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REVIEW

Trichoderma: Defence army against soil borne fungi

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Soil borne fungal pathogens are responsible for severe disease in vegetable production leading to substantial economic damage including yield loss and decreased quality of plant product. Disease management using synthetic fungicide is helpful to minimize the crop yield loss but its unscientific long term use led to development of fungicide resistance, new disease outbreaks and reduction in population of beneficial soil microorganisms. The increasing concerns regarding environmental and soil health necessitate the use of biocontrol methods, strategies and approaches for plant disease management. *Trichoderma* species are successful bio control agent which operates by triggering resistance responses, cross protection, systemic acquired resistance (SAR) and Induce systemic resistance (ISR). It also have ability to produce cell wall-degrading enzymes and antibiotics that helps in inducing plant resistance against various economically important soil borne fungi. The present review article highlight the current status of *Trichoderma*, its mechanism and effectiveness against various soil borne fungi.

Keywords: *Trichoderma*, competition,defense mechanism soil-borne fungi

INTRODUCTION

Soil borne plant fungi such as *Rhizoctonia* spp., *Fusarium* spp*., Verticillium* spp*., Sclerotinia* spp*., Pythium* spp*., and Phytophthora* spp*.* can cause 50%–75% yield loss for vegetables, fruit and ornamentals. They often survive for long periods in host plant debris, soil organic matter, free-living organisms or resistant structures like microsclerotia, sclerotia, chlamydospore or oospores (Panth *et al*. 2020).The term biological control was introduced with special concern to plant pathogens and insects (Maloy *et al.* 2003).

Use of biological control agents (BCAs), based on living microorganisms or their metabolites, and products of natural origin that control the population of plant pathogens (Tomah *et al.* 2020). *Trichoderma* is a common soil fungus that naturally grows in the rhizosphere. It not only parasitize plant pathogenic fungi but also help in the production of vitamins, increasing the solubility of nutrients contained in the rhizosphere (phosphates, Fe3+, Cu2+, Mn4+, ZnO), and supplementing necessary elements (mainly nitrogen, phosphorus, potassium, and microelements) for their proper growth of plants (Singh *et al*. 2018).

The systematics and taxonomy of *Trichoderma* fungi have evolved since 1794 when Persoon first introduced the generic name *Trichoderma*. Tulasne and Tulasne 1865 noticed the sexual state of a Hypocrea species and showed that Hypocrearufa is the telemorph of *Trichoderma virde* Pers. Based on their morphological features distinguished nine "aggregate" species: *T. harzianum* Rifai*, T. viride, T. hamatum* (Bonord) Bainier*, T. koningii* (Oudem.) Duche & R. Heim, *T. polysporum* (Link) Rifai*, T. piluliferum, T. aureoviride* Rifai*, T. longibrachiatum* Rifai*, T. pseudokoningii* Rifai (Btaszcczyk *et al.* 2018).

According to the current MycoBank classification, the *Trichoderma* genus belongs to the domain Eukaryota, kingdom Fungi, division Ascomycota, subdivision Pezizomycotina, class

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Sordariomycetes, order Hypocreales, and family Hypocreaceae. There are more than 370 *Trichoderma* spp. including *T. harzianum*, *T. viride*, *T. asperellum*, *T. hamatum*, *T. atroviride*, *T. koningii*, *T. longibrachiatum*, and *T. aureoviride* (Sanchez-Montesinos *et al*. 2021; Sun *et al*. 2022). This study systematically and comprehensively elaborated on the research progress on *Trichoderma* spp. and its mechanism in plant disease management, and the current status of *Trichoderma* as an antagonistic agent soil borne fungi.

Trichoderma as a bio control agent

The genus *Trichoderma* belongs to ascomycetic fungi that are present in nearly all soils and other diverse habitats. *Trichoderma* is widely used for the control of many soil borne plant pathogens (Table 1). *Trichoderma* was first reported as a biocontrol agent against *Rhizoctonia solani* for the control of citrus seedling disease since then *Trichoderma* got attention as fungal antagonist (Singh *et al.* 2002). It also has a good control effect on *Phytophthora* blight pepper and potato.

It can inhibit the growth of *Phytophthora* blight in soil, reduce the number of pathogenic fungi, and effectively reduce the rate of dead seedlings (Kappel *et al*. 2020).

