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Trichoderma spp. as Bio-Pesticides: Exploring Diverse Modes of Action

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ABSTRACT

Effective disease management in economically important crops is essential for maintaining high quality and yield. Traditionally, synthetic fungicides have been the mainstay for controlling plant diseases. However, growing concerns about the health risks and environmental impact of these chemicals, along with increasing pesticide resistance, have driven research towards non-chemical alternatives. Among these alternatives, biocontrol agents like *Trichoderma* spp. have emerged as promising candidates. These biological agents offer a range of modes of action that can effectively manage plant diseases while being eco-friendly, cost-efficient, and safer for human health. These include competition for essential nutrients, production of antibiotics, secretion of cell wall-degrading enzymes, hyperparasitism, and the stimulation of plant defense mechanisms. Many successful *Trichoderma* spp. leverage a combination of various modes of action to achieve upgraded antagonistic effects. This review explores the various mechanisms by which *Trichoderma* spp. act as bio-pesticides and their potential benefits in sustainable crop management.

Keywords: *Trichoderma* spp., biocontrol agents, bio-pesticides, plant disease management, mycoparasitism, enzyme production, sustainable agriculture.

INTRODUCTION

Trichoderma spp. had gained significant scientific interest due to its effective biocontrol properties against a variety of economically important plant pathogens (Riccarda et al., 2008). These fungi, which are free-living and commonly found in soil, decaying organic matter, and plant residues, were first documented as biocontrol agents in the 1930s, particularly for managing root rot caused by *Armillaria mellea* in citrus crops (Pellegrini et al., 2014). Trichoderma species are widespread globally and frequently associate with plant roots, soil, and debris (Jash and Sitansu, 2007). Rifai (1969) nine unique morphological species groups were identified. DNA-based techniques have introduced additional essential criteria for the taxonomy of Trichoderma, thereby advancing current efforts in identification and phylogenetic classification. Numerous isolates within the Trichoderma genus, recognizecd as mycoparasites of various economically important soil-borne pathogens, have been classified as T. harzianum, as shown in Table 1.

Table 1. Examples of some commercial products of *Trichoderma* spp. (available world)

	Name Product	Species/strain of Trichoderma	Pathogens controlled	Country	Agency/Company	Reference
1	Binab T	*T. harzianum, T. polysporum*	*Botryitis, Verticillium, Pythium, Fusarium, Phytophthora, Rhizoct*	Sweden	BINAB (http:// www.algonet.se)	Biswas and Datta, 2013
3	Binab T	*T. harzianum, T. polysporum*	*Botryitis, Verticillium, Pythium, Fusarium, Phytophthora, Rhizoct*	United Kingdom	Henry Doubleday Research Association	Ng et al., 2015
4	Plant Shield	*T. harzianum*	damping-off diseases	USA	http:// www.agreoBiologicals.com	Parveen and Kumar, 2004
11	Promot PlusWP Promot PlusDD	*Trichoderma spp., Trichoderma koningii Trichoderma harzianum*	Wilt, Root rot diseases	Vietnam	Tan Quy, Vietnam	Ha, 2010
12	*Antagon TV*	*T.viride, T.harzianum*	*Macrophomina* spp	Coimbatore, India	Green Tech	Gupta et al., 2005
13	Gliostar	*T.virens*	*Fusarium, Rhizoctonia, Sclerotium, Pythium*	Pantnagar, India	GBPUAT	Gupta et al., 2005
14	Monitor	*Trichoderma spp*	*Fusarium, Rhizoctonia,*	Rahuri, India	Agricultural and Biotech Pvt. Ltd. Gujarat Department of Plant Pathology, MPKV	Chaudhary and Prajapati, 2004
15	Bioderma	*T.viride/T. harzianum*	*Fusarium*	India	Biotech International Ltd.	Kexiang et al., 2002

