Trichoderma Species as Biocontrol Inoculant in Crop Rhizosphere

Subjects: Plant Sciences
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The fungal species belonging to the genus *Trichoderma* has been globally recognized as a potential candidate of biofertilizer and biocontrol agent to prevent devastating soil-borne fungal pathogens and enhance growth and productivity of agricultural crops. The antagonistic activity of *Trichoderma* to pathogenic fungi is attributed to several mechanisms including antibiosis and enzymatic hydrolysis, which are largely associated with a wide range of metabolites secreted by the *Trichoderma* species. Besides suppressing target pathogens, several metabolites produced by *Trichoderma* species may act against non-pathogenic beneficial soil microbial communities and perform unintended alterations within the structures and functions of microbial communities in the crop rhizosphere. Multiple microbial interactions have been shown to enhance biocontrol efficacy in many cases as compared to bioinoculant employed alone.

Trichoderma metabolites root exudates

1. *Trichoderma* Species as a Commercial Biofungicide

Trichoderma is a filamentous fungus beneficial for its multi-prong action against numerous plant pathogens [1]. Biofungicide is an important approach against some notable plant pathogens. Several *Trichoderma* strains have been recognized as a potential source to formulate biofungicide because of their suitability to reduce disease incidences caused by several fungal plant pathogens [2]. Species belonging to the *Trichoderma harzianum* complex are mostly found in various soil habitats and on plant decay materials, and have shown parasitism to other fungi [3]. Recently, a few commercial strains, such as *Trichoderma afarasin*, *T. afroharzianum*, *T. atrobrunneum*, *T. camerunense*, *T. endophyticum*, *T. guizhouense*, *T. harzianum*, *T. inhamatum*, *T. lentiforme*, *T. lixii*, *T. neotropicale*, *T. pyramidale*, *T. rifaii*, and *T. simmonsii*, have been identified as effective biofungicide formulations [4]. *T. afroharzianum* is the mostly reported strain used as an active ingredient in several commercial biocontrol products [4][5]. The taxonomy of the *T. harzianum* complex formalized the phylogenetic progenies and opened new prospects for the revelation of biological utilities, particularly controlling the plant pathogens. For instance, newly recognized *T. lentiforme* and *T. neotropicale* showed strong antagonistic actions against the *Moniliophthora roreri* pathogen causing frosty pod rot disease of the cacao tree (*Theobroma cacao*) [6].

T. viride has also been extensively used as a well-known biofungicide that protects the plant from fungal diseases striving with systemic negative effects on foliar leaves and seedcoat. Bio-formulations based on *T. viride* work as potential biofungicides against seed-borne and soil-borne fungal pathogens including *Armillaria*, *Pythium,* and *Rhizoctonia* [7]. Moreover, *Trichoderma* species play a significant role against seed-borne fungi, such as *Fusarium* sp., *M. phaseolina,* and *R. solani,* which cause pre-harvest and post-harvest losses in cotton, cowpea, mungbean, sorghum, soybean, and tomatoes [7]. The dry powder or dust of *Trichoderma* is used to coat seed for seed treatment just before sowing [8][9]. *T. harzianum*, *T. virens,* and *T. viride* were proven as potential seed protectants against the *Pythium* sp. and *R. solani*. Incubation of *Trichoderma*–treated seeds under warm and humid conditions right before radical emergence, results in rapid and uniform seedling emergence [10]. *Trichoderma* germinates conidial masses on the seed surface and forms a layer surrounding the primed seeds. These primed seeds are capable of tolerating the adverse conditions of soil habitats, such as vegetable seedlings treated with *Trichoderma* spore or cell suspension showed antagonistic to damping-off disease. *Trichoderma* was successfully applied in aerial plant parts to control the decay fungi in wounded shrubs and trees [10]. For instance, across the globe, several *Trichoderma*–based commercial bioformulations are used in controlling plant pathogenic fungi are listed in **Table 1**.

Table 1. *Trichoderma*–based commercial bioformulations controlling plant pathogenic fungi.