Trichoderma exhibit antagonistic behavior against several phytopathogenic fungi by competing for nutrients and space, modifying the environmental conditions, or promoting plant growth and plant defensive mechanisms and antibiosis, or directly, by mechanisms such as mycoparasitism (Figure 1).*Trichodermaviride*, *T. viridescens* and *T. atroviride* to inhibit mycelium growth of *Fusariumculmorum* and *F. cerealis* (Modrzewska *et al*. 2022). Pavitra *et al*. (2022) showed strong antagonistic potential of *T. virens* against *Pythiummyriotylum* and *P. aphanidermatum* followed by *T. asperillum* and *T. aureoviridae*. The biocontrol effect of *Trichoderma* spp. against various plant pathogens fungi are often the result of a combination of multiple biocontrol mechanisms presented in Figure 1.

In the current market for *Trichoderma* biological agents widely used in disease control mainly include Trichodex (Makhteshim Chemical Works Ltd., Israel), a commercial preparation of *T. harzianum* T-39; Root Shield (Bioworks, USA), a commercial preparation of *T. harzianum* T-22; Binab TF (Binab Bio Innovation AB, Sweden), a mixed-agent of *T. harzianum* and *T. polyspora*; Sentinel (Novozymes, Denmark), a commercial preparation of *T. atrovilide*; And Supervivit (Borregaard Bioplant, Denmark), a commercial preparation of *T. harzianum* (Yao *et al*. 2023).

Trichoderma have multiple biocontrol mechanisms presented in Figure 1.

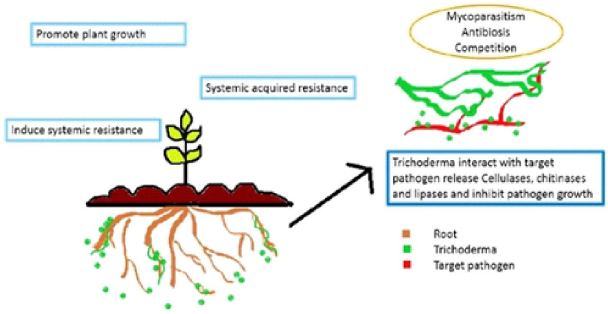

Fig.1: Model depicting mode of action of *Trichoderma* spp. against pathogen and plant growth

Interaction between Trichoderma plant and pathogen

Resistance response: SAR and ISR

Plant and *Trichoderma* interactions starts with the recognition followed by penetration, attachment and colonization. For root penetration, hyphae of *Trichoderma* form appressoria-like structures.It has been shown that attachment of appressoria is mediated by TasHyd1 and qid74 in *T. asperelloides* and *T. harzianum* respectively. Hydrophobins are small hydrophobic proteins present in the outer cell wall of *Trichoderma* whichmediate adherence to the root surface (Puyam, *et al*. 2016). Cellulose is recognized by these proteins which in turn modify plant cell wall architecture by secreting cellulolytic and proteolytic enzymes for root colonization facilitation**.** *T. harzianum* also produces enzymes like endopolygalacturonase which further, release specific oligalacturonides by breaking down plant pectin leds to degrade plant cell walls and thus facilitate root colonization **(** Behera *et al*. 2017).

A cysteine-rich cell wall protein and another protein swollenin TasHyd1 which has a binding domain for cellulose are encoded by the gene qid74. At present, there are more than 10 elicitors of *Trichoderma* that induce plant resistance, including Sm1, QID74 hydrophobic protein, chitin-degrading enzyme, MRSP1, xylanase, cellulase, endo-polygalacturonase, sucrase, and antibacterial peptides. TaSWO1, a swollenin secreted by *T. atroviride*, can induce resistance in *Capsicum annum* plants against *A. solani* and *R. solani* (Guzman-Guzman *et al.* 2023).

Growth of *Trichoderma* in the epidermal and cortical intercellular spaces is restricted by callose-enriched wall appositions which prevents its entry into the vascular tissues of the host (Contreras-Cornejo *et al*. 2009). Initial responses of host plant to microbes, whether beneficial or pathogenic, are to consider them as foreign bodies, that trigger immune responses through MAMP (microbe-associated molecular patterns)and by recognition receptors (PPRs) which are localized on the surface of plant cells. Thereby, initiate the MTI (MAMPS triggered) and ETI (effector triggered) immunity in plants, respectively. MTI activated by *Trichoderma* spp. includes defence responses such as oxidative burst, callose deposition, Ca2+ and reactive oxygen species (ROS) signaling as well as the induction of phytoalexins and by a rapid but transient activation of MAPK cascades through G heterotrimeric proteins(Chakraborty*et al*. 2020).

Interaction between Plant and *Trichodema* involves in exchanges of molecular signals and deposition of fungal elicitors in root apoplast. These elicitors triggered chemical and biological immunity of plants which keeps the plant primed and are expressed during pathogen attack in future. Plants recognize elicitors or pathogen-associated molecular patterns (PAMPs) which can be lipopolysaccharides, peptidoglycan, B-glucans, chitin or flagellin, and leads to typical plant defence responses such as strengthening of cell walls, enhanced accumulation of PR proteins and phytoalexin biosynthesis (Chakraborty, 2005).

