

Review Article

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Review on Plant-*Trichoderma*-Pathogen Interaction

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ABSTRACT

Trichoderma spp. are the most successful biocontrol agents as more than 60% of the registered bio-fungicides used in today's agriculture belongs to *Trichoderma*-based formulation. Plant-*Trichoderma*-pathogen is a complex network of multiple mechanisms. Presently many labs tried to dissecting the networking of three way cross talk in Plant-*Trichoderma*-Pathogen interaction. Proteome and genome analysis have greatly enhanced the ability to conduct holistic and genome-based functional studies as they have identified and determined the role of a variety of novel genes and gene-products, including ABC transporters, enzymes and other proteins that produce or act as novel elicitors of induced resistance, proteins responsible for a gene-for-gene avirulent interaction between *Trichoderma* spp. and plants, antagonism related gene, plant proteins specifically induced by *Trichoderma*, etc. but there is still much more left than what has been searched. Understanding these mechanisms at the molecular level would help in designing the strains with superior biocontrol properties. Here we review our current understanding of the genetics of interactions of *Trichoderma* with plants and phytopathogens and their role in mode of action. These factors are expected to enhance not only the rapid identification of effective strains and their applications but also indicate the potentials for improvement of natural strains of *Trichoderma*.

Keywords

Plant-*Trichoderma*-Pathogen network, Biocontrol genes, PGPF, MAMPs, Induced resistance, Mode of action

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Introduction

World population of 9.1 billion people in 2050 would require raising of overall food production by some 70% (FAO, 2009). The substantial increase in food grain production over the years has helped to meet the food security needs of the country, but the number of biotic and abiotic stress causes the yield losses up to a large extent. Biotic constraints include fungi, bacteria, virus, nematodes weeds, and insects which causes yield loss up to 31-42% (Agrios, 2005). Therefore pesticide consumption was also increases year by year

as 45.39 thousand tons pesticides were consumed in the year 2012-13 (Krishijagan, 2015). Besides affecting the environment and non-target organisms, continuous and tremendous use of chemical pesticides creates high selection pressure on pathogens which force to mutation inside the pathogens and development of pesticide resistance races such as dodine and metalaxyl resistance in *Venturia inaequalis* and *Phytophthora infestans* and respectively (Meszka *et al.*, 2008, Matson *et al.*, 2015). Pesticide resistance and environment threat due to injudicious use of chemical pesticides for disease management

employs the introduction of a new alternative as biological control. The use of biofertilizers and biopesticides is an alternative for sustaining high production with low ecological impact. Besides the classic mycorrhizal fungi and *Rhizobium* bacteria, other plant-growth-promoting fungi such as *Trichoderma* spp. (Teleomorph: *Hypocrea*) can stimulate plant growth by suppressing plant diseases (Van Wees *et al.*, 2008). Biological control agents, comprises a number of fungus and 90% of such application have been carried out from different strains of *Trichoderma*, the antagonistic properties of which are based on the activation of multiple mechanisms.

Biological control is a key constituent of integrated pest management that has generated interest among farmers for ecological and sustainable disease management. The genus *Trichoderma* possessing reasonable biological control attributes belonging to species *T. Harzianum*, *T. resseyi*, *T. asperellum*, *T. viridae*, *T. virens*.

Trichoderma spp. are ubiquitous and often predominant components of the mycoflora in soil, litter, organic matter and rhizospheric ecosystem of all climatic zones as saprophytes. Recent discoveries show that they are opportunistic, avirulent plant symbionts, as well as being parasites of other fungi. Strains of *Trichoderma* Spp. are endophytes establish robust and long-lasting colonizations of root surfaces and penetrate into the epidermis. However, the ability of these fungi to sense, invade, and destroy other fungi has been the major driving force behind their commercial success as biopesticides. *Trichoderma* defend the plants by their direct and indirect effect on plant-pathogen-soil environment interaction. These fungi not only protect plants by killing the pathogens mainly other fungi and nematodes but also induce resistance against plant pathogens, impart

abiotic stress tolerance, improve plant growth and vigor, nutrients uptake and bioremediation of heavy metals and environmental pollutants. In addition, this genus comprises fungi that produce secondary metabolites of clinical significance and enzymes with widespread industrial application. They produce and/or release a variety of compounds that induce localized or systemic resistance responses. These root-microorganisms interaction cause significant changes to the plant metabolism. Plants are protected from numerous pathogens by responses that are similar to systemic acquired resistance and rhizobacteria-induced systemic resistance. Root colonization by *Trichoderma* spp. also frequently enhances root growth and development, crop productivity, uptake and use of nutrients and resistance to biotic and abiotic stress. Detailed study as how *Trichoderma* evolved to interact with other fungi and with plants will improve and expand their applications in biological control programme. The ability to attack on soil borne plant pathogens dominated the interest in *Trichoderma* for many years. From past few years the researchers show their interest on plant disease resistance as [induced systemic resistance (ISR); to some extent, systemic acquired resistance (SAR)] induced by the *Trichoderma*-root symbiosis (Harman *et al.*, 2004 and Hermosa *et al.*, 2012).

