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EDITED BY
Jonathan Spencer West,
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University of Sargodha, Pakistan

*CORRESPONDENCE
Abhay K. Pandey
abhaykumarpandey.ku@gmail.com
Pranab Dutta
pranabdutta74@gmail.com

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Trichoderma- from lab bench to field application: Looking back over 50 years

Pranab Dutta[1]*, Lipa Deb[1] and Abhay K. Pandey[2]*

[1]School of Crop Protection, College of Post-Graduate Studies in Agricultural Sciences, Central Agricultural University (Imphal), Umiam, Meghalaya, India, [2]Department of Mycology and Microbiology, Tea Research Association, North Bengal Regional R & D Center, Nagrakata, West Bengal, India

Biological control of plant pathogens has become increasingly possible with the use of fungi, which have a high reproductive rate (both sexually and asexually) and a short generation time and are very specific to their target. *Trichoderma* species are found in diverse habitats and experience various interactions with other organisms. They are used as bio-fungicides owing to their plant-protecting abilities, and they produce a large number of secondary metabolites (SMs) accompanied by enrichment in secondary metabolism-associated genes. This article aims to review and discuss the SMs produced by *Trichoderma* species, including their physiology, mode of action, mass production, and industrial and field applications for the control of plant diseases. We also discuss the evolutionary history, taxonomical gradient, classification, and ecology of *Trichoderma* species, as well as indirect and direct mechanisms used as plant protectors with gene improvement strategies. Aside from the bioactivity of SMs derived from *Trichoderma* species, compatibility with fungicides, mass formulation techniques, and industrial applications of *Trichoderma* species, the review focuses on its advent and progress as a global research pioneer.

KEYWORDS

microbial biocontrol agents, ecology, mode of action, disease control, industrial application

Background

The use of novel agricultural technologies has improved production, but some modern practices damage the environment. Increasing yields in an environment-friendly manner has become one of the recent challenges of advanced farming (Weller et al., 2014). There are a number of diseases that can be caused by bacteria, fungi, viruses, nematodes, and mycoplasmas in crops. Fungal pathogens are one of these plant pathogenic organisms that cause significant damage to agricultural crops around the world that reduce crop yields with an estimated loss of 15–17% during cropping and

harvesting (Weller et al., 2014; Pandey et al., 2018). Mycotoxin production also results from fungal contamination of food commodities. Many approaches have been used to manage these pathogens, including cultural, mechanical, microbial biocontrol agents, and the use of resistant cultivars and chemical fungicides. The use of fungicides for the treatment of plant diseases may cause serious health and environmental effects (Suryanarayanan et al., 2016). Some of the negative effects of plant diseases on our everyday lives may go unnoticed. It is sometimes hard to get food if our crops do not succeed. Therefore, it is crucial for us to diversify our foods and develop eco-friendly agricultural technologies, so that we can grow healthier crops.

Existing disease management options in crops

Synthetic fungicides are currently used to control plant diseases, but they play a major role in limiting the availability of nutritionally adequate and safe food (Russell, 2005). In order to ensure a sustainable production in the future, plant disease management strategies are needed (Russell, 2005; Weller et al., 2014). In contemporary agriculture systems, agrochemicals are important to reduce crop losses (Carvalho, 2006). In general, agrochemicals can be divided into fertilizers and pesticides. Nitrogen, phosphorus, and potassium are all elements found as chemical compounds in growth regulators and pesticides (Carvalho, 2006). The four main types of pesticides are insecticides, fungicides, nematicides, and herbicides. The majority of plant diseases are caused by fungi and oomycetes, and fungi can also cause chronic and acute health problems in human beings (Weller et al., 2014). For instance, in addition to causing Fusarium head blight, *Fusarium graminearum* also produces a mycotoxin, deoxynivalenol, that has a harmful effect to both animals and humans (Weller et al., 2014). Increasingly, widespread availability and greater efficacy of these fungicides have been attributed to increased crop productivity and combating fungal pathogens. Therefore, fungicides are essential for plant disease control (Reuveni and Reuveni, 1998).