***Trichoderma*–Based Bioformulation/Tradename**	***Trichoderma* Species**	**Target Pathogens**	**Manufacturer**	**References**
Agroguard WG™	*T. harzianum*	*Phoma, Pythium, Rhizoctonia, Sclerotinia,* and *Sclerotium*	Life Systems Technology S.A. (Colombia)	[8]
Antagon WP™	*T. harzianum*	*Botrytis, Ceratocystis, Fusarium, Pythium, Rhizoctonia, Rosellinia, Sclerotinia,* and *Sclerotium*	Bio Ecologico Ltd. (Colombia)	[8]
Binab TF	*T. polysporum*	*Fusarium, Pythium, Rhizoctonia, Sclerotinia,* and *Sclerotium*	BINAB Bio-Innovation AB (USA)	[9]
Bioderma H	*T. harzianum*	*Alternaria, Ascochyta, Cercospora, Colletotrichum, Fusarium, Phytophthora, Pythium, Macrophomina, Myrothecium,* and *Ralstonia*	Biotech International Ltd. (India)	[8]
BioFungo™	*T. virens*	*Botrytis cinerea* and *Sphaerotheca pannosa*	Orius Biotecnologia (Colombia)	[8]
ECO-77™	*T. harzianum*	*Botrytis* and *Eutypa*	Plant Health Products (South Africa)	[8]
ECO-T™	*T. harzianum*	*Fusarium*, *Phytophthora, Pythium,* and *Rhizoctonia*	Plant Health Products	[8]

***Trichoderma*–Based Bioformulation/Tradename**	***Trichoderma* Species**	**Target Pathogens**	**Manufacturer**	**References**
			(South Africa)	
Ecoderma	*T. virens*	*Botrytis, Fusarium, Pythium, Rhizoctonia, Rosellinia, Sclerotinia,* and *Sclerotium*	BigHaat Agro Ltd. (India)	[9]
Ecotrich ES™	*T. harzianum*	*Rhizoctonia solani, Pythium,* and *Sclerotinia*	Ballagro Agro Tecnologia Ltd. (Brazil)	[8]
Esquive	*T. atroviride*	*Pythium* and *Rhizoctonia*	Agrauxine (France)	[9]
Floragard	*T. hamatum*	*Fusarium, Pythium, Rhizoctonia solani,* and *Sclerotinia homeocarpa*	Sellew Associates LLC (USA)	[9]
FoliGuard™	*T. hamatum*	*Alternaria, Botrytis cinerea, Cladosporium, Oidium,* and *Sphaeroteca pannosa*	Live Systems Technology S.A. (Colombia)	[8]
Lycomax	*T. viride*	Soil-borne pathogens	Russell IPM (UK)	[8]
Natibiol™	*T. viride*	*Rhizoctonia*	Probiagro S.A. (Venezuela)	[8]
PlantShield™/RootShield™	*T. harzianum*	*Fusarium, Pythium, Rhizoctonia solani,* and *Sclerotinia homeocarpa*	Bioworks (USA)	[8]
T-Gro	*T. harzianum*	*Botrytis, Ceratocystis, Fusarium, Pythium,* and *Rhizoctonia*	Dagutat Biolab (USA)	[9]
Trianum™	*T. harzianum*	Soil-borne pathogens	Koppert BV (The Netherlands)	[8][9]
Tricho™	*T. harzianum*	*Alternaria, Arrmilaria, Botrytis, Fusarium, Pythium, Rhizoctonia, Rosellinia, Sclerotinia,* and *Sclerotium*	Orius Biotecnologia (Colombia)	[8]

Trichoderma–Based Bioformulation/Tradename	*Trichoderma* Species	Target Pathogens	Manufacturer	References
Trichodermil™	*T. harzianum*	*Botrytis ricini, Fusarium, Phytophthora capsici, Phytophthora palmivora, Rhizoctonia,* and *Sclerotinia sclerotiorum*	Itaforte BioProdutos (Brazil)	[8]
Trichodex	*T. harzianum*	*Colletotrichum, Fusarium, Phytophthora,* and *Pythium, Macrophomina*	Makhteshim chemical works Ltd. (USA)	[9]
Trichosav	*T. harzianum*	Soil-borne pathogens	Centros de Reproduccion de Medios Biologicos (Cuba)	[8]
Trichosoil	*T. harzianum*	*Fusarium*	Lage S.A. (Uruguay)	
Tusal [11]	*T. asperellum*	*Fusarium, Pythium,* and *Rhizoctonia solani*	Isagro (USA)	[9]
Virisan	*T. asperellum*	*Phytophthora,* and *Pythium*	Isagro (USA)	[9]
VinevaxTM–Trichoprotection™ [12]	*T. harzianum*	*Armillaria, Botryosphaeria stevensii, Chondrostereum purpureum, Eutypa lata,* and *Phaeomoniella chlamydospor*	Agrimm Technologies Ltd. (New Zealand)	[8][9]

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signals that help to colonize in plant roots [13]. Auxin-induced root formations (e.g., increased number of root hairs) increase the total area of the absorptive surface in the root zones, making nutrient absorption easier and resulting in increased plant growth [14].