Trichoderma spp. is most successful bio-fungicides in present agriculture as more than 60 % of the registered biofungicides worldwide arrived from *Trichoderma*-based formulations (Verma, *et al.*, 2007). In India alone, about 250 products are available for field applications but the percentage share of bio-fungicides is only a small part of the fungicides market and dominated by synthetic chemicals (Singh, *et al.*, 2009). The major drawback of bio fungicides are slow to act, and influenced by environmental factors. Hence their efficacy under field conditions is restricted. Here, “genetic manipulation” to

design new strains that are more effective than the native ones might prove useful. It could be achieved by gaining knowledge on the molecular mechanisms of interactions of these organisms with other biotic and abiotic factors. We summarize here the recent findings on the genetics of three way interactions of *Trichoderma* with plants and pathogens and their mode of action.

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. At present the, genome sequences of seven species: *Trichoderma harzianum*, *Trichoderma asperellum*, *Trichoderma reesei*, *Trichoderma virens*, *Trichoderma atroviride*, *Trichoderma longibrachiatum* and *Trichoderma citrinoviride* are available (Sharma *et al.*, 2011). 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.). Several laboratories have recently started or planned to use proteomic and genomic analysis to frame the changes that occur in the *Trichoderma*, plant, and pathogen when they interact to each other, especially when an increase in disease resistance is generated.

Plant-*Trichoderma* interaction

Plant growth promotional activity

Positive effect on plant development has been demonstrated for several *Trichoderma*

Secondary Metabolites. Koninginins, 6-pentyl-a-pyrone, trichocaranes A – D, harzianopyridone, cyclonerodiol, harzianolide and harzianic acid are examples of isolated compounds that affect plant growth in a concentration dependent manner (Vinale *et al.*, 2014).

Effect on seed germination

Seed biopriming and seed treatment with *Trichoderma* spp. trigger the release and/or production of enzymes and phytohormones which are involved in seed germination. It also enhances the speed of germination and seedling vigor. Enhanced germination percent have been found in okra, maize, beans, mustard, chilli, soyabean, chickpea, tomato etc. (Mukhtar, 2008, Okoth *et al.*, 2011, Rahman *et al.*, 2012, Lalita *et al.*, 2012, Kumar *et.al.*, 2014, Babychan and Simon, 2017). Many seed invading pathogens such as *Pythium* are unable to attack on host due to faster seed germination and seedling vigor (Matsouri, *et al.*, 2010). Bezuidenhun *et al.*, (2012) reported that *Trichoderma harzianum* produces a metabolite as gliotoxin that may mimic the plant growth hormone gibberellic acid which is involved seed germination process. Seed and/ or soil treatment with *Trichoderma* enhances seed germination percentage, directly by activating enzymes and phytohormones and indirectly by altering soil microflora and nutrient availability in soil. By this way farmers get better field stand.

Effect on plant morphology

The rhizosphere supports microbial populations capable of exerting beneficial, neutral, or detrimental effects on plant growth. *Trichoderma* spp. are able to enhance rice growth components including plant height, leaf number, tiller number, root length and root fresh weight. In maize (*Zea mays*) plants, *Trichoderma* inoculation affects root

system architecture including enhanced root biomass and increased root hair development (Bjorkman *et al.*, 1998; Harman *et al.*, 2004). The root system is important for plant fitness because it provides anchorage, contributes to water use efficiency, and facilitates the acquisition of mineral nutrients from the soil. The two *Trichoderma* species, *Trichoderma harzianum* and *Trichoderma virens* has been found for growth promotional activity which was correlated with prolific formation of lateral roots (Contreras-Cornejo *et al.*, 2009). The ability of *Trichoderma spp.* to produce phytohormones is the key factor in the increase in rice plant height (Chowdappa *et al.*, 2013). Many lines of evidence strongly support a role for auxin in the regulation of root system architecture. *T. virens* is able to produce auxins as indole-3-acetic acid (IAA), indole-3-acetaldehyde (IAAld), and indole-3-ethanol (IET), which has been play roles in plant growth and development (Contreras-Cornejo *et al.*, 2009). Cai and coworker (2013) reported that harzianolide produced by *Trichoderma spp.* can improve the early stage of plant development through the enhancement of root length. Leaf number and tiller number has been found significantly higher in *Trichoderma spp.* treated rice plants compared to NPK treatment and control (Doni *et al.*, 2014). Line of evidence for enhancement of number of leaves, tillers, branches, flowers, fruits and plant height by *Trichoderma spp.* are available (Neumann and Laing, 2006, Sajeesh, 2015). Cai *et al.*, (2013) reported that harzianolide produced by *Trichoderma spp.* can improve the early stage of plant development through the enhancement of root length. These morphological modification are possible because of the ability of the *Trichoderma spp.* to act through several mechanisms such as environmental buffering (against pH, drought, waterlogging, cold and heat), Phosphorus solubilization, organic matter

decomposition, chilation and siderophore production.