It is believed that the first generation of fungicides was derived from the Bordeaux mixture, which was discovered in 1885, and powdery and downy mildew on grapes can be controlled with this chemical (Weller et al., 2014). Second-generation fungicides include organic chemicals, such as dithiocarbamates, and were first synthesized in 1934 (De Waard et al., 1993). These synthetic fungicides only affect plants on the surface and make no contact with the plant's inner tissue. Organic fungicides of the third generation (1970–80) penetrated host tissues and controlled infections caused by fungal pathogens (De Waard et al., 1993). Fungicides of the fourth generation (from 1980 to the present) inhibit fungi from penetrating plant tissue, thus causing plant resistance (Russell, 2005). As a result of pesticide use, humans and ecosystems suffer adverse effects. Agrochemicals adversely affect the environment, food chain, and soil and disrupt the ecological balance in the environment (Anderson et al., 2004). In the long run, nitrogen fertilizers can contaminate ground water, and fertilizers based on ammonium can decrease pH levels and make soils more susceptible to Fusarium wilt (Carvalho, 2006). In particular, fungicides negatively affect saprobic fungi such as *Penicillium* species and *Trichoderma* species in soils (Suryanarayanan et al., 2016).

Due to frequent use of the fungicides, fungicide resistance develops, resulting in failures in controlling disease (Vinale et al., 2008; Burketova et al., 2015). Gray mold is caused by *Botrytis cinerea* on vegetables, fruits, and ornamental flowers. *Botrytis cinerea* developed resistance to benzimidazoles due to a mutation in β-tubulin, a protein-coding gene. Currently, QoI (quinol oxidation inhibitor) fungicides such as strobilurins are important fungicides and azoxystrobin is the world's most popular fungicide, with extensive mitigation activity against many pathogens of food crops (Ishii, 2006). Nevertheless, QoI fungicides induce pathogen resistance. Melon and cucumber powdery mildew, as well as cucumber crops' downy mildew, developed a fungicide resistance to QoI groups of fungicides in Japan (Ishii, 2006). In addition, Fraaije et al. (2005) found that *Mycosphaerella graminicola*, a wheat pathogen, has developed resistance to strobilurin, a Qol groups of fungicide. A range of fungicides called DMI (demethylation inhibitors; also known as sterol biosynthesis inhibitors) are deployed to combat diseases in vegetables, cereals, fruit crops, and other plantation crops (Ishii, 2006). Apple scab fungi such as *Venturia inaequalis* and *V. nashicola* have developed resistance to DMI fungicides (Ishii, 2006). The use of pesticides at higher concentrations is required to curb pesticide resistance (Tranier et al., 2014) along with other strategies such as alternation or mixing with other modes of action (Mikaberidze et al., 2014). Consequently, pesticide effectiveness decreased (Widawsky et al., 1998). Since the use of synthetic fungicides causes environmental contamination and pathogen resistance, therefore, alternative methods for battling pathogens have increasingly become important in recent years (Hasan et al., 2013). In achieving high-quality crops, non-chemical products are a critical component.

In order to achieve sustainable agriculture, fertilizers and pesticides must be reduced or eliminated (Pandey et al., 2021). Most countries have implemented regulatory measures that minimize disease control based on chemical fungicides and encourage alternative mitigation strategies (Widawsky et al., 1998). The Integrated Plant Disease Management system is an effective alternative crop management method. Sustainable agriculture is achieved through combining synthetic

fungicides, organic fertilizers, biological control, better soil management, and water management (Carvalho, 2006; Suryanarayanan et al., 2016). One way to control pests and pathogens without using chemicals is to develop disease-resistant varieties of food crops (Widawsky et al., 1998). In addition to introducing disease-resistant cultivars, scientists are striving to increase yields by developing high-yielding varieties (Carvalho, 2006). Sustainable agriculture can also be achieved through organic farming. Natural bio-agrochemicals can be derived from organic debris such as phenolic compounds, flavonoids, terpenoids, alkaloids, and fatty acids (Chou, 2010). Using *Trichoderma* to manage crop diseases is not an exception. However, the findings of the research are scattered throughout the papers. Although, few researchers reviewed the use of *Trichoderma* for crop disease management. These reviews, however, were either crop specific (Olowe et al., 2022) or did not provide detailed information about the mode of action of *Trichoderma* in disease management (Al-Ani and Li, 2018; Meher et al., 2020) or its taxonomical and chemical characteristics (Asad, 2022). Thus, in this paper, we compiled a comprehensive review of *Trichoderma* species, their taxonomy, classification, and ecology, as well as indirect and direct mechanisms utilized as plant protective mechanisms. In addition, the review is focused on the compatibility, mass formulation techniques, and industrial applications of *Trichoderma* species more specifically on the advent and progress of *Trichoderma* research at a global level. The compiled reports will provide the scientific community with detailed information on the biology and multifaceted uses of the genus *Trichoderma*.

