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REVIEW

Harnessing Trichoderma Mycoparasitism as a Tool in the Management of Soil Dwelling Plant Pathogens

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Abstract

Maintaining and enhancing agricultural productivity for food security while preserving the ecology and environment from the harmful effects of toxicants is the main challenge in modern monoculture farming systems. Microbial biological agents can be a promising substitute for traditional synthetic pesticides to manage plant diseases. Trichoderma spp. are soil-dwelling ascomycete fungi and are common biocontrol agents against diverse phytopathogens. Trichoderma-based biocontrol techniques can regulate and control soil-borne plant diseases through mechanisms such as mycoparasitism, the production of antibiotics and hydrolytic enzymes, rhizo-sphere competence, the effective competition for available resources, induction of plant resistance and facilitation of plant growth. Numerous secondary metabolites produced by Trichoderma spp. are reported to prevent the development of soil-borne plant disease. Thus, Trichoderma spp. may have direct and indirect biological impacts on the targeted plant pathogens. Furthermore, this review discusses the convenient implications and challenges of applying Trichoderma-based strategies in agricultural settings. Overall, the assessment underscores the potential of Trichoderma as a sustainable and effective tool for mitigating soil-borne pathogens, highlighting avenues for future research and applications.

Keywords *Trichoderma* · Soil fungi · Biological control · Plant pathogens · Sustainable crop production

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Introduction

Near 2050, there will be 9.1 billion people on the planet, meaning that overall food production must increase by about 70% for food security [1]. Plant diseases have been a source of worry for humankind ever since the development of agriculture. These diseases played a significant part in the depletion of natural resources and were responsible for 16% of global crop yield losses [2]. Soil-borne plant pathogens economically affect crop production in tropical, subtropical, and temperate regions [3]. There are currently 2 million tons of pesticides used worldwide, with herbicides making up 47.5% of usage, insecticides making up 29.5%, fungicides making up 17.5%, and other pesticides making up the remaining 5.5% [4]. The top 10 countries in the world that use pesticides are China, the USA, Argentina, Thailand, Brazil, Italy, France, Canada, Japan, and India. It was observed that pesticide consumption worldwide increased by 20% over the past ten years [5]. Agricultural chemical pesticides are crucial for emerging nations to protect crops from insect pest attacks and increase crop yields. Pesticides can boost agricultural yield via direct control of phytopathogens. Still, their residual toxicity harms the environment, non-target organisms, biodiversity, food chain, human health, and food safety. Recent research on the environmental fate of chemical pesticides on soil, land, water, and living beings has been spurred by worry about the environment and human health [6]. Therefore, an urgent need is to explore and exploit biological control agents to manage phytopathogenic infections as an alternate and effective strategy.

Biocontrol is the term used to describe the function of naturally existing organisms in integrated pest management in reducing the number of plant pests [7]. Trichoderma species are the basis for more than 60% of the biofungicides currently licensed worldwide, making them the most effective biofungicides used in contemporary agriculture [8]. These fungi live in soil mostly confined to rhizospheric regions of plants. They colonize plant material like grains, leaves, and roots [9]. Trichoderma is the market leader for fungal bio-control agents on a global scale [10]. Due to its dual ability to prevent disease and act as soil compost, it has gained a unique place in agriculture as a potent biocontrol agent, plant growth stimulant, and soil fertility improver. Due to its rhizosphere competence, competitive saprophytic ability, capacity to manufacture or induce hormone production in plants, ability to release nutrients from the soil, and ability to increase root system architectural development, it acts as an effective plant growth promoting fungi (PGPF) [11]. Trichoderma can produce a variety of fungal enzymes, such as chitinases, glucanases, cellulases, and hemicellulases, responsible for the toxic action of fungi against soil-borne plant pathogens [12]. These enzymes are also used in the postharvest disease management of papaya, apple, tomato, pear, mango, banana, potato, and berries [13]. This genus has nine species, initially described in 1969 by Rifai and Webster [14]. The genus was further divided into five divisions based on conidiophore branching by Bissett (1991). *Trichoderma harzianum* and *T. viride* are most frequently used as biocontrol agents. The present review attempts to analyze and evaluate the biological control potential of Trichoderma spp. in managing fungal plant pathogens.

Trichoderma: Classification, Characteristics, and Benefits as a Biocontrol Agent

Trichoderma represents the asexual stage (anamorph), whereas *Hypocrea* corresponds to the sexual stage (teleomorph), according to their taxonomic classification [15]. In its asexual form, it falls under the division Deuteromycotina, while in the sexual stage, it is classified under Ascomycotina.

Trichoderma species (spp.) are widely distributed across agricultural regions in all climatic zones, thriving at temperatures ranging from 25 and 30° C, due to their saprophytic nature [16, 17]. For instance, *Trichoderma viride* and *Trichoderma polysporum* prefer mild temperatures, while *Trichoderma harzianum* prefers warm climatic conditions. These fungi are easily identifiable due to their unique smells, attributed to the volatile compound δ-lactone 6-pentyl-α-pyrone (6-PP), [18]. With their competitive saprophytic ability (CSA), Trichoderma spp. are also found in the rhizosphere of plants, where they induce systemic resistance against diseases and enhance plant growth and development [19]. Trichoderma spp. utilize a range of substances, including carbon and nitrogen sources for their sporulation activity [20], and produce abundant powdery masses with green conidia [21]. While the presence of *Trichoderma citrinoviride* has been reported in Southeast Asia, it is yet to be discovered in India [22]. Most of the Trichoderma spp. prefer acidic environments, however they can adapt to a wide pH ranging from 2.0 to 13.0 [23]. Typically, the conidial color morphology of Trichoderma spp. is green but can be grey, white, and yellow, depending on the species [24]. The dominant saprophytic ability of these fungi allows them to compete with other soil organisms and colonize plant roots effectively. Additionally, these fungi also produce secondary metabolites and enzymes that promote plant growth as well as enhance disease resistance against pathogens [25].