Effect on plant physiology

Trichoderma spp. are able to alter several physiological processes which include net photosynthetic rate, stomatal conductance, transpiration, internal CO₂ concentration, water use efficiency and nutrient uptake. Better nutrient uptake will enhance the physiological processes within the plants treated with *Trichoderma spp.* leading to good growth performance (Doni *et al.*, 2014, Saba *et al.*, 2012.) Micro nutrients such as Nitrogen and Magnesium are the component of chlorophyll and enzymes of m-RNA synthesis and gene regulation engaged in photosynthesis.

Trichoderma harzianum significantly increased the ability of rice plants to tolerate drought stress and increase rice water-holding capacity (Shukla *et al.*, 2012). Approximately three folds increase in net photosynthetic rate and stomatal conductance and two fold increase in water use efficiency in *Trichoderma* treated rice plants as compare to NPK treated plants has been observed (Doni *et al.*, 2014). High photosynthetic rates coupled with low transpiration rates in *Trichoderma* treated plants indicate high water use efficiency (Thakur *et al.*, 2010, Doni *et al.*, 2014). Low internal CO₂ concentration and high photosynthetic rate in *Trichoderma* treated plants are correlated as the activity of carboxylation by CO₂ fixation for glucose production during carbohydrate metabolism very active (Thakur *et al.*, 2010). The activity of *Trichoderma spp.* that contributes to the enhancement of root growth and distribution was also considered as a key factor to the prolonged photosynthetic activity and the delayed senescence in rice plants (Mishra and Salokhe, 2011). *Trichoderma* releases cellulases which degrade cellulose and enhance the organic matter and nutrients in

rhizosphere. Jiang *et al.*, (2011) Solubilization and chelation of minerals can enhance nutrient availability which is engaged in plant metabolism leading to the enhancement of plant physiological activity (Herman, *et al.*, 2004).

Effect on yield and quality of produce

Trichoderma effect on seed germination, plant morphology and physiology leads to better field stand and it also accelerates the vegetative and reproductive growth of plants. It enhances number of branches, spikes, flowers and fruits per plant. In many cases average weight of individual fruit is also comparatively higher. Higher yield by the application of *Trichoderma* species in mustard, wheat, corn, tuberose, sugarcane, tomato, okra etc. has been found (Haque *et al.*, 2012, Katatny and Idres, 2014, Naznin *et al.*, 2015., Shrivastava *et al.*, 2006, Tucci *et al.*, 2011, Idowu *et al.*, 2016).

Induced resistance against biotic and abiotic stress

Plants have an immune system that is able to detect motifs or domains with conserved structural traits typical of entire classes of microbes called as microbe-associated molecular patterns (MAMPs) (Hermosa *et al.*, 2012). The ability of *Trichoderma* spp. hyphae to release MAMPs for molecular recognition may contribute for signal cascade by signaling molecule within the plant such as salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). Earlier it was believed that JA and/or ET are the signaling molecule for *Trichoderma* induced resistance but recent finding shows that involvement of SA also. Colonization of *Arabidopsis* root by *T. asperellum* produces a clear ISR through an SA signalling cascade, and both the SA and JA/ET signalling pathways combine in the ISR triggered by cell-free culture filtrates of *Trichoderma*

(Yoshioka *et al.*, 2011). *Trichoderma* is able to trigger a long-lasting upregulation of SA gene markers in plants unchallenged by pathogens, although when plants are infected by a pathogen such as *B. cinerea*, the pretreatment with *Trichoderma* may modulate the SA-dependent gene expression and, soon after infection, the expression of defence genes induced through the JA signal transduction pathway occurs, causing ISR to increase over time (Tucci *et al.*, 2011); Elicitors released by *Trichoderma* spp. are also involved in triggering expressions of defense protein within the plant (Thakur and Sohal, 2013). In this way, plant immunity against pathogens is induced and in turn improves plant growth. A common feature of induced resistance responses of beneficial microbes is priming for enhanced defence. In primed plants, defence responses are not activated directly, but are accelerated upon attack by pathogens or other stress resulting in faster and stronger resistance to the attacker encountered (Van *et al.*, 2008). *Trichoderma* act locally and systemically that involve signaling cascade and activation and accumulation of defense related antimicrobial compounds which includes enzymes as Phenyl ammonia lyase (PAL), Peroxidase, polyphenol oxidase, Lipoxygenase; Proteins as PR (pathogenesis related protein), Terpenoid, phytoalexin as Rishitin, Lubimin, Phytoalexin, coumarin, solevetivone, Resveratrol and antioxidant as ascorbic acid, glutathione etc. (Howell *et al.*, 2000).