In the second stage, *Trichoderma* effectors are recognized by R-proteins to promote JA signaling by sustained MAPK (Mitogen-activated protein kinase) activation, and to suppress Salicylic acid signaling. The plant's receptors such as pathogen recognition receptors (PRRs) and resistance proteins involved in pathogen detection. The R proteins are mostly NB-LRR (nucleotide binding leucine rich repeat) proteins which interact with pathogen effector proteins. Later, a second peak in the amount of SA is observed, which may induce antioxidative enzyme activities to reduce the oxidative damage to biomolecules and cells. *Trichoderma*-induced systemic resistance (TISR) is very similar to *Rhizobacteria* mediated induced systemic resistance (RISR) since both are regulated by the jasmonic acid and ethylene (JA/ET) signaling pathway (Pacheco-Trejo *et al*. 2022).

Trichoderma releases the lytic enzymes in the rhizosphere, which catalyzes the cell wall damage to target fungi. After this, a signaling cascade is activated in *Trichoderma* cells which involves the activation of MAPK (mitogen-activated protein kinase) through G-protein-coupled receptors. Alteration in gene expression ultimately leads to PCD (programmed cell death) of pathogenic fungi.

Production of antibiotics and competition for the host receptor site

The phenomena of inhibition of one organism by metabolic products of the other is referred to as "Antibiosis". Weindling (1934) proposed "lethal principle" and showed that the factor behind the lethal principle is Gliotoxin secreted by *Trichoderma virens*. This led to the development of another mechanism behind the biocontrol potential i.e. antibiosis. *Trichoderma* produces low molecular weight diffusible compounds or antibiotics possessing antifungal and antibacterial properties.These substances can penetrate the host cell, inhibit cell wall synthesis of the target fungus (Puyam, 2016). *Trichoderma* produces a variety of secondary metabolites, including trichomycin, gliotoxin, viridin, antibacterial peptide, α-1, 3-glucanase, chitinase, polypeptides, polyketones, butyrolactones, sesquiterpene heptadecarboxylic acid, terpenes, and some volatile substances (hydrocarbons, alcohols, furans, aldehydes, alkanes, olefins, esters, aromatic compounds, heterocyclic compounds, and various terpenoids (Kappel *et al.* 2020).

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). Gliovirin and Gliotoxin are the two most important *Trichoderma* secondary metabolites belonging to Q and P group strains, respectively. "P group strains of *Trichoderma virens* (*Gliocladium virens*) is active against *P. ultimum*, but not against *R. solani* and Q group is more active against *R. solani* than *P. ultimum*" (Howell, 2000). Viridins obtained by diverse *Trichoderma* spp. (*T. viride, T. koningii, T. virens*) inhibit spore germination of *Penicillium expansum, Botrytis allii, Fusarium caeruleum, Colletotrichum lini, Stachybotrysatra*, and *Aspergillus niger* (Singh *et al.* 2005).

Antimicrobial activities could be the result of several secondary metabolites such as peptaibols, terpenes, polyketides, gliotoxin, and gliovirin produced by fungi (Vinale*et al.* 2008). Other metabolites include tricholin, harzianic acid, viridian, gliosoprnins, heptelidic acid, 6-pentyl-α-pyrone, and massoilactone (Mukherjee *et al.* 2012). In *Trichoderma* spp. several genes are involved in synthesis of secondary metabolites. During Interaction of *Trichoderma* spp. and *R. solani*, the pathogen is recognized by its (oligopeptides and small other molecules). In response of which peptides released by the action of proteases of *Trichoderma* spp. prior to contact. Also *R. solani* secrete ROS and secondary metabolites in response to *Trichoderma* spp. These molecules bind to G protein-coupled receptors (GPCRs; such as Gpr1) or nitrogen-sensing receptors (Target of rapamycin; TOR pathway), or adenylate cyclase receptors on the surface of *Trichoderma* spp. hyphae. After binding to the receptors, the molecules induce a signaling cascade involving G proteins and mitogen-activated protein kinases (MAPKs) or protein kinases (PKA), which then modulate the activities of transcription factors (TFs) and gene regulations. These substances then boost the expression of genes that code for enzymes involved in secondary metabolite production and lysis of the cell wall of *R. solani* (Abbas *et al*. 2022). In *Trichoderma* spp. several genes involved in secondary metabolite synthesis have been discovered. These genes encode secondary metabolites, such as pyrones, polyketides, peptaibols, gliotoxin, gliovirin, terpenoids, and other chemicals. Depending on the chemical and the target location, varying amounts of these compounds are poisonous to *R. solani*. (Rahimi Tamandegani *et al*. 2020). Some antimicrobial genes of *Trichoderma* spp. are involved in antagonism are described in Table1.