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	Name Product	*Species/strain of Trichoderma*	Pathogens controlled	Country	Agency/Company	Reference
16	Bio Fit	*T. viride*	*Pythium, Rhizoctonia, Sclerotium, other root rots*	India	Ajay Biotech (India) Ltd.	http://www.ajaybio.com
17	Ecofit	*T.viride*	*Fusarium*	India	Hoechst Schering Afgro Evo Ltd,	Yadav and Majumdar, 2005
18	Trichoguard	*T.viride*	*Sclerotium, other root rots*	Faridabad, India	Anu Biotech Int. Ltd.	Bunker and Mathur, 2001
19	Trichoguard	*T.viride*	*Fusarium*	Jorhat, India	Tocklai Experimental Station Tea Research Association	Komy et al., 2015
20	Ecofit	*Trichoderma viride*	*Fusarium*	India	Hoechest and Schering Agro. Evo. Ltd., Mumbai	Kumar et al., 2014
21	Funginil	*Trichoderma viride*	Tobacco mosaic virus	India	CHBRC, Gaziabad (UP)	Kumar et al., 2014
22	Trichogourd	*Trichoderma viride*	*Agrobacterium tumefaciens*	India	Anu Biotech international Ltd. Bangalore	Kumar et al., 2014
23	Defense SF	*Trichoderma viride*	*Agrobacterium tumefaciens*	India	Wockhardt Life Science Ltd., Mumbai	Kumar et al., 2014
24	Tricho-X	*Trichoderma viride*	*Fusarium oxysporum*	India	Excel Industries Ltd., Mumbai	Kumar et al., 2014
25	Biogourd	*Trichoderma viride*	*Botrytis cinerea*	India	Krishi Rasayan Export Pvt. Ltd., Solan (HP)	Kumar et al., 2014
26	Biocon	*Trichoderma viride*	*Sclerospora graminicola*	India	Tocklai Experimental Station Tea Research Association, Jorhat (Assam)	Kumar et al., 2014
27	Bip T	*Trichoderma viride*	*Tomato mottle virus*	India	Poland	Kumar et al., 2014
28	Pant biocontrol agent-1	*Trichoderma harzianum*	*Corynespora cassiicola*	India	Department of Plant Pathology, GB Plant University of Agriculture and Technology, Panatnagar, Uttarakhand	Kumar et al., 2014
29	Bioderma	*Trichoderma viride+ Trichoderma harzianum*	*Rhizoctonia solani*	India	Biotech International Ltd., New Delhi	Kumar et al., 2014
30	Ecoderma	*Trichoderma viride+ Trichoderma harzianum*	*Meloidogyne* spp	India	Morgo Biocontrol Pvt. Ltd., Bangalore	Kumar et al., 2014
32	Ecohope	*T. asperellum*	*Erwinia tracheiphila*	Japan	Ecohope-Dry (Kumiai Chemical Industry Co. Ltd.)	Hyder et al., 2017
33	Farroupilha	*T. asperellum*	*Peronospora tabacina*	Brazil	Quality WG (Laboratório de Biocontrole Farroupilha Ltda.)	Hyder et al., 2017
34	Trichodermax EC	*T. asperellum*	*Rhizoctonia solani*	Brazil	(TURFAL - Industria e comércio de produts biológicos e agronômicos Ltda.)	Hyder et al., 2017
35	Trichotech WP	*T. asperellum*	*Sclerotinia sclerotiorum*	Kenya	(Dudutech K Ltd)	Hyder et al., 2017
36	Antagon WP	*T. harzianum*	*Pythium aphanidermatum*	Colombia	(Bio Ecológico Ltda.)	Hyder et al., 2017
37	Trichobiol WP	*T. harzianum*	*Sclerospora graminicola*	Colombia	(Control BiológicoIntegrado ; Mora Jaramillo Arturo Orlando - Biocontrol)	Hyder et al., 2017
38	Unite WP	*T. harzianum*	*Meloidogyne* spp	Australia, New Zealand	(Agrimm Technologies Limited)	Hyder et al., 2017
39	Agroguard WG	*T. harzianum DSM 14944*	*Botrytis cinerea*	Colombia	Foliguard (Live Systems Technology S.A)	Hyder et al., 2017
40	Romulus	*T. harzianum isolate DB 104*	*Fusarium oxysporum*	South Africa	(DAGUTAT BIOLAB)	Hyder et al., 2017
41	Rootgard	*T. harzianum strain 21*	*Pythium ultimum*	Kenya	(Juanco SPS Ltd.)	Hyder et al., 2017
42	Eco-T	*T. harzianum strain kd*	*Pythium ultimum*	Zambia, Kenya and South Africa; in process FR, UK, Morocco, Tunisia and India	[Plant Health Products (Pty)Ltd.]	Hyder et al., 2017
43	Bio-Tricho	*T. harzianum strain SF*	*Pythium Spp*	South Africa	(Agro-Organics)	Hyder et al., 2017
44	Trichodermil	*T. harzianum strains ESALQ-1306, ESALQ-1303*	*Puccinia striformis*	Brazil	(ItaforteBioProdutos)	Hyder et al., 2017
45	Supresivit	*T. harzianum*	*Fusarium oxysporum*	Czech Republic	(Fytovita, Ltd.)	Hyder et al., 2017
48	Ecosom-TH	*T. harzianum IIHR-Th-2*	*Phytophthora medicaginis*	India	(Agri Life)	Hyder et al., 2017
50	Eco-77	*T. harzianum strain B77*	*Phytophthora capsici*	South Africa, Kenya, Zambia	(Plant Health Products)	Hyder et al., 2017
51	Tricho D WP	*T. harzianum T-22 (ATCC 20847)*	Penicillium digitatum	Colombia, Equador, Panama, Peru, Chile	(OriusBiotecnologia)	Hyder et al., 2017
52	Micover	*T. harzianum, Glomus intraradices and Pseudomonas*	*Cucumber mosaic virus*	European Union	Gold e Plus (Agrifutur)	Hyder et al., 2017
53	Promot WP	*T. harzianum, T. koningii*	*Phytophthora capsici*	R in Germany; Kenya (temp. 2010)	(Biofa AG, Bio-farming systems)	Hyder et al., 2017
54	Fitotripen WP	*T. harzianum, T. koningii, T. viride*	*Magnaporthe grisea*	Colombia	(Safer Agrobiologicos)	Hyder et al., 2017
68	Bio Traz, BioFit	*T. harzianum, T. virens*	*P. capsici*	Chile	(Biomycota)	Hyder et al., 2017
71	BW240 G,	*T. virens G-41*	*Meloidogyne* spp	USA	BW240 WP Biological Fungicide (BioworksInc)	Hyder et al., 2017
72	Trichonativa	*T. virens, T. harzianum, T. parceanamosum*	*Meloidogyne* spp	Chile	(Bio-InsumosNativaLtda)	Hyder et al., 2017
73	Biocure F	*T. viride*	*Rhizoctonia solani*	EU; available India	(T. Stanes and Company Limited)	Hyder et al., 2017
74	Bio-Shield	*T. viride*	*Stagonospora nodorum Berk.*	India	Bioveer (Ambika Biotech)	Hyder et al., 2017
76	Mycofungicyd, Trichodermin	*T. viride 16, T. lignorum*	*Aspergillus flavus*	Ukraine	Bizar-agro LTD	Hyder et al., 2017