Plant-*Trichoderma* networking

Plant immunity and development are interconnected in a network of hormone-signalling pathways (Pieterse *et al.*, 2009). There is a cross-communication between SA, JA and ET, the central players in defence and the response pathways of other hormones such as abscisic acid gibberellic acid and auxin commonly associated with plant development

and abiotic stress, IAA, related to plant growth and lateral root development, and gibberellins, which control plant growth by regulating the degradation of growth-repressing DELLA proteins (Hermosa *et al.*, 2012). In *Trichoderma*, the ACCD activity reduces the availability of ACC necessary for ET biosynthesis. Reductions in ET promote plant growth via gibberellin signalling by increasing the degradation of DELLA proteins. Moreover, gibberellins may control the onset of JA- and SA-dependent defence responses of the plant through the regulation of DELLA protein degradation (Brotman *et al.*, 2013). ET and IAA in the roots can reciprocally regulate each other's biosynthesis (Stepanova *et al.*, 2007). In *Trichoderma* IAA contributes to exogenous auxin-stimulated ET biosynthesis via ACC synthase (Hansen and Grossmann, 2000), which in turn triggers an increase in abscisic acid biosynthesis. Depending on the timing and outcome of *Trichoderma* stimuli, phytohormone homeostasis will control plant development and immune responses.

Trichoderma-pathogen interaction

Trichoderma prove antagonistic interaction with pathogen by following mode of action.

Mycoparasitism

The process of mycoparasitism involves direct attack of one fungal species on another one. Mycoparasitism is one of the main mechanisms involved in the antagonisms of *Trichoderma*. The events leading to mycoparasitism are complex, and take place as follows: Chemotropic growth of *Trichoderma*, recognition of the host, coiling and appressoria formation, secretion of hydrolytic enzymes, penetrations of the hyphae and lysis of the host. This complex process includes sequential events, involving cycle of recognition by the binding of carbohydrates in the *Trichoderma* cell wall to

lectins on the target fungus, hyphal coiling and appressoria formation which contains higher amount of osmotic solutes such as glycerol and induces penetration, attack on cellular machinery via producing several fungitoxic cell-wall-degrading enzymes glucanases, chitinases and proteases (Harman *et al.*, 2004), cumulative action of these compounds result in parasitism of the target fungus and dissolution of the cell walls. At the site of appressoria formation holes can be produced in the target fungus leads direct entry of *Trichoderma* hyphae into the host lumen and finally killing of the host (Kumar, 2013). There are at least 20-30 genes, proteins and other metabolites that are directly involved in this interaction. The functions of different glucanases and chitinases in the process of mycoparasitism are well studied from *Trichoderma* spp. using gene-for-gene experiments and future studies will definitely help us to understand this complex process (Daguere *et al.*, 2014).

Antibiosis

Antibiosis is an antagonistic interaction involving low molecular weight diffusible secondary metabolites or antibiotics produced by a microorganism that are detrimental for the growth of pathogens. *Trichoderma* spp. produces a variety of antibiotics, such as gliovirin, gliotoxin, viridin, viridol, koniginins, pyrones and peptaibols, against fungal phytopathogens (Howell, 2003; Harman *et al.*, 2004). Trichokonins VI, a type of peptaibol from *Trichoderma pseudokoningii* SMF2, exhibited antibiotic activities by inducing extensive apoptotic programmed cell death in fungal pathogens (Shi *et al.*, 2012). Gliotoxin and gliovirin are the two most important *Trichoderma* secondary metabolites belonging to P and Q group strain respectively "P group strains of *Trichoderma (Gliocladium) virens* is active against *P. ultimum*, but not against *R. solani*

and Q group is very active against *R. solani*, but less against *P. ultimum*" (Howell, 2000). "The *T. virens* *veA* ortholog *vel1* (VELVET protein Vel1) is involved in regulation of gliotoxin biosynthesis, biocontrol activity and many other secondary metabolism- related genes" (Mukherjee *et al.*, 2013). "Koninginin D also inhibited the growth of soil-borne plant pathogens, such as *Rhizoctonia solani*, *Phytophthora cinnamomi*, *Pythium middletonii*, *Fusarium oxysporum* and *Bipolaris sorokiniana*" (Dulop *et al.*, 1989). Viridins isolated from diverse *Trichoderma* spp. (*T. koningii*, *T. viride*, *T. virens*), prevents spore germination of *Botrytis allii*, *Colletotrichum lini*, *Fusarium caeruleum*, *Penicillium expansum*, *Aspergillus niger* and *Stachybotrys atra* (Singh *et al.*, 2005). Harzianic acid isolated from a *T. harzianum* strain showed in vitro antibiotic activity against *Pythium irregulare*, *Sclerotinia sclerotiorum* and *R. solani* (Vinale *et al.*, 2009). The isolation and over expression of *tri5* (trichodiene synthase) gene in *T. brevicompactum* *Tb41tri5* transformant increased the trichodermin production and fungal activity against *Aspergillus fumigates* and *Fusarium* spp. (Tijerino *et al.*, 2011). *T. asperellum* strain produces two asperelines (A and E) and five trichotoxins (T5D2, T5E, T5F, T5G and 1717A) which can be associated with antibiosis (Brito *et al.*, 2014).