Identification of Trichoderma Isolates

The genus Trichoderma includes a diverse range of fungi that exhibit a range of colony morphologies depending on the culture media used for their growth. For instance, when grown on potato dextrose agar (PDA) at 28 °C for seven days, Trichoderma cultures from soil samples displayed green pigmented colonies. Conversely, colonies from rhizospheric isolates grown at 25 °C and 30 °C appeared pale or yellowish, exhibiting rapid growth and conidia dispersion. The fungi can also be identified based on the arrangement of conidia and the phialides, which are projections of the conidiophores. Phialides, of these fungi in particular, were observed to be ellipsoidal, oblong, and bowling pinshaped [26]. Additionally, a study by Sekhar et al. (2017) reported that ten isolates from the rhizosphere of groundnuts exhibited various morphological and microscopic traits, including colony color, reverse color, and the shape and features of conidia, phialides, and conidiophores [27].

Culture Media for Trichoderma

Selective Media for Trichoderma (TSM)

Trichoderma selective medium (TSM) is recognized as the gold standard for the quantitative separation of Trichoderma spp. from the soil. To grow quickly and sporulate, the fungus contains low glucose-specific fungal inhibitors, including pentachloronitrobenzene, p-dimethyl amino benzene, diazo sodium sulfonate, and rose bengal. At the same time, chloramphenicol is used to stop bacterial development [28].

Trichoderma Selective Media (TSM) The ingredients and amounts required for Trichoderma selective medium are $MgSO_4{\bullet}7H_2O$ (0.2 g), K_2HPO_4 (0.9 g), KCl (0.15 g), NH_4NO_3 (1.0 g), glucose (3.0 g), rose bengal (0.15 g), agar (20 g), chloramphenicol (0.25 g), p-dimethyl amino benzene diazo sodium sulfonate (0.3 g), pentachloro nitrobenzene (0.2 g), distilled water (1.0 L). For media preparation, the ingredients are mixed properly and then autoclaved for 15 min at 121 °C. The mixture is then supplemented with 0.25 g of chloramphenicol and 0.2 g of pentachloro nitrobenzene. To avoid solidification, the media should be maintained or stored at 45 °C.

***Trichoderma harzianum* Selective Medium (THSM)** The ingredients and amounts required for *T. harzianum* selective medium are the same as those mentioned for TSM including the media preparation procedure. However, antimicrobial agents such as chloramphenicol, streptomycin, quintozene, and propamocarb are added to the medium to isolate a pure colony of Trichoderma sp. [29]. For instance, the media after autoclaving are supplemented with 0.25 g of chloramphenicol, 9.0 ml of streptomycin, 1.2 ml of propamocarb, and 0.2 g of quintozene. The use of THSM makes the comparison of aggressive and non-aggressive Trichoderma groups possible.

Biological Control Strategies Employed by Trichoderma spp.

Trichoderma spp. employ several strategies to function as biocontrol agents [30]. They can rapidly multiply or utilize available food sources more efficiently than soil-borne pathogens, outcompeting them and seizing control through efficient nutrient competition. They may also engage in mycoparasitism/hyperparasitism, feeding on a pathogenic species. Additionally, Trichoderma spp. also secrete secondary metabolites that inhibit or significantly delay the growth of infectious soil-borne pathogens in their vicinity, a process known as antibiosis [25]. For example, various secondary metabolites with antimicrobial potential have been identified, such as gliotoxin from *T. lignorum*, gliovirin from *T. virens*, alamethicin F30, a peptaibol from *T. viride*, and harzianolide, an antifungal butanolide compound from *T. harzianum*. Many other such metabolites have been extensively reviewed in the report by Khan et al. (2020) [31]. The secondary metabolites secreted by Trichoderma spp. exhibit antifungal and antimicrobial effects through various mechanisms of action. These include inducing cytotoxicity by producing toxins, inhibiting spore germination, hyphal elongation, and mycelial growth, as well as suppressing the formation of sexual structures. In bacteria, these metabolites interfere with cell division and cause cell wall degradation [32]. Furthermore, Trichoderma spp. can induce plants to produce chemicals that induce localized or systemic resistance in plants. Finally, their ability to grow endophytically supports the growth of plants (Fig. 1).