	Name Product	*Species/strain of Trichoderma*	Pathogens controlled	Country	Agency/Company	Reference
77	Excalibur Gold	*Trichoderma spp.*	*Rhizoctonia and Fusarium*	USA	Excalibur Green (ABM)	Hyder et al., 2017
78	Trichodermacontaining	*Trichoderma spp.*	*Ralstonia solanacearum*	China	products indicated, but not specified	Hyder et al., 2017
79	Tricho Plus	*Trichoderma spp.*	Sclerotiniose/Brassica campestris L	South Africa	[Biological Control Products (Pty)Ltd]	Hyder et al., 2017
80	Trichozam	*Trichoderma spp.*	*Botrytis cinerea*	Honduras, Colombia	Hardware & Lumber Limited (Agro Grace Division)	Hyder et al., 2017
81	Solstice	*Trichoderma Td82 and Td84*	*Fusarium oxysporum f.sp. lycopersici*	Australia	(Metcalf Biologicals)	Hyder et al., 2017
82	ICB Nutrisolo SC e WP	*T. viride, T. harzianum, T. koningii and Trichoderma spp.*	*Graminis* var. *tritici*	Brazil	(ICB BIOAGRITEC Ltd)	Hyder et al., 2017
83		*Trichoderma spp. (6 strains)*	*Botrytis cinerea*	Brazil		Hyder et al., 2017
84	Trichosav-34	*T. harzianum A-34*	*Fusarium* pathogen infection	Cuba	Research Institute Plant Protection	Hyder et al., 2017
85	Trichosav-55	*T. harzianum A-55*	*Fusarium oxysporum* f. sp. *radicis- lycopersici*	Cuba	[Institute for Research in Plant Protection (INISAV)]	Hyder et al., 2017
86	Remedier® Tenet®	*T. asperellum ICC 012* *T. gamsii ICC 080*	*Fusarium*	European market	Isagro S.p.A	Biswas and Datta, 2013
87	Tusal®	*T. asperellum T25* *T. atroviride T11*	*Mucor piriformis*	European market	Certis Europe B.V	Ng et al., 2015
88	T34 Biocontrol®	*T. asperellum T34*	*Rhizoctonia solani*	European market	Biocontrol Technologies SL	Parveen and Kumar, 2004
89	Xedavir®	*T. asperellum TV1*	*Pythium spp.*	European market	Xeda Italia S.r.l	Hyder et al., 2017
90	Esquive® Tri-Soil®	*T. atroviride I-1237*	*Xanthomonas axonopodis pv. glycines, Burkholderia glumae*	European market	Agrauxine S.A Certis Europe	Hyder et al., 2017

Trichoderma spp. have gained widespread recognition as potent biocontrol agents, offering environmentally friendly solutions for managing plant diseases (Elad, 2000; Mukesh et al., 2016). Their ability to inhibit pathogens through diverse mechanisms - such as antibiosis, mycoparasitism, and the stimulation of systemic resistance - makes them invaluable for sustainable agriculture. These fungi control pathogens and simultaneously improve plant growth, soil health, and nutrient availability for better yields of crops (Harman et al., 2004; Vinale et al., 2009). Having more than 250 commercial products being formulated in the world, the species *Trichoderma* spp. represent a nontoxic, efficient alternative to chemical fungicides, reducing environmental and health risks due to the increasing pesticide resistance noted by Mbarga et al. (2014) and Singh et al. (2021).

Choosing effective Trichoderma strains is crucial for creating safe and efficient bio-control strategies. Bio-fungicides, including those based on Trichoderma, serve as viable alternatives to synthetic fungicides, helping to reduce environmental damage and risks to animals and humans. The survival and dominance of Trichoderma in soil are attributed to their diverse metabolic capabilities, which enable them to outcompete other microorganisms (Ahmed et al., 2019; Elad, 2000). Approximately 90% of fungal biocontrol agents targeting pathogenic microorganisms are represented by various Trichoderma strains (Mukesh et al., 2016). These strains have developed a range of strategies to directly antagonize other fungi and indirectly promote plant and root development (Harman et al., 2004). Notably, *T. harzianum* strains are recognized for their ability to thrive in diverse environments, including acidic soils (Rhman et al., 2002). The increasing adoption of Trichoderma as a biofungicide among farmers can be attributed to its diverse mechanisms for inhibiting the growth and development of plant pathogens. Furthermore, various *Trichoderma* species utilize different antifungal strategies while offering additional benefits such as promoting plant growth and enhancing soil fertility (Ahluwalia et al., 2015; Jaroszuk-Scisel et al., 2019). Trichoderma strains also contribute positively to biodegradation and can outcompete fungal pathogens during their saprophytic stages, especially under nutrient-limiting conditions (Gajera et al., 2020). Trichoderma is also reported to excel in competing within the rhizosphere and exhibits notable mycoparasitic behavior compared to other microorganisms (Zeilinger et al., 1999; Jash and Sitansu, 2007). Their effective biodegradation and substrate colonization capabilities are attributed to their remarkable metabolic versatility and the production of a diverse array of hydrolytic enzymes (Reino et al., 2008). Cell wall-degrading enzymes in Trichoderma play a crucial role in mycoparasitism by hydrolyzing the cell walls of various host fungi (Keszler et al., 2000). Key enzymes involved include chitinases, β-1,3-glucanases, β-1,6-glucanases and α-1,3-glucanases (Elad, 2000; Adekunle et al., 2001; Ahmed, 2008). Some strains are particularly notable for their potential in production of secondary metabolites with significant potential, such as antibiotics including gliotoxin and viridin, α-pyrones (Keszler et al., 2000), terpenes, polyketides, isocyanide derivatives and complex peptaibols. Additionally, volatile compounds produced by *Trichoderma* spp. can induce or enhance plant resistance (Jash and Sitansu, 2007; Bansal et al., 2021). Trichoderma species synthesize several organic acids, including citric, gluconic, and fumaric acids, which play a crucial role in the mobilization and absorption of soil minerals. These acids contribute to altering the soil pH, thereby facilitating the solubilization and uptake of essential micronutrients (Vinale et al., 2009). In soils contaminated with pathogens, they not only promote plant development but also restrict pathogen growth via a variety of antagonistic mechanisms (Rhman et al., 2002; Chilosi et al., 2020). Certain globally utilized strains of Trichoderma have been shown to enhance plant growth by producing indole-3-acetic acid (IAA) through auxin-dependent pathways (Nakkeeran et al., 2006; Fu et al., 2015) (Tables 2 and 3).