Trichoderma: A multifunctional microbial biocontrol agent

The genus *Trichoderma* is one of the most prevalent culturable fungi in the family Hypocreaceae and can be found in all types of ecological diversity. The genus is soil-dwelling, free-living, cosmopolitan, facultatively anaerobic, filamentous, and asexually reproducing and is widely distributed in root and soil ecosystems and plant debris. This fungus has long been recognized as a microbial biocontrol agent that can replace chemical fungicides against the large range of fungi that cause root rot, soilborne, and foliar disease (Harman et al., 2006) and for increasing root and shoot development, crop productivity, resistance to abiotic stresses, and nutrient uptake (Saba et al., 2012). By enhancing crop productivity, it also contributes to food security in a sustainable way without causing ecological imbalance. Since the first recognized application of *Trichoderma* species in early 1930, they have been widely applied for the management of many plant pathogens and associated diseases (Howell, 2003; Harman et al., 2006). Some of them are wilt disease, dry root rot, damping off, and collar rot caused by *Fusarium* spp., *Rhizoctonia* spp., *Pythium* spp., *Phytophthora* spp., and *Sclerotium rolfsii*, respectively (Yang et al., 2011). *Trichoderma* shows diverse versatility, high competence, and profuse root-colonizing nature and also exists as a virulent plant symbiont (Papavizas, 1985). Characteristically, the fungus is identified through rapid growth, bright green to yellow-colored conidia and branched conidiophores (Kumar et al., 2019). Due to its eco-friendly nature, the fungus has been recognized as a substitute to commercial synthetic fungicides against a broad range of fungal pathogens. It is also extensively utilized as a model organism to understand biological interaction among antagonistic fungi, mechanisms, host-defense response, and plethora of heterologous proteins affecting plant metabolism and physiology.

Historical perspectives

Trichoderma was first described 200 years ago by Persoon (1794) in Germany. In India, it was first isolated by Thakur and Norris (1928) from Madras. In the early 20th century during World War II, this fungus was identified as cellulolytic and identified as *T. viride* QM6a but later renamed *T. reesei* by Elwyn T. Reese due to its ability to decay wood (Simmons, 1977). In 1932, the first ever evidence of *T. lingorum* (Tode) Harz. (*H. virens*) as a mycoparasite having biocontrol potential against *Rhizoctonia solani* was established, followed by discovery of gliotoxin as the first antimicrobial compound from *Trichoderma* species in 1934 (Weindling, 1932; Weindling, 1934). Earlier studies by Gutter (1957) also highlighted the discovery of an effect of light on conidiation of *T. reesei* in 1957. However, the genus *Trichoderma* was classified for the first time in 1969 by Rifai (1969), leading to a concept for the identification of species belonging to the genus *Trichoderma*, and by 2006, more than 100 distinct species had been described (Druzhinina et al., 2006).

The first evidence of *T. harzianum* suppressing *Sclerotium rolfsii* in the field was reported in 1972 (Wells et al., 1972). Research on cloning studies on *Trichoderma* species dates back to 1983 reported cloning of first cellulase of *T. reesei* (Shoemaker et al., 1983) followed by cloning of the first mycoparasitism-related genes *(prb1)* and its induction by cell walls in 1993 (Geremia et al., 1993). In 1986, the ability of *Trichoderma* to support plant growth was discovered for the first time (Chang et al., 1986). Specifically, the genus boosts plant immunity by induced resistance in 1997 (Bigirimana et al., 1997) and internal colonization of root system by *Trichoderma* in 1999 (Yedidia et al., 1999). The first commercial formulation of *Trichoderma*, Binab T, for biological control of plant diseases was registered in 1989.

