. This resistance may persist for long periods, at least several months. After termination a re-induction is necessary (Harman et al., 2012; Mathys et al., 2012;

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Salas-Marina et al., 2011; Contreras-Cornejo et al., 2011; Sriram et al., 2009; Perazzolli et al., 2008).

There is a large array of evidence showing how soil-borne microorganisms, such as rhizosphere fungi and bacteria, may play an important role in suppression of plant diseases by direct control of root and foliar pathogens as well as by induction of systemic resistance in plants. The ability of these microorganisms, called biological control agents (BCAs), to facilitate plant immunity has initiated their regular application in biological plant protection, resulting in decrease in pesticide use (Carreras-Villaseñor et al., 2012; Ryder et al., 2012; Harman et al., 2012; Hermosa et al., 2012; Salas-Marina et al., 2011; Mastouri et al., 2010; Perazzolli et al., 2008). Among BCAs there are microscopic fungi of the *Trichoderma* species, to which a lot of attention has been paid for several decades. Their ability to positively influence plants as well as their resistance to toxic compounds which allows to use these fungi with reduced doses of pesticides, are tested under laboratory and field conditions (Carreras-Villaseñor et al., 2012; Omann et al., 2012; Harman et al., 2012; Salas-Marina et al., 2011; Contreras-Cornejo et al., 2011; Katayama and Matsumura, 2009).

Trichoderma species form a diverse, belonging to Sordariomycetes, filamentous fungi group, common in the ecosphere. Friedl and Druzhinina (2012) suggest that a relatively small number is adapted to use soil as a habitat. These strains are often characterized by rapid growth and intensive production of spores under different environmental conditions, including changing nutrient status and pH (Harman et al., 2012; Carreras-Villaseñor et al., 2012; Hermosa et al., 2012; Steyaert et al., 2010; Schuster and Schmoll, 2010; Vinale et al., 2008b). Some are able to effectively colonize roots and shoots and efficiently communicate with plants by chemical signals (Carreras-Villaseñor et al., 2012; Harman, 2012; Hermosa et al., 2012; Contreras-Cornejo et al., 2011; Salas-Marina et al., 2011; Schuster and Schmoll, 2010). Depending on the strain, the positive influence of *Trichoderma* on plants may be associated with stimulation of plant growth and biomass production, and/or protection against pathogens. Some *Trichoderma* strains are able to provide plants with nutrients and hormones. Others change the internal plant phytohormone homeostasis and/or strenghten its photosynthesis and carbohydrate metabolism. Some strains are known mainly to supress diseases caused by pathogens or alleviate abiotic stress, where *Trichoderma* may exhibit mycoparasitic properties or be a pathogen antagonist (Harman, 2012; Hermosa et al., 2012; Carreras-Villaseñor et al., 2012; Contreras-Cornejo et al., 2011; Salas-Marina et al., 2011; Shoresh et al., 2010; Mastouri et al., 2010; Viterbo et al., 2010; Karolev et al., 2008; Djonović et al., 2006). However, the ability of the selected *Trichoderma* strains, avirulent endophytic symbionts, to induce plant defense response and systemic resistance is essential for plant protection against a wide spectrum of viral, bacterial and fungal pathogens (Carreras-Villaseñor et al., 2012; Harman, 2012; Contreras-Cornejo et al., 2011; Salas-Marina et al., 2011; Mastouri et al., 2010; Schuster and Schmoll, 2010; Sriram et al., 2009; Perazzolli et al., 2008). Taking into account that activation of defense mechanisms may use up energy and materials, limiting growth and development of plants, it is important that both plant growth and immunity are stimulated by the same strain (Bolton, 2009). Such abilities of *Trichoderma* strains allow to use some of them as BCAs in agriculture, where *Trichoderma* is a genus of particular interest (Carreras-Villaseñor et al., 2012).