Table 2. *Trichoderma* species produce phytohormones that play a role in their interactions with plants

Category	Function Performed	Trichoderma Species	References
IAA.	Plant growth and maturation, along with the development of their root systems.	*T. virens*	Contreras-Cornejo et al., 2009
GA3	Growth enhancement achieved by breaking down DELLA proteins that inhibit growth and by lowering ethylene levels.	*Trichoderma spp*	Hermosa et al., 2012; Guzmán- Guzmán *et al*., 2019
ABA	Transpiration is altered and stomatal openings are regulated by activating an ABA receptor.	*T. virens,* *T. atroviride*	Contreras-Cornejo et al., 2015
Ethylene	Enhanced resilience to both biotic and abiotic stresses by modulating the levels of SA and JA and their associated signaling pathways.	*T. atroviride*	Pieterse et al., 2012
JA	JA and/or ET serve as the signaling molecules for ISR induced by Trichoderma.	*T. asperellum*	Yoshioka et al., 2012
SA	Strengthens plant disease resistance by initiating systemic acquired resistance (SAR).	*T. atroviride*	Seyfferth and Tsuda, 2014

Table 3. Trichoderma species produce enzymes that are involved in their interactions with plants

Category	Function Performed	Trichoderma Species	References
Cellulolytic enzymes	Cleavage of β-1,4-D-glycosidic bonds in cellulose molecule.	*T. viride,* *T. harzianum*	Strakowska et al., 2014
Exo-β-1,4-glucanases	Breaking the β-1,4-D-glycosidic bonds within cellulose molecules.	*T. reesei,* *T. koningii*	Vázquez-Garcidueña et al., 1998
Endo-β-1,4-glucanases	During the enzymatic degradation of cellulose, the β-1,4-glycosidic bonds are randomly cleaved, likely within the amorphous regions of cellulose, resulting in the formation of cellulodextrins with varying chain lengths.	*T. viride,* *T. longibrachiatum,* *T. pseudokoningii,* *T. reesei*	Li et al., 2011
Xylanase	Facilitate the decomposition of xylans, resulting in the production of xylo-oligomers, xylobiose, and xylose.	*T. harzianum,* *T. koningi*	
Chitinase	Facilitate the breakdown of chitin into low molecular weight chitooligomers.	*T. longibrachiatum,* *T. pseudokoningii,* *T. reesei,* *T. viride Trichoderma harzianum,* *T. virens,* *T. asperellum,* *T. atroviride*	Harman et al., 1993
Endochitinases	Chitin is randomly hydrolyzed at internal sites, resulting in the formation of diacetylchitobiose dimers and low molecular weight GlcNAc multimers such as chitotriose and chitotetraose.		
Exochitinases	They are classified into two subgroups: 1. Chitobiosidases, which catalyze the sequential release of diacetylchitobiose from the non-reducing ends of chitin microfibrils; and 2. 1-4-β-glucosaminidases, which break down the oligomeric products produced by endochitinases and chitobiosidases, thereby generating GlcNAc monomers.		

Biocontrol Potential of *Trichoderma* spp. against Various Pathogens

The genus *Trichoderma* is renowned for its role as a natural bio-agent, effectively suppressing plant pathogens through multiple mechanisms. *Trichoderma* spp. are of particular interest as biocontrol agents because of their rapid growth and ability to utilize a variety of secondary metabolites. Certain *Trichoderma* spp. have been identified as promising bio-control agents against plant pathogenic fungi. Research highlights the remarkable ability of *T. harzianum* to control phytopathogenic fungi, which is attributed to its synergistic strategies (Hjeljord, 1998; Gajera et al., 2020). Using a *Trichoderma* isolate with multiple mechanisms of action can enhance biocontrol effectiveness. Furthermore, employing multiple isolates may create synergistic effects against pathogens (Abd El Moity, 1985; Ali, 2021). Anand and Reddy (2009), recommended including several *Trichoderma* strains in formulations to broaden the spectrum of control. Nowadays, *Trichoderma* spp. are among the most frequently utilized fungal biological control agents globally, according to their efficacy and accessibility for commercial production. Approximately 250 different Trichoderma-based products are available in countries including Belgium, Sweden, the USA, Denmark, India, and New Zealand, and are used on various crops for agricultural use (Singh et al., 2021; Mbarga et al., 2014). *Trichoderma* spp. are widely recognized as leading fungal agents for biological control, with over 60% of the registered biofungicides globally being formulated with various strains of this genus (Keswani et al., 2014; Mohdly et al., 2024). Various strains of Trichoderma and product formulations exhibit different levels of effectiveness in managing fusarium and charcoal rot diseases (Orojnia et al., 2021). In one of the early studies, Petcu et al. (2023) investigated the use of a combination of Trichoderma harzianum and Bacillus subtilis to enhance maize yield under field conditions. Their findings demonstrated that treatments with Trichoderma harzianum strain 179 and Bacillus subtilis strains 84 and 284, applied to seeds and vegetation, promoted plant growth and increased maize yield. Additionally, the treatment showed secondary benefits, such as improved plant height and reduced maize weevil infestation.