Competition

Competition for substrates is the most important factor for fungi as is competition for light in the case of evolution of plants (Garrett, 1956). The most common reason for the death of many microorganisms growing in the vicinity of *Trichoderma* strains is the starvation due to scarcity of limiting nutrients and for rhizospheric colonization. Root exudates and rhizosphere are rich source of nutrients such as sugar, amino acids, iron, vitamins, organic acids etc. Competition for

carbon is effective mode not only in *Trichoderma* but also some other fungi such as strains of *Rhizoctonia solani*, *F. oxysporum* (Sarrocco, *et al.*, 2009; Alabouvette *et al.*, 2009).

The proficient mobilization of immobile nutrients and their utilization makes it more efficient and competitive than many other soil microbes. This process could be related also to the production of organic acids, such as gluconic, citric and fumaric acids, which decrease soil pH and allow the solubilization of phosphates, micronutrients and mineral cations like iron, manganese and magnesium (Vinale *et al.*, 2008).

"In the aerobic environment (with oxygen and neutral pH) iron exists mainly as Fe³⁺ and tends to form insoluble ferric oxide, making it unavailable for root absorption and microbial growth (Miethke, 2013). Iron act as cofactor of numerous enzymes and an essential nutrient for growth of plants and other microorganisms. *Trichoderma* secrete siderophore, an iron chelating compounds which bind with insoluble iron (Fe^{III}) and converted to soluble form(Fe^{II}) for plant absorption, and and inhibit the growth of plant pathogens by depriving them of iron sources (Leong, 1986).

"Siderophore bound Fe (III) undergoes reduction to Fe (II), which is catalyzed by free extracellular or membrane-standing ferric chelate reductases. If not already released extra cytoplasmatically, the iron has to be removed from the Fe (III)-siderophore complex in the cytosol. This is mediated either by intracellular ferric-siderophore reductases or, in a few cases, by ferric-siderophore hydrolases" Siderophores produced by some *Trichoderma* isolates are highly efficient chelators for iron Hence, *Trichoderma* spp. outcompetes with *Pythium* for available iron in soil and effectively controls its growth.

Table.1 Biocontrol genes of *Trichoderma* spp.