Trichoderma as a Safeguard for the Health of Plants

Trichoderma species either actively attack their hosts in their defense mechanisms or succeed by stopping the pathogen from proliferating in the host's surroundings. They use lytic enzymes, proteolytic enzymes, ABC transporter membrane pumps, diffusible or volatile metabolites, etc. Ascomycetes, basidiomycetes, and oomycetes fungus as well as nematodes are all controlled by Trichoderma species [33]. Protease, chitinase, glucanase, tubulins, proteinase, xylanase, monooxygenase, galacturonase, cell adhesion proteins, and stress tolerance genes are a few

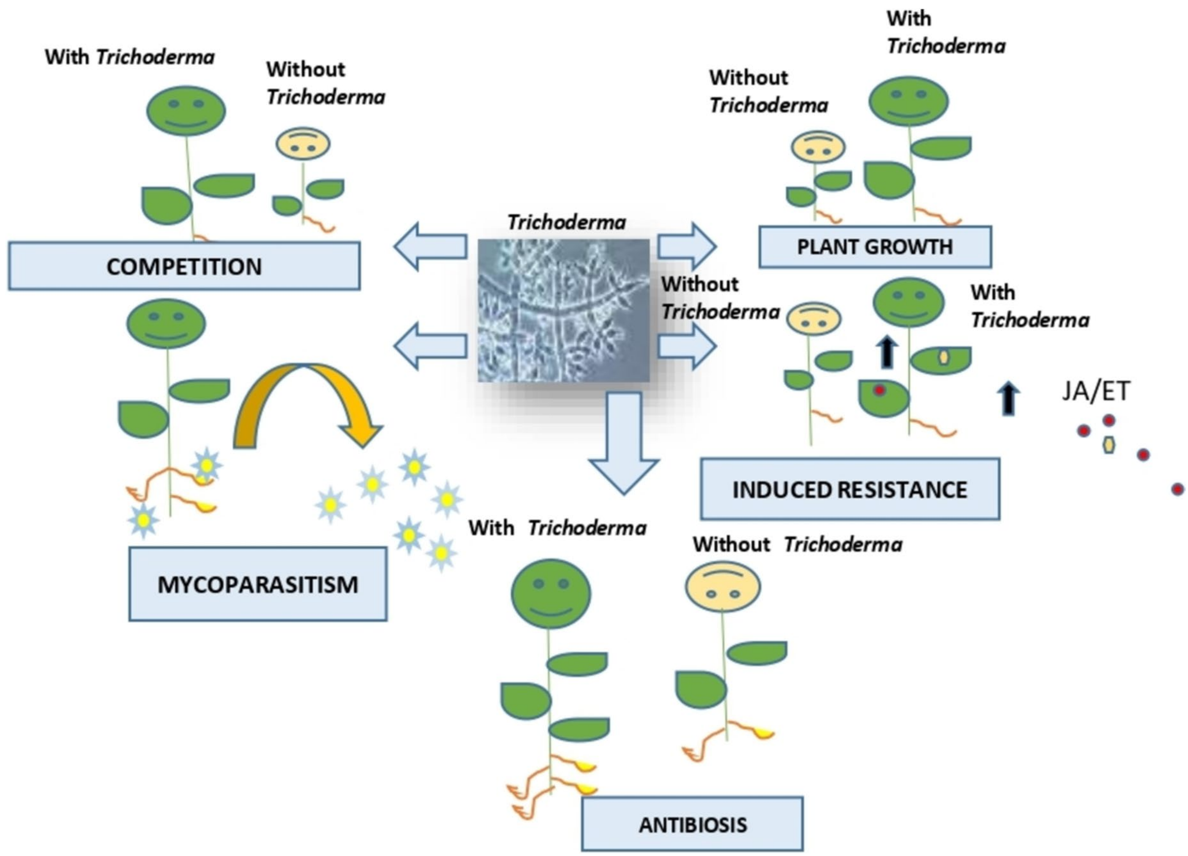

Fig. 1 The model illustrates how Trichoderma spp. functions to boost plant development and control pathogens biologically

significant categories of biocontrol genes that are readily isolated, cloned, and reported. These genes carry out particular tasks in a biocontrol mechanism, including cell wall disintegration, hyphal growth, stress tolerance, and parasite activity. The structural proteins known as tubulins, composed of microtubules, are useful for analyzing the composition of pathogen cell walls. Chitinase facilitates the hydrolysis of glycosidic linkages, while glucose oxidase catalyzes the conversion of D-glucose into D-glucono-1, 5-lactone, and hydrogen peroxide, all of which have antifungal properties. Xylanase assists in the hydrolysis of hemicellulose, which is a major component of plant cell walls [34]. Genes related to biocontrol and mycoparasitism are triggered by several signal transduction pathways, such as the cAMP pathway and mitogen-activated protein kinase (MAPK) cascades [35]. Particularly important in the heterotrimeric G protein signaling pathway is the MAP-kinase TVK1, which was identified in *T. virens* and its orthologs in *T. asperellum* (TmkA) and *T. atroviride* (TMK1) [36]. TGA1 is crucial in managing coiling around host hyphae and generating antifungal compounds. When TGA1 is missing, the growth of host fungi is significantly more hindering [37]. TGA3, on the other hand, is essential for biocontrol since strains created after the homologous gene was deleted were not pathogenic. Recently, a significant function in the biocontrol of *T. virens* has been attributed to the homolog of the VEL-VET protein, which is currently mostly recognized as the light-dependent regulator protein [38].