Competition with fungal pathogen

Trichoderma genus are widely known for very rapid growth and are regarded as aggressive competitors. The hyphae quickly wrap the roots of crops to form a protective layer that seize the invasive part of the plant's pathogenic fungi and hinders the invasion of the pathogen fungi (Mohiddin *et al.* 2021). Its rapid growth and reproduction seize nutrients and space near the plant rhizosphere, which results in nutrient deficiency and inhibiting the growth and reproduction of the pathogen fungi (Bazghaleh *et al*. 2020; Halifu *et al.* 2020; Oszust*et al.* 2020; Panchalingam *et al*. 2022. Competition for iron is intense in weakly- acidic, neutral or alkaline soils, when iron (Fe3+) forms insoluble complexes of Fe (OH) 3 and thus, becomes unavailable. Most bacteria and fungi produce siderophores (sid = iron, phore = bearer), that sequester or chelate the scarce iron and sideophore is known for uptake of any other element. Organisms that produce siderophores with greater sequestering power and with higher stability constants have a competitive edge over those having comparatively less efficient siderophores (Dube, 2021).

Hyper parasitism

Hyper parasitism is common in soil. The hyphae, resting spores, and sclerotia of several fungi and invaded parasitized (mycoparasitism) or lysed (mycolysis) by several non-pathogenic fungi. *Trichoderma* releases low levels of extracellular exochitinase induced by the cell-wall oligomers of the target fungi and endochitinase gene is activated before coming into touch with the target fungus. After entering the soil for 24h, *Trichoderma* can quickly adsorb to the roots of crops for propagation, and the hyphae quickly wrap the roots of crops to form a protective layer then it detect the pathogen and degrade its cell

Table.1: Some Antimicrobial Genes of *Trichoderma* against Soil Borne Fungi

Gene	*Trichoderma*	Function
Tvsp1	*T. virens*	Tvsp1 is not necessary for the normal growth or development of *T. virens*, but plays a role in the biocontrol process
tri5	*T. brevicompactum, T. rodmanii, T. albolutescens, T. taxi*	Gene responsible synthesis of trichodiene which act as a signaling molecule and inhibit protein and DNA synthesis of pathogen
pgy1 and ecm33 genes	*T. virens*	Hyperparasite ability
tbrg-1 gene	*T. virens*	Increase in gliotoxin production
Gv29–8	*T. virens*	Hyperparasite ability against *R. solani*, *Sclerotium rolfsii*, and *Fusarium oxysporum.*
egl1.	*T. longibrachiatum*	gene showed biocontrol activity against *P. ultimum* in damping-off of cucumber
tac1	*T. virens*	This gene has its role in mycoparasitic activity against *R. solani* and *P. ultimum*
qid74	*T. harzianum*	Protect its own cell from mucolytic activity and help in binding to the hydrophobic surfaces of the fungus toward the mycoparasitism against *R. solani*
tac1	*T. virens*	Helps in mycoparasitism on *R. solani* and *P. ultimum*

Pozo *et al.* (2004); Gutierrez *et al.* (2021); Halifu *et al.* (2020)

wall by releasing fungitoxic cell wall degrading enzymes like extracellular β-(1, 3) glucanase, proteases, lipases and chitinases. Root colonization by *Trichoderma* is enhanced by root secretions such as polysaccharides, monosaccharides and disaccharides and also the mucigel layer. This enhanced endosymbiosis in turn activates plant defences (Vargas *et al*. 2009). Ultimately, this action kill the nearby pathogenic fungi and protect the roots of crops from the invasion of fungus. *Trichoderma hebeiensis* and *Trichoderma erinaceum* strains controlled four important rice pathogens, i.e., *Rhizoctonia solani* (100%), *Sclerotium oryzae* (84.17%), *Sclerotium rolfsii* (66.67%), and *Sclerotium delphinii* (76.25%) (Viterbo *et al.* 2007).Many research done by researcher worldwide prove the success of *Trichoderma* spp. as an effective biocontrol agent against various plant pathogens fungi. Some of the successful management efforts against soil bore pathogens are listed in table 2.