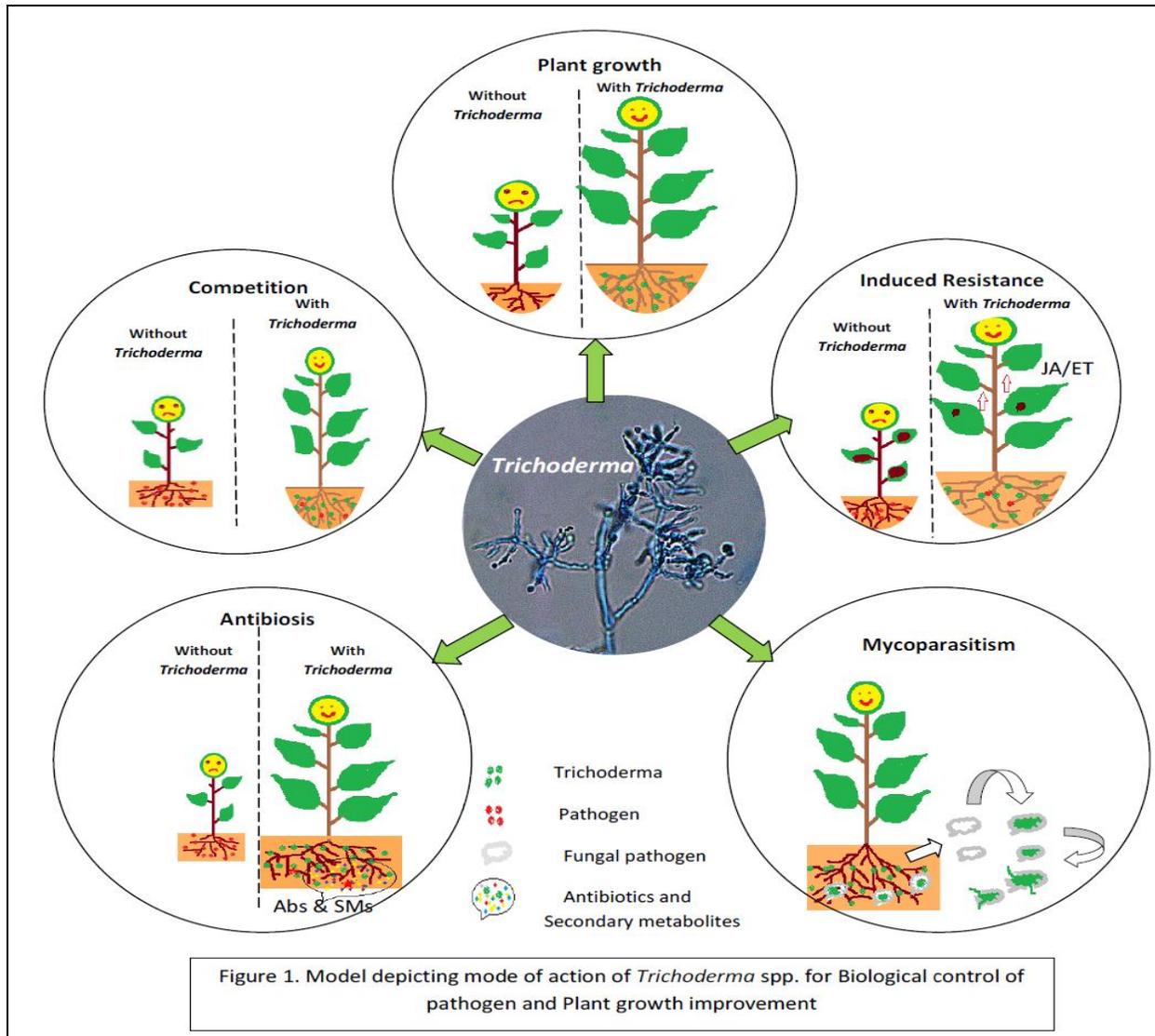
Genes	<i>Trichoderma</i> spp.	Product/Function	Pathogen/Abiotic stress	References
<i>Tvsp1</i>	<i>T. virens</i>	Serine protease in cotton seedlings	<i>Rhizoctonia solani</i>	Pozo <i>et. al.</i> , 2004
<i>tri5</i>	<i>T. harzianum</i>	Trichothecene inhibitor of protein and DNA synthesis	Soil borne pathogens	Cardoza <i>et. al.</i> , 2011
<i>erg1</i>	<i>T. harzianum</i>	Squalene epoxidase, for ergosterol synthesis and <i>erg1</i> silencing provides resistance to terbinafine, an antifungal compound.	-	Godio <i>et. al.</i> ,2007
<i>exc1,exc2, chit42,chit3, bgn13.1,prb1</i>	<i>T. harzianum</i>	NA Gases, Chitinases, Glucanases, Proteases synthesis	<i>Fusarium oxysporum</i>	Mondizar <i>et.al.</i> , 2011
<i>TgaA,TgaB</i>	<i>T. virens</i>	Antagonist activity	<i>R. solani</i> and <i>S. rolfsii</i>	Mukherjee, <i>et.al.</i> , 2004.
<i>ThPG1</i>	<i>T. harzianum</i>	Endopoly-galacturonase for cell wall degradation.	<i>R. solani</i> and <i>P ultimum</i>	Moren-Diez <i>et al.</i> , 2009
<i>Th-Chit42</i>	<i>T. harzianum</i>	Mycoparasitic activity	<i>Sclerotinia sclerotiorum</i>	Steyaert, <i>et. al.</i> , 2004
<i>tri5</i>	<i>T. brevicompactum</i>	Trichodermin for antifungal activity.	<i>C. albicans</i> <i>A.fumigatus</i>	Tijerino <i>et al.</i> , 2011
<i>Sm1</i>	<i>T. harzianum</i>	Elicitor for triggering of plant defence	Biotic/abiotic stress	Frietas <i>et al.</i> , 2014
<i>Thkel1</i>	<i>T. harzianum</i>	Regulate glucosidase in <i>A. thaliana</i>	Salt, Osmotic stresses	Hermosa <i>et al.</i> , 2011
<i>egl1.</i>	<i>T. longibrachiatum</i>	Biocontrol activity	<i>P. ultimum</i>	Migheli <i>et al.</i> , 1998
<i>qid74</i>	<i>T. harzianum</i>	Surface adherence in mycoparasitism	<i>R. solani</i>	Rosado <i>et al.</i> , 2007
<i>tac1</i>	<i>T. virens</i>	Mycoparasitic activity	<i>R.solani</i> and <i>P.ultimum</i>	Abbas <i>et al.</i> , 2017
<i>TrCCD1</i>	<i>T. reesei</i>	Carotenoid metabolism for conidial and hyphal growth	<i>T. reesei</i>	Zhong, <i>et al.</i> , 2009