Secondary Metabolites

The Trichoderma fungus is incredibly adept at occupying many ecological niches and its varied metabolism allows it to produce various secondary metabolites and catabolize many substrates. The secondary metabolites include about 370 distinct kinds of chemical compounds with antagonistic effects which play a crucial role in safeguarding plant health [39, 40]. The peptide antibiotic Paracelsin was one of the earliest secondary metabolites from Trichoderma spp. to be described. Trichoderma spp. produces secondary metabolites, including antifungal metabolites from some chemical com-pound classes, depending on the strain. Ghisalberti and Sivasithamparam divided them into three groups: Water-soluble substances, such as koningic or peptidic acid, volatile antibiotics, which include δ-lactone 6-pentyl-α-pyrone (6-PP) and most isocyanide derivatives

Table 2 Secondary metabolites of certain Trichoderma isolates

Sources	Secondary metabolites	Biological task	Other applications	References
T. hamatum, T. pseudokoningii	Mannitol		Antimutagenic	[44]
T. koningii	Methyl benzoate p-hydroxy benzyl alcohol			[45]
T. pseudokoningii	2,5-dimethoxybenzoquinone		Cytotoxic	[45]
T. pseudokoningii	Succinic acid, Itaconic acid			[45]
Trichoderma sp.	Carolic acid			[46]
T. viride ATCC74084	Viridiofungin A, Viridiofungin B Viridiofungin C	Antifungal	Squalene synthase Inhibitor	[47]
T. viride PRL 2233	1,8-dihydroxy-3-methyl anthraquinone	Anticeptic, viricide	Cytotoxic	[48]
T. viride PRL 2233	1,6,8-trihydroxy-3-methyl Anthraquinone			[48]
T. viride	1,3,6,8 tetrahydroxy-4-aacetyl anthraquinone 1,3,6,8-tetrahydroxy Anthraquinone	Antibacterial		[49]
T. longibrachiatum ATCC2449	Sorbicillin, Bisvertinolone, Trichodimerol, Trichodermolide, Sorbiquinol		Inhibitor tumor necrosis factor	[50]
T. harzianum IMI298371	Harzianopyridone	Antifungal		[51]
T. harzianum IMI 311092	Dehydro harzianolide	Antifungal		[52]
T. harzianum SY-307	Harzianic acid	Hypercholesterimic		[53]
T. harzianum	Trichoharzin	Inhibit fungal activity, Antimicrobial activity	Regulate plant growth	[54]
Trichoderma spp.	Massoilactone	Antifungal activity	Regulate plant growth	[55]
Trichoderma spp	δ-decenolactone	Antifungal activity		[55]
T. harzianum IMI 311090	Koninginin E	Antifungal activity	Regulate plant growth	[56]
T. virens ATCC74180	3,4,14-trihydroxycarotane-14-oleate	Antifungal activity	Antitrichomal, Mycotoin	[57]
Trichoderma. polysporum CMI40624 T. sporulosumn CMI104643	Trichodermin	Antifungal activity	Mycotoxin	[58]
T. pseudokoningii	Epifridelenol	Antibiotic	Immunosuppressive	[55]
T. hamatum HLX 1379	Isonitrinic acid F	Antibiotic		[44]
HLX 1360 T. hamatum	Dermadin	Antibiotic		
TK-1 T. koningii	Dermadin methyl ester	Antibiotic		
UC 4875 T. viride	Epoxy diol	Antibiotic		
T. polysporum	Spirolactone Antibiotic	Antibiotic		
HLX 1379 T. hamatum	Diol isocyanide	Antibiotic		
HLX 1379 T. hamatum	Epidiol isocyanide	Antibiotic		
HLX 1379 T. hamatum	Isonitrin A	Antibiotic		
HLX 1379 T. hamatum				
IMI 3208 T. hamatum				

[33, 41]. According to Vinale et al. (2008), peptaibols are linear oligopeptides with 12–22 amino acids that are rich in α-aminoisobutyric acid, N-acetylated at the N-terminus, and amino alcohol phenylalaninol (Pheol) or tryptophanol (Trpol) at the C-terminus [42]. The most investigated secondary metabolites are peptaibols, polyketides, pyrones, terpenes, and molecules like diketopiperazine [43] (Table 2).

A Crucial Aspect of Successful Biocontrol: Mycoparasitism

Mycoparasitism is a condition in which an antagonistic fungus, known as a mycoparasite, parasitizes another fungus, referred to as the host [39]. Necrotrophic mycoparasites are the general classification for the fungus of the Trichoderma genus [59]. Around 75 Trichoderma spp. are known to have a strong propensity to become mycoparasitic [60]. Trichoderma necrotrophs physically combat fungal diseases by vigorously branching and coiling around the host's hyphae, as well as by chemotactically attaching to the host and sensing prey. This action is known as mycoparasitism. Trichoderma can also produce pathogen appressoria homologs or penetrate using structures resembling appressoria [61, 62]. It produces antifungal compounds and hydrolytic enzymes that chemically degrade and break down the cell wall of the pathogen, eventually leading to the death of host in the final stage of the mycoparasitic interaction [59, 61]. The necrotrophic mycoparasitic effect was noted in the study by Błaszczyk et al. [63] when *T. atroviride* AN240 and *T. viride* AN255 strains interacted with *F. graminearum* and *F. avenaceum*, respectively. Similarly, it was found that the *R. solani* hyphae benefited from the mycoparasites *T. virens* [64] and *T. harzianum* [65]. Furthermore, the mycoparasitic *T. cerinum* Gur1 strain reduced chickpea wilt disease in vivo [66].