Taxonomy, phylogeny, and classification of *Trichoderma*

Trichoderma was historically described as a genus of anamorphic fungi found primarily in rotting plant material and soil (Persoon, 1794) with *T. reesei* as the first evidence for the existence of the genus. As early as 1865, Tulasne and Tulasne (1865) postulated a sexual relationship between *Hypocrea* (*H. jecorina*) and *Trichoderma* (*T. reesei*). Their hypothesis was confirmed 100 years later (Kuhls et al., 1996). As a consequence, Rossman et al. (1999) described the genera *Hypocrea*, *Podostroma*, and *Sarawakus* belonging to the Hypocreaceae family and class Ascomycetes as teleomorphs of *Trichoderma*. According to Bisby (1939), for many years, due to morphological similarity in the majority of *Trichoderma* species as rapid growth, bright green conidia with repetitive branched conidiophore, it was considered as a single species, *T. viride*. Earlier classification of the genus *Trichoderma* included consolidated taxonomical scheme proposed by Rifai (1969) that introduced the concept of "species aggregate" and identified nine species under the genus based on morphological characterization in a monograph. In later studies, Bissett (1991) attempted to classify *Trichoderma* by integrating similar forms within species concept based on morphology, that is, conidiophore branching system into five sections such as *Pachybasium*, *Saturnisporum*, *Trichoderma*, *Longibrahiatum*, and *Hypocreanum*. Table 1 presents morphological characteristics used for identification of important *Trichoderma* species. In the 20th century, several new DNA-based approaches, such as rDNA sequence analysis, random amplified polymorphic DNA (RAPDs) analysis and PCR fingerprinting methods were used in fungal systematics and taxonomical studies including identification and phylogenetic classification of various *Trichoderma* species. Several studies demonstrated great genetic diversity among *Trichoderma* species by identifying four distinct species within the *T. harzianum* aggregate as *T. harzianum s. str., T. atroviride, T. longibrachiatum* and *T. asperellum* (Hermosa et al., 2000). The biotypes within *T. harzianum s. str.* as *T. harzianum* Rifai and *T. hamatum* (Bon.) Bain were linked to biocontrol and mycoparasitic activity, whereas, *T. aggressivum* was associated with green mold of mushroom (Samuels et al., 2002). Phylogenetic studies based on 18S rDNA sequence analysis (Kulling-Gradiner et al., 2002), where, small mitochondrial rDNA subunit, ITS1, 5.8S rDNA, ITS2, 28S rDNA, translation elongation factor (TEF-1), and endochitinase 42 were used to construct a phylogenetic tree, suggested *Trichoderma* as a monophyletic branch under *Hypocreaceae* and identified 46 species under three sections, namely, *Trichoderma*, *Pachybasium*, and *Longibrachiatum*. In a recent study, Gu et al. (2020) identified four new species of *Trichoderma* in the *Harzianum* clade (Figure 1) based on ITS, RPB2, and TEF1-alpha sequence data set.

TABLE 1 Identification features of *Trichoderma* species based on morphological characteristics.

Species name	Mycelial characteristics	Conidiophores	Conidia
T. harzianum	Watery white to light green, colorless ring-like zones on reverse side, 7–8 cm diam. in 5 days	Highly branched, loose tufts, short-skittle shaped phialides of size 7.2–11.2 × 2.5–3.1 µm	Sub globose or short ovoid conidia with truncate base, size 2.8–3.2 × 2.5–2.9 µm, 12h spore germination time
T. asperellum	Smooth, hairy, yellowish green, cotton pattern, 1–2 ringed Concentrics, emit coconut odor	Compact form, nine-pin shaped phialides attenuated into long neck arise singly/opposite pairs along branches, usually 6.8–7.2 × 3.0–3.4 µm	Globose or short ovoid, green colored, size 3.6–4.0 × 3.4–4.0 µm, 12–13h spore germination time
T. viride	Green to dark yellowish green after 2–3 days, no odor, smooth surface, cottony white mycelial mat, aerial hyphae	Long, slender phialides, swollen in middle, horn-shaped, size 6.2–10.5 × 3.1–3.9 µm	Globose to obovoid, smooth walled, usually 2.6–3.0 × 2.0–2.4 µm, 13h spore germination time
T. atroviride	Watery white, submerged, translucent smooth, floccose, changed yellowish green to artemisia green after 2 days, dull yellowish at reverse, odorless	Highly branched, oblong shaped, curved phialides, constricted at base, appear in ampulliform, swollen at middle, narrow at tips, 5.2–10.5 × 2.4–2.8 µm	Globose, green colored, 2.4–3.6 µm, 12–13 spore germination time
T. longibrachiatum	Submerged transluscent/watery white, yellowish green to lily green after 2 days, no smell	Smooth, irregular tufts, singly/2–3 verticels, lageniform, constricted at base, 3.4–5.2 × 2.3–3.0 µm	Obovoid to ellipsoidal, dilute green, apex rounded, 2.4–3.6 µm, 12–13 spore germination time
T. koningii	Creamy white, white to terreverte, crusty, compact, glaucous -like	Intercalary/terminal, phialides narrow at base, alternate to conical apices, singly and laterally, nine-pin bowling shaped, 3.8–7.6 × 2.5-3.2 µm	Ellipsoidal/oblonged, rounded apex, acute base, 2.5–4.2 × 1.8–2.6 µm, 14h spore germination time
T. virens	Watery white to green color with dull blackish green granules, no odor, 7–8 cm in 5 days	Branched irregularly near apex, terminated by cluster of 3–6 bunched phialides, lageniform to ampuliform phialides, swollen at middle, attenuated at apex, 4.4–12.8 × 2.6–4.2 µm	Broadly ellipsoidal to obovoid, rounded ends, green color, usually 3.2–5.6 × 2.5–3.9 µm, 13 h spore germination time