The exchange of root exudates and other signaling molecules between *Trichoderma* and plants is complex and not well characterized [15]. Thus, several antibiotics, toxins, and plant antimicrobial agents affect the *Trichoderma* species in the crop rhizosphere. For example, benzoic acid, cinnamic acid, ferulic acid, phenolic acids, vanillic acid, 3-phenyl propionic acid, and 4-hydroxybenzoic acid can inhibit the growth of *Trichoderma* [16]. However, some *Trichoderma* species induce root branching and increase shoot biomass by the presence of auxin-like compounds, which help to exchange these root exudates and signaling molecules between *Trichoderma* and plants in crop rhizosphere [15]. The ATP cassette-binding cell membrane pump of *Trichoderma* species is an important part of a comprehensive, potent cell detox system that explains the ability of *Trichoderma* to cope with various chemical stresses. In addition to co-inoculating other useful organisms such as the AM fungi, the *Trichoderma* species appears to have a role to play in attenuating plant hormone reactions to the root colonization process [17]. The effective colonization of the *Trichoderma* species on the roots of their hosts implies a reprogramming of the plant, with improved growth, yield, and pathogen resistance [18].

3. Effects of *Trichoderma* Metabolites on Soil and Root Pathogens

Trichoderma species are commonly found on plant root surfaces in various soil habitats where they control the soil-borne pathogens causing plant root diseases [19]. The most versatile strains from the *Trichoderma* genus, including *Trichoderma arundinaceum, T. asperellum, T. atroviride, T. citrinoviride, T. cremeum, T. crissum, T. gamsii*, *T. hamatum, T. harzianum, T. pseudo-koningii, T. koningii, T. koningiopsis, T. longibrachiatum, T. longipile, T. ovalisporum, T. polysporum, T. reesei, T. saturnisporum, T. spirale, T. virens,* and *T. viride,* secrete diverse chemical compounds [20][21][22] (**Table 2**). A large number of soil-borne fungi are capable of generating chemicals that are recognized for their antifungal efficiency. *Trichoderma* species possess the fungicidal and fungistatic characteristics as they generate various cell wall-degrading enzymes and secondary metabolites (SMs) [23][24]. These metabolites enhance the plant defense response when attacked by phytopathogens. Secreted antimicrobial compounds during the *Trichoderma*–mediated defense response pathways are often associated with the barriers of pathogen entry into the plant cells [18]. For example, the accumulation of secondary phenolic metabolites plays a crucial role in plant defense mechanisms against various pathogens. *Trichoderma* produces various peptides, proteins, and low molecular weight compounds, which are involved in biochemical resistance to pathogens and induce resistance in plants [25].

Various groups of compounds are secreted by the *Trichoderma* species trigger to induce the defense reactions in plants. Celluloses produced by *T. harzianum* have been proven to act as an elicitor for systemic acquired resistance (SAR) by causing peroxides and chitinase activity. Systemic plant reactions occur via the JA/ethylene signaling pathway (**Figure 1**). *Trichoderma* has been shown to release these enzymes or otherwise functioning proteins, avirulence gene (*Avr*) encoded homologous proteins, oligosaccharides, and other low molecular weight compounds [26]. The chitinase enzymes are commonly known as plant gene-encoding enzymes, which degrade cell walls, and are used to induce plant resistance against phytopathogens. In terms of antifungal efficiency, the chitinase genes from *Trichoderma* showed dominant expression over the corresponding plant genes resulting in improved pathogenic resistance [27]. Therefore, it is expected that the transgenes inserted in the plant-host increase the resistance level against a variety of plant pathogens [28]. The *Trichoderma* gene *chit42* encodes a powerful endochitinase enzyme that exhibits strong antifungal activity against a broader range of plant pathogens as compared to other chitinolytic enzymes. The constitutive expressions of *Trichoderma* genes in plants have shown higher levels and improved resistance against soil-borne plant pathogens [29].

Table 2. A list of metabolites and chemical compounds secreted by *Trichoderma* species affects soil pathogenic fungi.