Synthesis of Antibiotics and Additional Antifungal Substances

Most Trichoderma strains primarily produce polyketides and peptidaibols, which are volatile organic chemicals [67]. Approximately 80% of the entries in the "Peptaibiotics Database" are related to different species within the genus *Trichoderma*, making it one of the most abundant sources of peptaibols [68]. Peptaibols are categorized as antimicrobial polypeptides with a molecular weight between 500 and 2200 Da. They are rich in non-proteinogenic amino acids, especially alpha-aminoisobutyric acid and isovaline. Peptidoglycan synthesis is carried out by non-ribosomal peptide synthetases [67]. Three major non-ribosomal peptide synthetase genes, tex1, tex2, and tex3 have been recognized in the Trichoderma genomes [60]. Depending on the strain, Trichoderma spp. produce secondary metabolites that include antifungal substances from several chemical class components. The polyketides produced by these fungal species are a structurally diverse class of physiologically active chemicals found in bacteria, plants, and fungi [69]. These include pigments, mycotoxins, and antibiotics (such as macrolides and tetracyclines) [70]. Numerous Trichoderma spp. produce secondary metabolites classified as pyrones, anthraquinones, terpenoids, and epipolythiodioxopiperazines [71]. The terpenoids produced by the Trichoderma spp., include tetracyclic diterpenes (like harziandion), sesquiterpenes (like trichothecenes, like trichodermin and harzianum A), and triterpene viridian [69]. Additionally, *T. viride*, *T. harzianum*, and *T. koningii* manufacture the volatile antibiotic 6-phenyl-α-pyrone, which is responsible for the biological barrier against *F. oxysporum* having the unique coconut odour [72].

Plant Resistance Induced by Trichoderma: the Battle for Space and Nutrients Amid Biological Stress

Pathogens can be deprived of space and nutrients when antagonistic fungi invade shared habitats such as rhizospheres, plant tissues, or phyllospheres [73]. This depends on their traits, the degree to which the host plant has colonized them, and the degree to which they have adapted to their environment [67]. Trichoderma should be common in a niche where there is a rivalry with other fungi and have effective plant colonization strategies to effectively compete with diseases for nutrients and habitats. In terms of glucose and sucrose, the Trichoderma fungus grows quite quickly [74]. Compared to other microbes, the fungus from the genus Trichoderma is far more adept in mobilizing and absorbing nutrients from the soil [75]. This procedure yields the formation of citric, gluconic, fumaric, and organic acids, which decrease the soil's pH and encourage the solubilization of phosphates and microelements like manganese, iron, and magnesium [42]. Of particular importance in the competitive dynamics of plant–microbe and Trichoderma tripartite interaction is the production of siderophores, which is formed during an iron-deficiency stress. Siderophores are low molecular weight compound with a high affinity for iron (Fe), and help the fungi compete for iron by binding to the insoluble form (Fe^{3+}) [76]. Later the insoluble Fe3 + is converted into Fe^{2+}, which is readily taken up by microbes and plants [42]. Based on their chemical structure and iron coordination sites, the microbial siderophores are typically categorized into three classes, such as hydroxamate, catecholate, and carboxylate [60]. This process of iron bioavailability under stress due to siderophore production and iron solubilization ultimately triggers plant resistance by enhancing nutrient availability and strengthening the plant's defenses against pathogens.

Moreover, the Trichoderma spp. can also indirectly influence dangerous microbes through plants by triggering their systemic or local defensive mechanisms [67, 77]. Different elicitors secreted by the cells of microbes and plant tissues cause the induction of plant resistance. There are two categories for the elicitors: (1) Race-specific elicitors only cause gene-to-gene type defence in specified host cultivars (2) Nonrace-specific defence is induced in both host and non-host plants by generic elicitors delivered from pathogenic and non-pathogenic strains simultaneously. The discovery of conserved domains, such as the microbe- or pathogen-associated molecular patterns (MAMP/PAMP), is the major foundation for the plant defence response (Fig. 2) [78]. These domains activate two types of innate immunity in plants: PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI) [79].

Antibiosis

It is an antagonistic relationship between two bacteria, where the release of antibiotics or metabolites by one negatively impacts the other. According to chemical and analytical reports, 373 distinct secondary metabolites, including non-volatile and volatile terpenes, peptaibols, pyrones, and compounds containing nitrogen, were obtained from Trichoderma species and showed great potential for the production of antibiotic and secondary metabolites [11, 77]. Some of the examples that are effective against the target pathogen in situ are alkyl pyrones, trichodermin, diketopiperazines, viridin, polyketides, isonitriles, peptaibols, and sesquiterpenes isolated from Trichoderma spp., and 6-Pentyl-2H-pyran-2-one [83].