Different Modes of Action of *Trichoderma* spp.

1. Antibiosis

Antibiosis refers to the inhibition or suppression of one microorganism by another through the production of secondary metabolites. *Trichoderma* spp. exhibit antibiosis by secreting a variety of antimicrobial compounds that hinder the growth or proliferation of phytopathogens (Cruz-Quiroz et al., 2018). Antibiosis in *Trichoderma* spp. is triggered during interactions with pathogens and plants, leading to the production of antibiotics that suppress the growth of phytopathogens. More than 180 secondary metabolites have been identified in *Trichoderma* spp., representing diverse chemical classes. These include cell wall-degrading enzymes such as cellulase, xylanase, pectinase, glucanase, lipase, and protease, as well as volatile compounds like 6-n-pentyl-2H-pyran-2-one (6-PAP) (Reino et al., 2008; Sood et al., 2020). Trichoderma also produces a variety of antibiotics, including trichodermin, gliovirin, gliotoxin, viridin, herzianolide, peptaibols, and formic aldehyde (Mironenka et al., 2020; Bansal *et al*., 2021). Strains of T. virens with high biocontrol efficacy are particularly noted for their production of gliovirin (Bansal *et al*., 2021). Additionally, many Trichoderma strains are capable of synthesizing both volatile and non-volatile toxic metabolites, including low molecular weight compounds and specific antibiotics, to suppress plant pathogens (Gajera et al., 2013). For example, the volatile antibiotic 6-phenyl-pyrone, known for its role in controlling *Fusarium oxysporum,* is produced by *T. viride, T. harzianum,* and *T. koningii* (Blaszczyk *et al*., 2014). Additionally, *T. harzianum* produces harzianic acid, a tetrameric acid with notable antifungal properties, which also stimulates plant growth (Vinale et al., 2009). Pathogenic tissue degradation is facilitated by the enzymatic breakdown of cell walls, with *Trichoderma* spp. producing hydrolytic enzymes like chitinase, β-1,3-glucanase, and cellulase (Hjeljord et al., 1998; Zin and Badaluddin, 2020). Also, antibiotics are involved in activities such as encircling the host and forming appressorium-like structures (Dennis and Webster, 1971; Lu et al., 2004). Lectins present in the host cell wall induce the *Trichoderma* hyphae to encapsulate the host's hyphae following direct contact (Harman et al., 2004). In *T. atroviride*, the *nag1* gene, responsible for encoding N-acetylglucosaminidase, is pivotal in chitinase induction and enhancing biocontrol effectiveness (Brunner et al., 2003). During interactions between *Trichoderma* and *Rhizoctonia solani*, host-released dispersal factors stimulate the transcription of the *ech42* gene, which encodes endochitinase 42, even prior to direct physical contact (Zeilinger et al., 1999; Harman et al., 2004) (Figure 1).

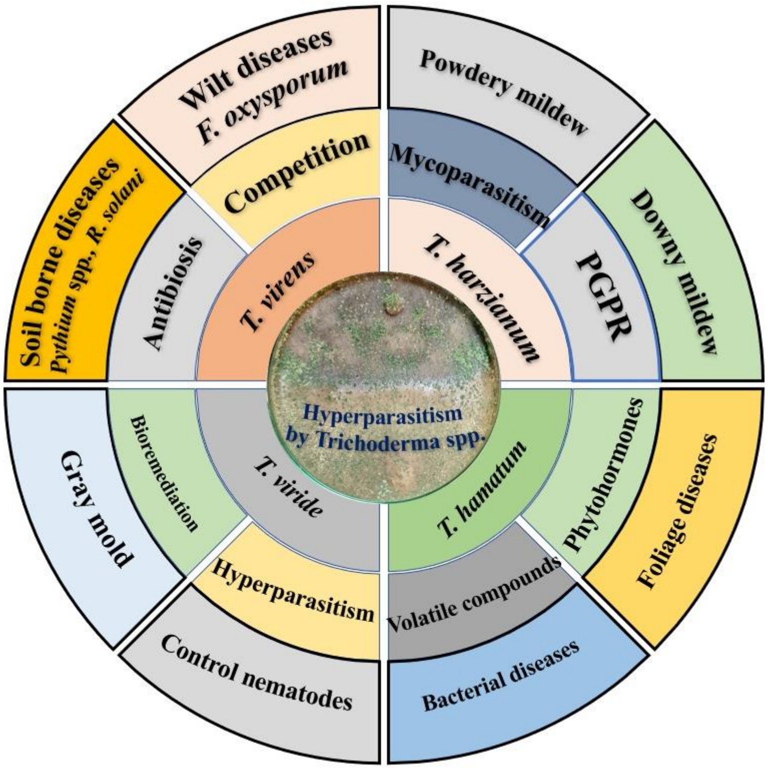

Figure 1. Different *Trichoderma* spp., mode of action and group of diseases control using this bio-control agent