Metabolites	Compound	*Trichoderma* Species	Target Fungal Pathogens	References
Anthraquinones	1,8-dihydroxy-3-methylanthraquinone, 1-hydroxy-3-methylanthraquinone	*T. harzianum*	*Fusarium oxysporum, Macrophomina phaseolina, Rizoctonia*	[30]

Metabolites	Compound	*Trichoderma* Species	Target Fungal Pathogens	References
	and 6-methyl-1,3,8-trihydroxyanthraquinone		*solani*, and *Sclerotium rolfsii*	
	1,8-dihydroxy-3-methylanthraquinone and 1-hydroxy-3-methylanthraquinone	*T. harzianum*	*Gaeumannomyces graminis* var. *tritici*, and *Pythium ultimum*	[31]
Azaphilones	Harziphilone, Fleephilone and T22azaphilone	*T. harzianum*	*G. graminis* var. *tritici*, *P. ultimum*, and *R. solani*	[32]
	T22azaphilone	*T. harzianum*	*Leptosphaeria maculans*, and *Phytophthora cinnamomi*	[33]
Epipolythiodio-xopiperazines	Gliotoxins	*T. virens*	*M. phaseolina, Pythium aphanidermatum, Pythium deharyanum, Rizoctonia bataticola, R. solani*, and *S. rolfsii*	[34]
	Gliovirin	*T. longibrachiatum*	*R. solani*	[34]
	Gliovirin	*T. virens*	*P. ultimum*	[34]
Koninginins	koninginins A, B, D, E, and G	*T. aureoviride T. harzianum* and *T. koningii*	*G. graminis* var. *tritici*	[35]
	koninginins A, B, and D	*T. koningiopsis*	*F. oxysporum*, *F. solani*, and *S. rolfsii*	[35]
	koninginin D	*T. harzianum* and *T. koningii*	*Bipolaris sorokiniana, F. oxysporum, P. cinnamomi*, and *Pythium middletonii*	[36]
Lactones	aspinolide C	*T. arundinaceum*	*Fusarium sporotrichioides*	[37]
	Cerinolactone	*T. cerinum*	*Rosellinia necatrix*	[37]
	Cremenolide	*T. cremeum*.	*F. oxysporum* and *R. solani*	[37]
Peptaibols	trichokonins VI, VII, and VIII	*T. koningii*	*F. oxysporum*, *R. solani*, and *Verticillium dahliae*	[30]

Metabolites	Compound	*Trichoderma* Species	Target Fungal Pathogens	References
	Trichokonin VI	*T. pseudokoningii*	*F. oxysporum*, *Phytophthora parasitica*, and *V. dahlia*	[30]
Polyketides	Harzianolide and Dehydro Harzianolide	*T. harzianum*	*F. oxysporum* and *R. solani*	[38]
	6-pentyl-α-pyrone	*T. harzianum* *T. koningii* *T. viride* and *Trichoderma* spp.	*R. solani*	[38]
	6-pent-1-enyl-α-pyrone	*T. harzianum* and *T. viride*	*R. solani*	[38]
	Massoilactone δ-decenolactone	*Trichoderma* spp.	*R. solani* and *S. rolfsii*	[38]
	Koninginia E, B, and A	*T. harzianum* and *T. koningii*	*G. graminis* var. *tritici*	[32]
	Koninginin D and Seco-koninginin	*T. harzianum*	*G. graminis* var. *tritici*	[32]
	Koninginin C	*T. koningii*	*G. graminis* var. *tritici*	[32]
Pyridones	Harzianopyridone	*T. harzianum*	*G. graminis* var. *tritici*, *L. maculans, P. cinnamomi, P. ultimum*, and *R. solani*	[32]
Pyrones	6-Pentyl pyrone (6-PP)	*T. harzianum, T. koningii*, and *T. viride*	*F. oxysporum* and *R. solani*	[39]
	Viridepyronone	*T. viride*	*S. rolfsii*	[39]
Steroids	Stigmasterol	*T. harzianum* and *T. koningii*	*F. oxysporum, M. phaseolina*, *R. solani*, and *S. rolfsii,*	[32]
Terpenes (trichothecenes)	Trichodermin	*T. polysporum* *T. sporulosum* *T. reesei* and *T. virens*	*R. solani*	[40]
	Harzianum A	*T. harzianum*	*F. oxysporum*	[40]
	Mycotoxin T2	*T. lignorum*	*R. solani* and *S. rolfsii*	[40]
Terpenes (triterpenes) (sterols)	Ergokonin A	*T. koningii* *T. longibrachiatum* and *T. viride*	*Phoma* spp.	[41]