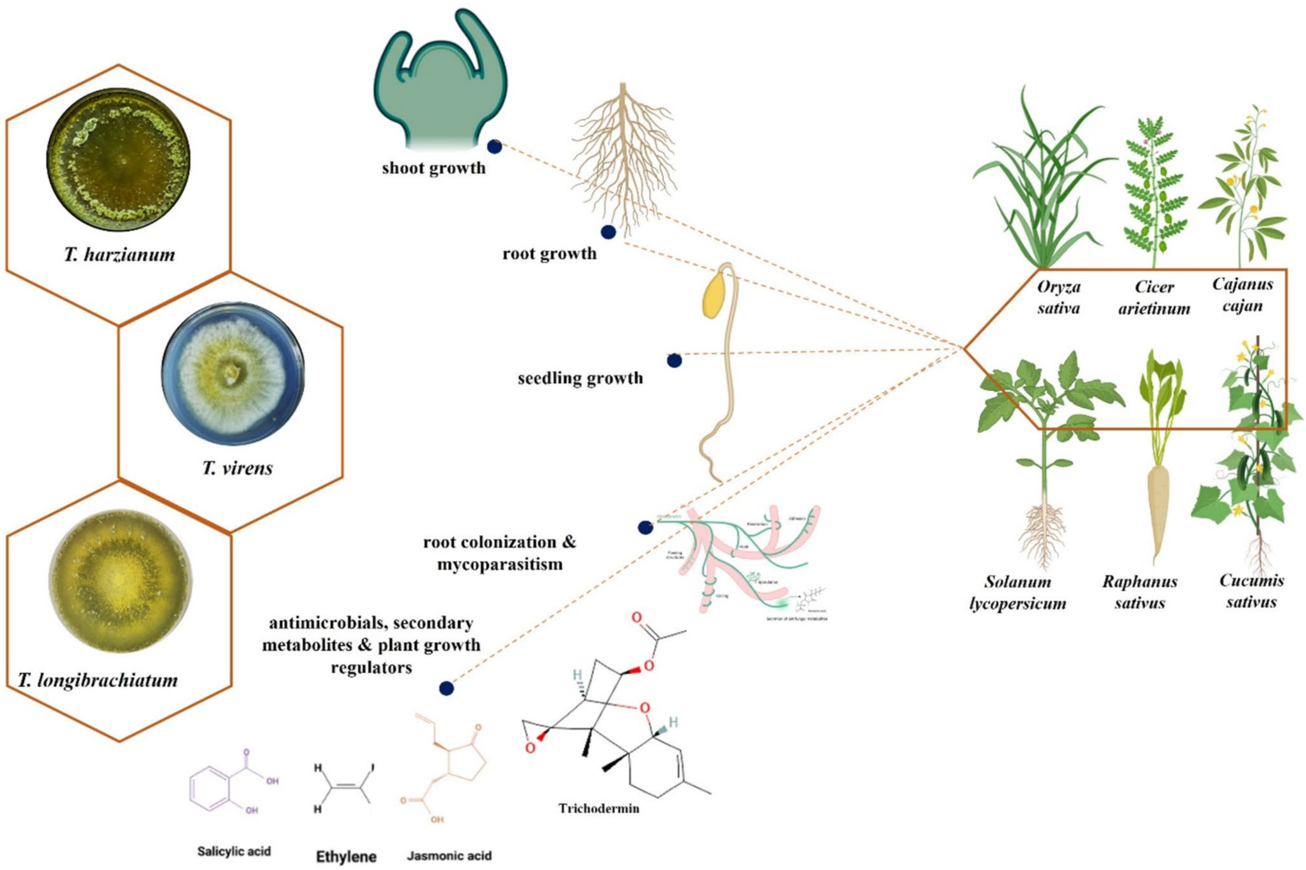

Fig. 2 Tricoderma spp. function as biocontrol agents in various crops to improve plant growth promotion. The different Trichoderma species such as *T. harzianum*, *T. virens*, and *T. longibrachiatum* are used in different field crops and horticultural crops that promote plant growth and development by regulating shoot growth, root growth, seedling growth, root colonization, and mycoparasitism, production of antimicrobial substance such as trichodermin, trichdermamide, viridine, harzianum, etc. as well as the production of plant growth regulators such as jasmonic acid, salicylic acid, and ethylene that help in plant defense processes [Figures made using Biorender (https://app.biorender.com/signin) and adapted from [79–82]

Application of Trichoderma as a Protective Measure for Plant Health

Trichoderma as a Bioremediation Agent

Trichoderma spp. thrives in plant roots and soil, where they combat fungal infections and demonstrate resilience against most agrochemicals. Furthermore, they exhibit high resistance to various environmental pollutants such as tannery effluents, organometallic compounds, heavy metals, and hazardous chemicals like cyanide. As a result, these fungal genera are well suited to investigate as a genetic re-source for use in the phytoremediation of harmful contaminants [84]. Trichoderma bioremediation techniques for inorganic contaminants including heavy metals and others can be categorized into four categories:

Biosorption

Biosorption is the ability of biological materials to extract heavy metals from wastewater via physicochemical or metabolic absorption mechanisms. It entails attaching to free groups of negatively charged molecules in a variety of biopolymers that make up the microbial cell wall in a metabolism-independent manner. For example, using the batch approach, the dried biomass of Trichoderma sp. was tested for removing harmful heavy metal ions at concentrations ranging from 0.5 to 2.0 mg/L at different pH levels [85]. The biomass of *T. harzianum* was found to significantly absorb Cr (VI) ions from the aqueous solution. FTIR spectroscopy revealed that the amine in chitin and the chitosan in the fungal cell wall play a crucial role in metal binding [86].

Bioaccumulation

The energetically dependent metal inflow mechanism living cells use during bioaccumulation is the active removal of the metal procedure. The ability to withstand and gather heavy metals like cadmium, zinc, copper, and arsenic in vitro have been demonstrated for various Trichoderma species. Trichoderma spp. has been shown to improve the solubility of soil micronutrients like Zn, Cu, Fe, and Mn. Cu (II) binding in the cell wall surface was demonstrated by *T. viride* as a metal tolerance mechanism. At pH 5.0 and 100 mg/L of Cu (II) at 30 °C, a maximum of 80% of the copper was eliminated in 72 h. Copper was rendered less dispersed and accessible in the media by binding to the cell surface, which decreased the metal's toxicity [87].

Biovolatilization

It involves the enzymatic conversion of organic and inorganic metalloid compounds into their volatile by-products, a process known as biomethylation. *T. viridian* and *T. asperellum* have been shown to be arsenic in liquid surroundings and should be volatilized. The fungal strains Rhizopus sp., Neocosmospora sp., Trichoderma sp., and sterile mycelial strain were found to have the most effective at removing arsenic from soil [88].