2. Mycoparasitism

Mycoparasitism is a key mechanism in biological control, involving a fungus directly attacking another fungus through a series of steps: recognizing the pathogen, attacking, penetrating the host cell, and ultimately causing its death. During this process, *Trichoderma* spp. initially produce low levels of cell wall-degrading enzymes to locate their target. Once the pathogen is recognized, *Trichoderma* increases its growth towards the pathogen and enhances the production of cell wall-degrading enzymes (Sharma et al., 2017; Almeida et al., 2021). Mycoparasitism is a complex, sequential process involving three main steps: chemotrophic growth and pathogen recognition, hyphal coiling and interaction, and the secretion of specific lytic enzymes (Dix and Webster, 1995). Studies have also shown the mycoparasitic behavior of Trichoderma species against Pythium ultimum and Sclerotium rolfsii (Papavizas, 1985). *Trichoderma* spp. attach to their fungal targets by binding their carbohydrates to the lectins on the pathogen’s surface. They then wrap around the pathogen’s hyphae and form appressoria to penetrate them. The hyphae are subsequently attacked and broken down through the secretion of hydrolytic enzymes and secondary metabolites. Additional enzymes, such as those that degrade β-1,6-glucans, α-1,3-glucans, chitin, and proteins, further ensure the full degradation of fungal mycelia or conidia (Chao and Wen-ying, 2019) (Table 4).

Table 4. Compounds synthesized (Proteases) by *Trichoderma* spp. involved in plant interaction

Category	Function Performed	Trichoderma Species	References
Exopeptidases	Induce the breaking of peptide bonds at either the amino or carboxy terminal ends.	*T. viride, T. harzianum, T. aureoviride, T. atroviride*	Flores et al., 1997
Lipase	Lipase breaks down the ester bonds in triacylglycerols, leading to the production of mono- and diacylglycerols, free fatty acids, and sometimes glycerol.	*T. lanuginosus, Trichoderma reesei*	Bhale and Rajkonda, 2012
Glucose oxidase	Cause generation of reactive oxygen species (ROS).	*T. virens, T. asperelloides*	Gupta et al., 2014
Antioxidative enzymes	Strengthen the antioxidative defense mechanisms in plants.	*Trichoderma spp.*	Mastouri et al., 2012

3. Competition

Starvation is a primary cause of death among microorganisms, making the competition for limited micro- and macro-nutrients a key factor in biological control of phytopathogens (Poveda and Baptista, 2021). The main biological mechanisms of *Trichoderma* is direct antagonistic activity against plant pathogenic fungi include competition for nutrients, mycoparasitism and antibiosis (Marzano et al., 2013). Its competitive edge over other microorganisms is due to its high growth rate and superior ability to mobilize and utilize nutrients from soil and substrates (Fu et al., 2015). *Trichoderma* spp. are highly effective rhizosphere colonizers and soil competitors. Consequently, the biocontrol of fungal pathogens using *Trichoderma* relies heavily on nutrient competition among its various strategies, highlighting its importance (Mukesh et al., 2016). In filamentous fungi, iron uptake is crucial for survival. When iron is scarce, many fungi release low molecular-weight ferric-iron chelators, known as siderophores, to mobilize environmental iron (Devi et al., 2016). Specific strains of *Trichoderma* are known to produce siderophores, which sequester ferric ions from the surrounding environment, effectively limiting the growth and activity of soil-borne pathogens (Deng et al., 2019). *Trichoderma* is also noted for its aggressive competitive behavior, characterized by rapid growth and efficient substrate colonization, which allows it to control slower-growing pathogens (Costa et al., 2021). Competition for macro- and micronutrients is crucial in the interaction between *Trichoderma* and plant pathogens (Vinale et al., 2008). *Trichoderma* species compete with bacteria in the crop rhizosphere for both nutrients and infection sites (Ahluwalia et al., 2015). Compared to other rhizosphere fungi, *Trichoderma* demonstrates superior capabilities in nutrient acquisition and utilization, making it effective in managing pathogens like *Botrytis cinerea* through nutrient competition (Bargaz *et al*., 2018; Jalal *et al*., 2024). Additionally, *Trichoderma* colonization of plant roots typically enhances nutrient absorption, crop yield, stress tolerance, and root growth and development (Boominathan *et al*., 1992).

4. Induced Systemic Resistance

Trichoderma can activate a host plant’s defense mechanisms, limiting pathogen proliferation and promoting the development of local or systemic disease resistance (Singh et al., 2021). This resistance induction is associated with increased production of defensive metabolites and enzymes, including those involved in phytoalexin biosynthesis, such as phenylalanine ammonia-lyase and chalcone synthase, which are part of the phenylpropanoid metabolism pathway (Brunner et al., 2003). Additionally, enzymes like chitinases and glucanases enhance plant resistance, along with pathogenesis-related proteins involved in systemic acquired resistance and antioxidative defense responses (Nakkeeran et al., 2006; Cruz-Quiroz et al., 2018). Yedidia et al. (1999) Studies have shown that inoculation of *T. harzianum* in cucumber roots enhances peroxidase and chitinase activities, thereby boosting the plant's resistance to pathogenic attacks. Trichoderma induces plant disease resistance through two primary mechanisms: first, by modulating or introducing elicitors that activate the plant's defensive responses, and second, by releasing oligosaccharides through cell wall-degrading enzymes produced by Trichoderma, which stimulate plant resistance (Gomes et al., 2015). Furthermore, Saravanakumar et al. (2016) reported that corn seeds treated with Trichoderma exhibited a marked increase in peroxidase and phenylalanine ammonia-lyase activities, resulting in enhanced resistance against *Curvularia* leaf spot in corn.