Table.2 *Trichoderma* associated MAMPs

MAMP/effector	<i>Trichoderma</i> Spp.	Activity	Reference
Proteins			
Xylanase Xyn2/Eix	<i>T. viride</i>	A xylanase that elicits ET biosynthesis and hypersensitive response in tobacco leaf tissues	Rotblat <i>et al.</i> , (2002)
Cellulases	<i>T. longibrachiatum</i>	Activated and heat-denatured cellulases elicit melon defences through the activation of the SA and ET signalling pathways,	Martinez <i>et al.</i> , (2001)
Cerato-platanins Sm1/Epl1	<i>T.virens/T.atroviride</i>	Hydrophobin-like SSCP orthologues that can induce expression of defence responses in cotton and maize	Djonovic <i>et al.</i> , (2006),
Swollenin TasSwo	<i>T. asperelloides</i>	Expansin-like protein with a cellulose-binding domain capable of stimulating local defence in cucumber roots and leaves and affording local protection against <i>B. cinerea</i> .	Brotman <i>et al.</i> , (2008)
Endopolygalacturonase ThPG1	<i>T. harzianum</i>	Involved in active colonization of tomato root and ISR-like defence in <i>Arabidopsis</i>	Moran-Diez <i>et al.</i> , (2009)
Secondary metabolites			
Alamethicin	<i>T. viride</i>	Elicitation of JA and SA biosynthesis in lima bean	Engelberth <i>et al.</i> , (2001)
Trichokonin (20mer peptaibol)	<i>T. pseudokoningii</i>	production of ROS, the accumulation of phenolic compounds at the application site and virus resistance in tobacco plants through multiple defence signalling pathways	Luo <i>et al.</i> , (2010)
6-Pentyl-a-pyrone, harzianolide harzianopyridone	Various	Low-concentration metabolite activating plant defence and regulating plant growth in pea, tomato and canola	Vinale <i>et al.</i> , (2008)

Table.3 Mode of action of *Trichoderma* spp.

<i>Trichoderma</i> spp.	Mode of application	Biotic /Abiotic stress	Crop	Effect	Reference
<i>T. harzianum</i>	Soil and seed treatment	<i>Pseudomonas syringae</i> <i>Pvr phaseolicola</i>	Bean	Defensive enzymes Peroxidase, (PO) and Polyphenoloxidase (PPO)	Gailiti 2005
<i>T. virens</i> Gv29-8	Seedling treatment	<i>Colletotrichum graminicola</i>	Maize	<i>AOS, OPR7, OPR8, HPL</i> and <i>LOX10</i> Gene expression	Djonovic <i>et al.</i> , 2007
<i>T. harzianum</i> and <i>T. asperellum</i>	Soil treatment	<i>Xanthomonas campestris vesicatoria</i>	Tomato	Chitinase and β 1,3-Glucanase	Saksirirat <i>et al.</i> , 2009
<i>T. harzianum</i>	Seed biopriming	Salt stress	Rice	Proline, Malondialdehyde content, total phenol.	Rawat <i>et al.</i> , 2012
<i>T. harzianum</i>	Soil treatment and soil drenching	<i>Fusarium oxysporum</i> f. sp. <i>radicis cucumerinum</i> <i>Botrytis cinerea</i>	Cucumber, <i>Arabidopsis thaliana</i>	<i>PAL1, CHIT1, β1,3-Glucanase, PR-1, LOX 1</i> gene expression	Alizadeh, <i>et al.</i> , 2013
<i>T. harzianum</i>	Seed biopriming	<i>Pythium aphanidermatum</i>	Cucumber	Phenyl Ammonia Lyase (PAL), PO and PPO	Devi and Shivprakash 2013
<i>T. harzianum</i>	Seed biopriming	Drought	Wheat	Osmotic potential, Phenolics, Proline, lipid peroxidation and PAL	Shukla <i>et al.</i> , 2014
<i>T. viridae</i>	Seed biopriming	<i>Fusarium oxysporium</i> and <i>Alternaria alternate</i>	Pigeon pea, Moong bean	PO, PPO, PAL, Catalase, Total phenols and antioxidants.	Rao, <i>et al.</i> , 2015
<i>T. harzianum</i>	Seed treatment	<i>Phytophthora melonis</i>	Cucumber	PAL, Lipoxygenase and Galactinol synthase and Cucumber pathogen induced 4 gene expression	Sabbagh <i>et al.</i> , 2017
<i>T. harzianum</i>	Seed biopriming	Drought	Rice	Proline, SOD, lipid peroxidation and DHN/AQU transcript level	Pandey <i>et. al.</i> , 2016
<i>T. harzianum</i>	Soil and seedling treatment	<i>Sclerotinia sclerotiarum</i>	Oilseed rape	AOC3,PDF1.2 and ERF2 genes expression	Alkooranee <i>et al.</i> , 2017
<i>T. harzianum</i>	Seed biopriming	Drought	Tomato	Flavonoides, phenols, IAA, IBA, Gibberellin, Proline,	Mona <i>et al.</i> , 2017



There are many more examples about effective application of competition for the biocontrol of pathogens such as *B. cinerea*, (Latorre *et al.*, 2001). These reports suggest that the molecular and proteomic assembly of *Trichoderma* is more efficient to mobilize and take soil nutrients as compared to many other pathogens and other organisms.