Phytoremediation

Microbe-assisted utilizing plants and microbes to remove toxins biologically are called phytoremediation, also known as phytobial remediation. Trichoderma spp. aids in phyto extraction processes that promote the absorption of other ions, including nitrates, in the root area and adopt certain hazardous metals and metalloids. *Pteris vittata*, an arsenic-accumulating fern, grows more roots when *T. harzianum* strains are used because they can detoxify potassium cyanide (Table 3).

The Implications of Trichoderma in Agriculture

Biological control is a method of reducing crop pests by employing helpful microbial organisms. Among the many beneficial bacteria, Trichoderma sp. is frequently utilized as a biocontrol agent against various plant diseases. Trichoderma sp. is active rhizosphere colonizers that also infiltrate cortex cells in roots and live as endophytes. Examples include *Trichoderma harzianum*, *T. longibrachiatum*, *T. virens*, and *T. asperellum*, etc. These species contribute significantly to plant growth and metabolism, promoting increased shoot and root lengths, enhanced overall plant growth, and improved vigor and emergence seedling in many crops such as beans, brinjals, cauliflower, chickpeas, cucumbers, lentils, pigeon peas, radishes, tomatoes, and rice. Figure 2 provides a schematic representation illustrating the plant growth-promoting activities of Trichoderma species. Trichoderma antibiotics such as viridin, gliotoxin, enzymatic breakdown of cell walls, and physiologically active heat-stable metabolites like ethyl acetate are engaged in preventing illness and promoting plant development. Examples of important categories of biocontrol genes include xylanase, chitinase, tubulins, protease, glucanase, proteinase, galacturonase, genes encoding cell adhesion proteins, monooxygenase, and stress tolerance genes that are easily isolated, cloned, and described. These genes carry out particular tasks within the biocontrol mechanism, including cell wall disintegration, hyphal growth, stress tolerance, and parasite activity. Tubulins are microtubule-derived structural proteins that facilitate the examination of the content of pathogen cell walls. Chitinase facilitates the hydrolysis of glycosidic

Table 3 Trichoderma spp.–based bioremediation of various pollutants

Sl no	Pollutants	Trichoderma spp.	References
1	A solvent that is organic	Trichoderma spp.	[89]
2	Dichlorvos, an organophosphate insecticide	*T. atroviride*	[90]
3	Phenanthrene, Crude oil, naphthalene, and benzopyrene	*11 Trichoderma* strains	[91]
4	Tolerance to arsenic in *Eucalyptus* globules	*T. harzianum*	[92]
5	Cd and Ni-contaminated soils for phytoextraction	*T. atroviride*	[93]
6	Eucalyptus's resistance to aluminium	*T. harzianum*	[94]
7	Metal-contaminated soil using PGPR	*T. harzianum*	[95]
8	Polyresistance pesticide	Trichoderma spp.	[96]
9	Cyanide	Trichoderma spp.	[97]
10	Contaminants in the soil and water	Trichoderma spp.	[98]
11	Diesel-contaminated soil	Trichoderma	[99]
12	Agrochemicals like dieldrin, penta-chloro-nitrobenzene, DDT, endosulfan, and penta-chloro-phenol)	*T. harzianum*	[100]

bonds. D-glucose is converted by glucose oxidase into hydrogen peroxide, 5-lactone, and D-glucono-15-lactone, all of which have antifungal qualities. One important component of plant cell walls, hemicellulose, is broken down with the help of xylanase [101].

Effectiveness of Trichoderma Species Against Fungus that are Found in the Soil

Trichoderma spp. is used as plant growth enhancers and antagonistic fungal agents against various pests. Faster metabolic rates, antimicrobial metabolites, and physio-logical conformation are important elements that primarily lead to these fungi's antagonistic interactions. It is commonly recognized that Trichoderma fungi are antagonistic to several bacteria, invertebrates, and other soil-phytopathogens [19]. The efficiency of Trichoderma species against soil-dwelling fungi is shown in (Table 4).

Timber Preservation

Ejechi studied *T. viride*'s capacity to prevent *G. sepiarium* and *Gloeophyllum* sp. from decomposing obeche (Triplochiton sceleroxylon) wood over an 11-month period, during the wet and dry seasons in tropical climate. *T. viride* successfully suppressed the decay fungus through mycoparasitism and nutritional competition, [112]. Trichoderma isolates can inhibit and kill wood decay fungi by the release of volatile organic compounds, with production varying based on the specific Trichoderma isolate [113]. Trichoderma fungi are found on freshly cut sawn wood of many different softwood and hardwood species as well as in soils across all latitudes. The fungi that develop on wood surfaces have the potential to reduce the value of sawn objects by reducing the functional aesthetics of lignocellulosic materials. Under favorable conditions, the Trichoderma fungi can even cause soft rot in wooden materials because they produce a wide variety of enzymes, including cellulase, hemi-cellulase, xylanase, and chitinase [113]. Overall, the diverse capabilities of Trichoderma fungi highlight their significant impact on both wood preservation and degradation processes.