Commercially Available *Trichoderma* spp. Bioproducts

Trichoderma spp. is extensively studied as a microbial biocontrol agent (MBCA) in agriculture and is available commercially in various forms, including bio-pesticides, bio-fertilizers, growth promoters, and natural resistance inducers. Despite their benefits, bio-pesticides numbers for a relatively small portion of the commercial market, with chemical pesticides still holding over 95% of the market for controlling pests and diseases. The effectiveness of microbial pesticides in field conditions is often inconsistent due to several factors, including the limited shelf-life of the microorganisms, instability within formulations, competition with native soil microorganisms, and the negative impacts of various abiotic stresses on these organisms in the field.

Developing a formulation that is safe, cost-effective, and easy to handle, while maintaining the microorganism's viability, is crucial for creating an efficient and reliable biocontrol agent. Formulation involves blending active ingredients, such as fungal spores, with inert carriers like diluents and surfactants to enhance physical properties (Kumar et al., 2014). Combining different *Trichoderma* spp. strains in formulations is more effective than using single strains alone for controlling crop pests and diseases, as well as for enhancing plant growth. Potential *Trichoderma* isolates are formulated using various organic and inorganic carriers, through either solid or liquid fermentation technologies (Peng and Xia, 2011). An effective strategy for creating a successful microbial biocontrol consortium involves combining biocontrol agents with complementary disease-suppressive mechanisms. Mixtures of various *Trichoderma* strains offer better protection compared to single-strain applications (Marzano et al., 2013). *T. viride* combined with *T. harzianum* proved more effective than single-strain applications in managing *Maydis* leaf blight in maize (Yassin et al., 2021). There are numerous *Trichoderma* species and strains tailored to specific plant pathogens. Singh and Singh (2012), observed that a mixture of two different *T. harzianum* isolates resulted in greater disease reduction and yield improvement against *Sclerotinia sclerotiorum* compared to individual strains. Therefore, using *Trichoderma* in consortium form, with compatible isolates of the same or different species, provides more significant benefits than individual applications due to their synergistic effects. Kumar et al. (2023) *Trichoderma spp*. demonstrate significant efficacy in controlling fungal plant pathogens through several mechanisms, including the secretion of hydrolytic enzymes, mycoparasitism, coiling, and antibiosis. Species like *T. virens*, *T. asperellum*, and *T. harzianum* have been widely researched for their biocontrol potential against various phytopathogens (Table 5).

Table 5. Trichoderma species produce biosynthetic and signaling compounds that participate in interactions with plants

Category	Function Performed	Trichoderma Species	References
PAL and CHS	Production of phytoalexins	*Trichoderma spp.*	Ahluwalia et al., 2015
Glucan and Chitin synthases	Trichoderma produces these compounds to mend damage to its own cell wall inflicted by pathogens during their interactions.	*Trichoderma spp.*	Suriani Ribeiro et al., 2019
MAPK	Transmit information from receptors to initiate cellular signaling and defense responses.	*Trichoderma spp.*	Shoresh et al., 2005
ETR1 and CTR1	Plays a role in ethylene (ET) signaling.	*Trichoderma spp.*	Shoresh et al., 2005
ACC synthase	Promote ethylene biosynthesis.	*Trichoderma spp.*	Mastouri et al., 2012
δ-cadinene synthase	Act as precursor for phytoalexin synthesis.	*T. virens*	Yoshikuni et al., 2006

Formulations for Biocontrol Applications

An efficient biocontrol formulation using fungal propagules should be easy to prepare, maintain key properties such as viability, germination potential, and enzymatic activity during storage, and facilitate easy application. Carrier materials are essential in prolonging the shelf life of these formulations while enhancing conidial resistance to environmental stressors, including UV radiation (Sokhandani et al., 2016; Thabet et al., 2023; Khalil et al., 2024). Common formulation types for biocontrol agents include powders, granules, liquids, and seed treatments, each designed for specific agricultural uses. Advances in formulation technology have improved the encapsulation and efficient delivery of microbial biocontrol agents, leading to a variety of commercially available Trichoderma-based products. The main formulation categories are wettable powders and water-dispersible granules. Wettable powders are fine, dust-like mixtures of clay and silica, combined with surfactants to form stable suspensions when mixed with water (Kala et al., 2020). In contrast, granules are larger particles that dissolve or disperse rapidly in water, creating a uniform suspension (Ghoneem et al., 2019). These formulations are suitable for a range of applications, including ground and aerial spraying, root drenching, dipping, and seed treatments.

- Dry Formulations

Dry formulations represent the most widely adopted approach for producing Trichoderma-based products and dominate the commercial market. From a production standpoint, they provide the advantage of reduced susceptibility to contamination compared to liquid formulations. The powdered form allows for easy distribution and incorporation into soil or plant surfaces. Common dry formulation carriers for *Trichoderma* products include vermiculite and biochar. Biochar is particularly advantageous as a carrier because it is easy to handle and enhances the sporulation of *Trichoderma* spp. in the field. Additionally, biochar improves soil water-holding capacity, reduces fertilizer leaching, and promotes plant growth (Li et al., 2021; Wong et al., 2022). Granular formulations are commonly employed for soil applications, intended to gradually release Trichoderma into the soil and support ongoing microbial activity. These granules can either be applied directly to the soil or blended with other soil amendments.