Trichoderma-pathogen networking

The seven transmembrane G protein coupled receptor *Gpr1* is involved in sensing the fungal prey in nearby vicinity (Oman *et al.*, 2012). *Vellof Trichoderma virens* is involved in hydrophobin expression for adherence to the

host and mycoparasitism (Zeilinger *et al.*, 2005). Ligand binding with such receptors leads to downstream signaling events via activation of G-protein cascades. *Trichoderma* spp. have three MAPK cascades comprising MAPKKK, MAPKK and MAPK and MAPK signaling pathways may act in mycoparasitism and biocontrol (Reithner *et al.*, 2007, Kumar *et al.*, 2010). Production and release of Cell wall degrading enzymes (CWDEs) and antibiotics are the most important members of the chemical arsenals deployed by *Trichoderma* to kill pathogens. Glucan and Chitin synthases are produced by the *Trichoderma* to repair their self-cell wall damage by pathogen during *Trichoderma*-pathogen interaction.

Simultaneously genes encoding hydrolytic enzymes like chitinases and glucanases, and those for secondary metabolism like NRPSs path are expressed to kill the pathogens (Kubicek *et al.*, 2011). Earlier evidences suggested the involvement of *chit42*, *chit3*, *bgn13.1*, *Bgn2* *Bgn3* and *prb1* are involved in chitinases, glucanases and proteases in biocontrol (Mondizar *et al.*, 2011). Certain species like *T. atroviride* produce the volatile metabolite 6-pentyl-2H-pyran-2-one (6-PP) which plays an important role in *Trichoderma*–fungal interactions (Hasan *et al.*, 2008, Vinale *et al.*, 2009). Recently, genetic evidence has been provided for the assembly of 11- and 14-modules peptaibols by a single NRPS Tex2 of *T. virens* (Mukherjee *et al.*, 2011). Given the fact that these peptaibiotics are strongly antimicrobial (by being able to form voltage-gated membrane channels as peptaibol trichokonin VI of *T. pseudokoningii* are involved to induce programmed cell death in *Fusarium oxysporum* (Shi *et al.*, 2012).

Trichoderma spp. possess many qualities and attributes, they have great potential use in agriculture such as plant growth development by improving germination, morphological features and physiological alteration by alleviating uptake of nutrients in plants, enhancing nitrogen-use efficiency in different crops, and assisting to improve photosynthetic efficiency. Several strategies have been applied to identify the main genes and compounds involved in this complex, three-way cross-talk between the fungal antagonist, the plant, and microbial pathogens. They also stimulate defence in response of biotic and abiotic stress and antagonism including mycoparasitism, antibiosis and competition against pathogens. *Trichoderma* elicits ISR by JA/ET-dependent pathways and triggers priming responses in the plant. On the other hand, the *Trichoderma*–plant interaction is dynamic and the expression of defence-related genes of the JA/ET and/or SA pathways may overlap, depending on the *Trichoderma* strains and their concentration, the plant material, the developmental stage of the plant, and the timing of the interaction.

Trichoderma also produces the phytohormones ET and IAA, which play roles in interconnecting plant development and defense responses. The genome of *Trichoderma* spp. has been extensively investigated and has proven to contain many useful genes, along with the ability to produce a great variety of expression patterns, which allows these fungi to adapt to many different environments (soil, water, dead tissues, inside the plants, *etc.*). The metabolomics of *Trichoderma* spp. are incredibly complex, especially in terms of antibiotics and secondary metabolites production but with the help of advanced genomic and proteomic approaches, it is possible to explore new pathways, novel functions of compounds produced by this genus. The expression of *Trichoderma* genes in plants has beneficial results, mainly in the control of plant diseases and resistance to adverse environmental conditions. The experimental evidence indicates that *Trichoderma*–plant interactions have features in common with other beneficial microbe associations but that they also display their own characteristics due to *Trichoderma*'s particular lifestyle. Nevertheless, there is a need for more studies aimed at gaining insight into the signalling transduction pathways, related to defense and development, resulting from *Trichoderma*–plant interactions in the presence of pathogens and/or different types of abiotic stress (Table 1–3 and Fig. 1).

Future prospects

Genetics of three way cross talk among Plant – *Trichoderma* –Pathogen interaction should be investigated including the process of induction and regulation of enzyme expression. Additionally, the environmental cues along with the transmission of the respective signal to the promoters of the output pathways should be considered. Such knowledge of the physiology will further improve enzyme production in the microbial cell factory and enhance the mycoparasitic potential of biocontrol strains.

The identification of the plant receptors for

Trichoderma elicitor proteins and effectors that may reprogram a host's genetic machinery can serve as the foundation for understanding how these symbionts trigger the host defense reaction.

Trichoderma compatibility with chemical fungicides as the part of integrated disease management should be evaluated.

Needs to enhance popularity of *Trichoderma* based formulation among the farmers for ecofriendly management of diseases.

The ecological impact of large-scale applications of a single fungal species and their secondary metabolites for biocontrol should be evaluated to establish a knowledge base for the safe and sustainable use of *Trichoderma*.

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