Conclusion and future outlook

The repeated use of chemical fungicides are not only effecting soil health and non-target microorganism but also reduces sensitivity of a pathogenic fungi to a specific chemical. *Tricoderma*, an alternative option for the next-generation fungicide can improve crop health by triggering the immunity and promoting plant growth. *Trichoderma* strains have no adverse effect on soil microflora and microfauna as well as do not leave toxic residues.In this review we described multiple mechanisms of *Trichoderma* including nutrient competition, mycoparasitism, synthesis of antibiotic and hydrolytic enzymes, and induced plant resistance. Research on the mechanisms have led to a better understanding on the role of several secondary metabolites,antimicrobial genes, lytic enzymes and components involved in signaling pathway (SAR & IAR) responsible for building effective defence system against pathogens.Indeed, *Trichoderma* has been a godsend in the treatment

Table. 2: List of successful *Trichoderma* species used against various soil borne phytopathogenic fungi

Treatment	Target Pathogen spp.	Crop	Reference
T. longibrachiatum	*Fusarium oxysporum* f. sp*. cepa*	Onion	Abdelrahman *et al*. (2016)
T. asperellum	*Fusarium oxysporum* f. sp.*solani*	Eggplant, tomato	Adhikary *et al*. (2017); Attia *et al.* (2023)
T. harzianum	*Fusarium oxysporum* f. sp*. capsici*	Chilli	Jamil *et al*. (2020)
T. asperellum	*F. oxysporum* f. sp.*cucumerinum*	Cucumber	Li *et al*. (2019)
T. asperellum, T. harzianum, T. pseudokoningii	*F. solani*, *F. avenaceum*	Snow pea	Boakye *et al*. (2022)
T. longibrachiatum	*F. oxysporum* f. sp. *lycopersici.*	Tomato	Yogalakshmi *et al*. (2021)
T. atroviride	*F. oxysporum* f. sp. *spinaciae*	Spinach	Bhale *et al*. (2012)
T. asperellum	*Rhizoctonia solani*	Tomato	Sehim *et al*. (2023)
T. brevicrassum	*Rhizoctonia solani*	Cucumber	Halifu *et al*. (2020)
T. harzianum, T. atroviride, T. orientalis	*Rhizoctonia solani*	Sugar beet	Stankov *et al*. (2023)
T. harzianum	*Rhizoctonia solani*	Brinjal	Koka *et al*. (2019)
T. harzianum, T. asperellum, T. virens	*Pythium aphanidermatum*	Tomato	Elshahawy and Mohamedy. (2019)
Trichoderma spp.	*Pythium aphanidermatum*	Tomato, cauliflower	Sharma *et al*. (2023)
T. viride, T. harzianum	*Pythium aphanidermatum*	capsicum	Muthukumar *et al*. (2011)
T. aggressivum f. *europaeum*	*Pythium aphanidermtum*	Melon	Montesino *et al*. (2021)
T. asperellum	*Sclerotinia. cepivorum*	Onion	Mendez *et al*. (2020)
T. atroviride, T. auroviride, T. hamatum, T. harzianum, T. koningii, T. longibrachiatum, T. virens, T. viride	*Sclerotinia sclerotiorum*	Pea	Khan *et al*. (2022)
T. harzianum , T. asperellum	*Sclerotinia sclerotiorum*	Brinjal	Singh *et al*. (2021)
T. koningii, T. viride , T. harzianum	*Sclerotiumrolfsii*	Tomato, bean and cabbage	Kamel *et al*. (2020)
T. harzianum	*Sclerotium rolfsii*	Chilli	Yadav *et al*. (2022)
T. harzianum	*Verticillium dahliae*	Tomato, Potato	Chliyeh *et al*. (2014); Chen *et al*. (2014)

T. harzianum	*Sclerotium rolfsii*	Chilli	Yadav*et al*. (2022)
T. harzianum	*Verticillium dahliae*	Tomato, Potato	Chliyeh *et al*. (2014); Chen *et al*. (2014)
T. virens	*Phytophthora infestans*	Potato	Lalaymia *et al.* (2022); Mollah *et al*. (2023)
T. asperellum,	*Phytophthora capsici*	Capsicum	Tomah *et al*. (2020)
T. atroviride	*Phytophthora nicotianae*	Tomato	La Spada *et al*. (2020)
T. asperellum, T. virens, T. gliocladium, T. viride, T. hamatum,	*Macrophomina phseolina*	Okra	Bhojani *et al*. (2022)
T. harzianum	*Macrophomina phseolina*	Sugar beet	Stankov *et al*. (2023)

of fungal diseases and developing country. All these promising results are opening the door for sustainable agriculture to exploit the potential of *Trichoderma* in an eco-friendly way.

DECLARATIONS

Conflict of interest: Authors declare no conflict of interest.

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