- Liquid and Gel Formulations

Liquid and gel formulations preserve Trichoderma propagules by employing oil or water-soluble polymer networks to keep them hydrated. In contrast to dry formulations, these liquid and gel-based types encounter difficulties in prolonging shelf life due to increased water activity, which can cause spontaneous germination (Gervais et al., 1988), or imbibition damage from prolonged water exposure. Common types of liquid and gel formulations include oil-based and natural polymers. Natural polymer-based formulations, such as those using alginate, provide a different stabilization approach. Oil-based formulations involve mixing biocontrol propagules with vegetable oil and mineral oil-based formulations have proven effective for biocontrol activities, with or without the addition of water (Peng and Xia, 2011; Perinotto et al., 2017). These formulations exhibit better resistance to leaching by water improved UV tolerance and protection against incompatible water-soluble pesticides (Luz and Batagin, 2005; Lopes et al., 2011; Fernandes et al., 2015). Liquid formulations of *Trichoderma* are utilized for applications on plant leaves or as soil treatments. These formulations are particularly useful for extensive applications and can be applied with conventional spraying equipment. Typically, these liquids have a high concentration of active spores. For *Trichoderma* spp., Mbarga et al. (2014) demonstrated that *T. asperellum* PR11 conidia, when formulated in an oil dispersion primarily using soybean oil, maintained 50% conidial germination after 22.5 weeks at 25°C. Notably, this formulation effectively protected cacao pods from *Phytophthora megakarya* in the field, surpassing the performance of some conventional synthetic fungicides. Advanced formulations sometimes blend *Trichoderma* with additional biocontrol agents or chemicals to boost their efficacy. These combined products can provide synergistic benefits and a wider range of disease control. The combination of *Trichoderma asperellum* and *Streptomyces rochei* recorded significant effectiveness in reducing chia charcoal rot disease and enhancing plant growth parameters (Mergawy et al., 2022). In summary, good formulations offer high viability during extended storage, provide UV protection, enhance biocontrol performance, and improve adhesion to hydrophobic surfaces, which is crucial for foliar applications (Birnbaum et al., 2021).

Trichoderma spp. has garnered substantial scientific attention as effective biocontrol agent against a myriad of economically important plant pathogens. These fungi are ubiquitously present in soil, decaying organic matter, and plant residues, where they naturally associate with plant roots and debris (Jash and Sitansu, 2007; Riccarda et al., 2008). The biocontrol efficacy of *Trichoderma* spp. stems from their diverse mechanisms, including antibiosis, mycoparasitism, competition, and the induction of systemic resistance in host plants. For example, Trichoderma harzianum produces a range of hydrolytic enzymes such as chitinases and β-1,3-glucanases that degrade the cell walls of pathogenic fungi, thereby inhibiting their growth and proliferation (Hjeljord et al., 1998; Keszler et al., 2000). Additionally, the production of secondary metabolites like gliotoxin and viridin enhances their antagonistic capabilities, offering a sustainable alternative to synthetic fungicides and mitigating environmental risks (Gajera et al., 2020; Bansal et al., 2021). The ability of *Trichoderma* spp. to outcompete other soil microorganisms through efficient nutrient acquisition and rapid growth further solidifies their role as dominant biocontrol agents in agricultural ecosystems (Elad, 2000; Mukesh et al., 2016).

The commercial application of *Trichoderma* spp. has expanded significantly, with approximately 250 Trichoderma-based products available worldwide for various agricultural uses (Mbarga et al., 2014; Singh et al., 2021). These bioproducts are formulated in multiple forms, including dry powders, granules, and liquid formulations, to enhance their stability, shelf-life, and ease of application under diverse field conditions (Kumar, 2014; Sokhandani et al., 2016). Dry formulations, such as wettable powders and granules, are favored for their lower susceptibility to contamination and ease of distribution, while liquid and gel-based formulations offer advantages in terms of application flexibility and rapid colonization of plant surfaces (Ghoneem et al., 2019; Kala et al., 2020). Moreover, the use of mixed Trichoderma strains in formulations has been shown to create synergistic effects, broadening the spectrum of pathogen control and enhancing overall biocontrol efficacy compared to single-strain applications (Marzano et al., 2013; Yassin et al., 2021). These advancements in formulation technologies not only improve the practical usability of *Trichoderma* spp. in large-scale agricultural operations but also contribute to sustainable farming practices by reducing dependency on chemical pesticides and promoting environmental health (Peng and Xia, 2011; Birnbaum et al., 2021).

CONCLUSIONS

This paper summarizes the use of *Trichoderma* spp. for biocontrol of plant pests and diseases. The results in this study have pointed out the application potential of Trichoderma as a more eco-friendly and safer alternative compared to chemical pesticides. By acting through various modes of action, such as antibiosis, mycoparasitism, nutrient competition, and induction of systemic resistance in host plants, Trichoderma has provided satisfactory results by improving sustainable agriculture.

The research has highlighted the use of Trichoderma-based products worldwide, with over 250 commercially produced formulations for various application purposes in agriculture. These products have also been found effective against a wide range of phytopathogens and can ameliorate soil health and productivity. The study also emphasized developing innovative formulations that can maintain the viability and effectiveness of Trichoderma under diversified field conditions. Besides, the combination of different strains of Trichoderma has also been considered as one of the means for improving efficiency in biocontrol and broadening the spectrum of suppressed pathogens. This will reduce dependence on chemical pesticides and further contribute to sustainable farming through environmental safety and agricultural resilience.

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