Metabolites	Compound	*Trichoderma* Species	Target Fungal Pathogens	References
	Viridin	*T. koningii* *T. virens* and *T. viride*	*F. oxysporum* and *R. solani*	[41]
Trichothecenes	Trichodermin	*T. brevicompactum*	*R. solani*	[42]
	Trichodermin	*T. harzianum*	*F. oxysporum* and *R. solani*	[43]

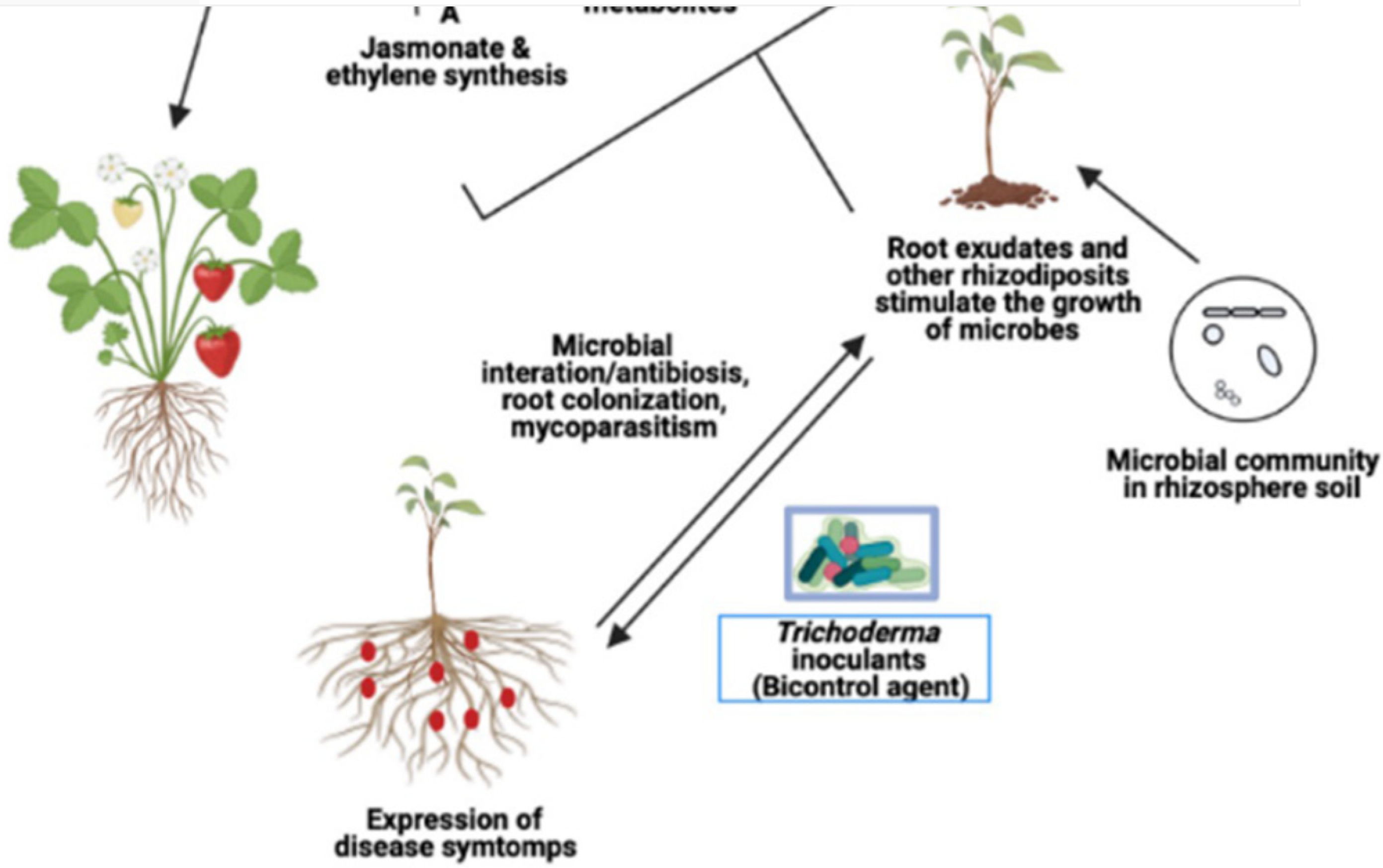

Figure 1. Metabolites (antibiotics and enzymes) produced by *Trichoderma* induce plant defense responses against the pathogens: (A) *Trichoderma* released antibiotics, enzymes, and secondary metabolites (SMs) through metabolic pathways leading to antagonize the phytopathogens. (B) Signals involved in *Trichoderma*–plant interaction enhanced the plant defense responses.

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