There is a large body of literature describing *Trichoderma* species, among which BCAs useful for different necrotrophs, hemibiotrophs or biotrophs are being looked for. The number of known microorganisms able to induce resistance in the dicots or monocots belonging mainly to *Brassicaceae*, *Graminaceae*, *Solanaceae* or *Cucurbitaceae* is growing constantly (Mukherjee et al., 2012; Baker et al., 2012; Mathys et al., 2012; Salas-Marina et al., 2011; Mastouri et al., 2010; Maischak et al., 2010; Segarra et al., 2010). It is important that resistance induction may vary because of the influence of abiotic environmental factors, as well as presence of microscopic pathogens and symbionts in the rhizosphere (Contreras-Cornejo et al., 2011; Schuster and Schmoll, 2010). There are known examples of strains whose positive impact on plants has been observed only under unfavorable environmental conditions. Mastouri et al. (2010) showed that influence of *Trichoderma harzianum* T22 was particularly pronounced under abiotic stress conditions and during plant contact with pathogen *Pythium ultimum*, against which defense mechanisms evolved. Analogously, in the Sriram et al. (2009) and Morán-Diez et al. (2009) investigations the *Trichoderma*-induced resistance associated changes were observed mainly in plants inoculated with pathogens i.e. *Rhizoctonia solani* or *Phytophthora capsici*. The fact that *Trichoderma* induces various resistance pathways in different biotic and abiotic conditions call for further physiological, biochemical and more often molecular analyses.

2. *Trichoderma* elicitors involved in the induction of plant resistance

Although molecular and biochemical processes underlying *Trichoderma*-induced plant resistance have not been fully elucidated yet, it is known that resistance development is tiggered by the exchange of microbial and plant elicitors essential for interactions between organisms. Therefore, plant defense mechanisms do not necessarily require stimulation by a living fungus (Mukherjee et al., 2012; Osbourn, 2010; Schuster and Schmoll, 2010; Djonović et al., 2006). Depending on the involved elicitors released by *Trichoderma* hyphae, interaction of these molecules with plant receptors may determine the adhesion and recognition of *Trichoderma*, and then the induction of resistance in plants. Below are the examples of molecules released by *Trichoderma* whose ability to induce resistance is emphasized (Mathys et al., 2012; Salas-Marina et al., 2011; Shoresh et al., 2010; Sriram et al., 2009; Djonović et al., 2006).

Elicitors involved in induction of resistance include secondary metabolites released by *Trichoderma* hyphae e.g. proteins with enzymatic activity as well as plant and *Trichoderma* cell wall components (López-Mondéjar et al., 2011; Sriram et al., 2009; Djonović et al., 2006). Pectins, phospholipids and saccharides have been noticed among plant molecules able to activate defense against pathogens (Mathys et al., 2012). Some *Trichoderma* elicitors which can induce a battery of changes in plants are similar to the avirulence gene products as well as microbe-associated molecular patterns (MAMPs), also known as pathogen-associated molecular patterns (PAMPs), common slowly evolving molecules unique to microorganisms (Bolton, 2009; Djonović et al., 2006). Elicitors released by fungi fall into several classes, the most important of which are proteins or peptides with low molecular weight ranging from 6 to 42 kDa (Salas-Marina et al., 2011; Sriram et al., 2009), enzymes i.e. serine proteases, xylanases chitinases, cellulases or glucanases (Shoresh et al., 2010; Aidemark et al., 2010; Morán-Diez et al., 2009), indole compounds (Gravel and Tweddell, 2007), fatty acids, lipids and their derivatives, such as glycosphingolipids (Mukherjee et al., 2012; Uchiyama et al., 2009), and also polysaccharides or oligosaccharides, including chitin and chitin-like compounds (Mathys et al., 2012; de Jonge et al., 2010; Bolton, 2009).

It is known that certain classes of proteins participate in plant – *Trichoderma* interaction and act directly against pathogens. Small extracellular cysteine-rich proteins produced by *Trichoderma* strains, secreted by fungal hyphae, especially in the presence of a host plant, are an important group of compounds involved in mycoparasitism and resistance induction (Djonović et al., 2006). Small proteins 1 (Sm1) required, for example, in *Trichoderma*