Tolerance to Abiotic and Biotic Stresses

Trichoderma species, an excellent natural protein source, can help plants with-stand biotic and abiotic stress conditions. It has also been reported that the cloned and characterized hsp70 gene from *T. harzianum* T34 isolate encodes a protein that, when expressed and produced in Arabidopsis, increases tolerance to heat and other abiotic stimuli. This gene codes for a protein product that allows the fungus to resist heat and other stresses, such as oxidative, salt, and osmotic tolerances, to reach higher levels. With the recent sequencing of the genomes of seven Trichoderma species,

Table 4 Effectiveness of Trichoderma species against fungus that are found in the soil

Trichoderma strains	Pathogens	Plant/crops	Disease with efficacy	References
TH-3 T. harzianum	*Rhizoctonia solani*	Tomato	Wilt (5%)	[102]
T. harzianum	*Fusarium solani*	Tomato	Root rot (70–72%)	[103]
T. harzianum	*R. solani*	Tomato	Damping off (51%)	[103]
T. harzianum Mutants	*R. solani*	Tomato	Damping off (40%)	[103]
T. viride (Tv-R) *T. harzianum*	*M. phaseolina* *R. bataticola*	Chickpea Mungbean	Root rot (62%) Dry root (87%) rot	[104]
T. harzianum T-22	*F. verticillioide*	Maize	Ear and kernel Rot (65% reduce size of necrotic area)	[105]
T. viride	*F. oxysporum f. sp. Adzuki*	Soybean	Root rot	[106]
T. harzianum	*Cucumerinum*	Cucumber	Stem and root (12–79%) Rot	[107]
T. harzianum	*Alternaria tenuissima*	Sorrel	Leaf spot (67–76%)	[107]
T. viride	*F. verticilloid A. alternate*	Tomato	Root rot and wilt 67%	[107]
T. harzianum *T. longibrachiatum*	*A. porri*	Onion	Purple blotch 73%	[108]
T. viride	*Colletotrichumcapsici*	Chilli	Fruit rot 58%	[109]
T. harzianum	*F. udum*	Pigeon pea	Wilt (*T. harzianum* is more successful when applied to the soil than when seed is used)	[110]
T. hamatum	*F. oxysporum*	Lentil	Vascular wilt (33%)	[111]

there is promising potential for developing transgenic plants that may provide effective resistance to changing climate conditions [114].

Reaction Sensitivity to Agrochemicals

The efficacy of the bioagents is decreased by the toxic character of the fungicides used in crop production technologies. Consequently, researchers have investigated Trichoderma sensitivity and tolerance [115]. Studies have been conducted on the impact of different fungicides in combination with Trichoderma species on treating illnesses holistically. Trichoderma spp. has been proven to be more resistant to broad-range fungicides than many other soil microbes because of their capacity to colonize pesticide-treated soil more quickly [116]. Because numerous unusual contaminants can be treated simultaneously and have a wider range of uses, trichomoniasis alone, in conjunction with bacteria or immobilized formulations, can show enormous potential. This will boost the overall cost-effectiveness of the method.

Future Prospects

Numerous studies have shown that Trichoderma spp. can tolerate and detoxify environmental contaminants from contaminated areas. The synthesis of amylases from *T. harzianum*, cellulases from *T. reesei*, 1,3 β-glucanases from *T. harzianum*, *T. koningii*, and chitinases from *T. aureoviridae* and *T. harzianum* is well known. The genus Trichoderma is a good source of various hydrolytic and industrially important enzymes. They have been used in the manufacture of extracellular gold nanoparticles using *T. koningii* and the fabrication of silver nanoparticles (AgNPs) using *T. reesei* [104]. However, further investigation is needed to examine the long-term consequences on the stability and rehabilitation of the contaminated sites before these interactions between Trichoderma and plants can be fully exploited. The survival of Trichoderma depends on the diverse metabolic capabilities of this group of fungi. A deeper understanding of these processes will lead to better, more affordable environmental protection techniques and increased crop output in contaminated areas. Due to their broad spectrum of biotic and abiotic stress tolerance, Trichoderma species have the potential to be exploited in sustainable agriculture and biofuel crops with the help of modern plant biology methods and techniques.

Conclusion

The overuse of chemical fertilizers and pesticides has negatively impacted human health and the environment. Consequently, research on organisms as biocontrol agents has emerged as a promising approach to finding sustainable and eco-friendly alternatives. Trichoderma**,** due to its multiple biocontrol traits, is one of the most extensively studied beneficial microbes for managing various plant pathogens. These are free-living soil fungi that colonize decomposing organic matter and form beneficial endophytic associations with plants. They inhibit phytopathogenic fungi while stimulating plant defenses, promoting root development, and enhancing plant growth under biotic and abiotic stresses. It is effective not only against fungi and oomycetes but also against insects, pests, and nematodes. This is achieved through enhanced plant defenses or by directly inhibiting pathogen growth via competition, antibiosis, or parasitism. However, a deeper understanding of these underlying processes can significantly improve the effectiveness of Trichoderma in managing plant-pathogen interactions. This would make Trichoderma a highly effective biocontrol agent, biofungicides, and biofertilizers thereby reducing dependence on synthetic chemicals and promoting sustainable agriculture. Although numerous formulations containing different Trichoderma species are available for sustainable crop production, their high cost often limits accessibility for small-scale farmers. Species like *T. atroviride* and *T. harzianum* are notable mycoparasites, while newly discovered strains hold promise as cost-effective alternatives for farmers. Additionally, the production of hydrolytic enzymes and N-acetylglucosamine (GlcNAc) from Trichoderma spp, which influences signaling and virulence properties in bacteria, highlights its diverse biocontrol functions. Despite their potential, broader accessibility and cost reduction are needed to maximize their application in sustainable crop production.

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Declarations

Competing Interests The authors declare no competing interests.

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