Source: Kumar et al. (2019).

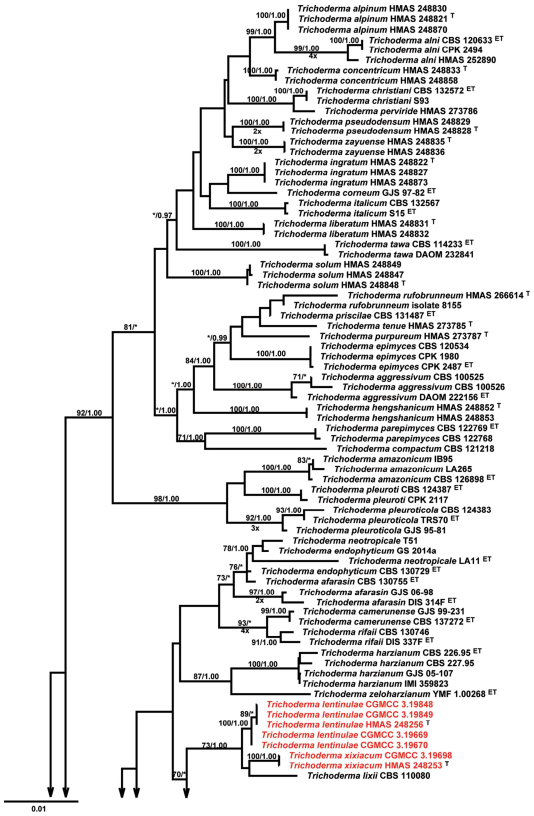

FIGURE 1
Phylogenetic tree of four new species of *Trichoderma* identified by Gu et al. (2020) based on Maximum Likelihood analysis of a combined ITS, RPB2, and TEF1α sequence data set.

As per Kirk's classification, taxonomy based on molecular phylogeny in the Ainsworth and Bisby's dictionary of fungi (10th edition), teleomorphic stage of the genus *Trichoderma* belongs to the domain Eukarya, kingdom Fungi, phylum Ascomycota, class Sordariomycetes, subclass Hypoceromycetidae, order Hypocreales, family Hypocreaceae, and genus *Hypocrea* species (Voigt and Kirk 2011). A total of 75 *Trichoderma* species have been identified; the majority of which are considered as important microbial biological control agents. These include *T. harzianum, T. hamatum*, *T. koningii* Oud., *T. polysporum* (Link ex Pers.) Rifai, and *T. virens* (J. Miller, Giddens, and Foster) von Arx (Harman et al., 2004). Complete genome-sequencing analysis of the genus *Trichoderma* was assembled, annotated, and analyzed for the first time in the case of *T. reesei* as cellulase producer (Martinez et al., 2008) followed by *T. virens*, *T. atroviride*, *T. harzianum*, and *T. asperellum* (Kubicek et al., 2011) as microbial biocontrol species enabled studies on evolution in the context of ecological fitness. In recent years, identification and characterization of newly isolated *Trichoderma* species has been elucidated by development of phenotypic arrays investigating carbon utilization patterns (Kubicek et al., 2003), oligonucleotide barcode (TrichoOKEY), and similarity search tool (TrichoBLAST) (Kopchinskiy et al., 2005). At present, Index Fungorum Database listed 471 different names for *Hypocrea* species and 165 records for *Trichoderma*, whereas, International Sub commission on *Trichoderma/Hypocrea* listed 104 species (Internationally) and 13 species (From India) based on characterization at molecular level (Table 1).

Environment-induced changes in *Trichoderma* ecology

Trichoderma species are ubiquitous, fast growing, cosmopolitan, and widely distributed as dominant microflora in soil including agricultural, orchard, forest, soil with organic matter (OM), pasture land, and desert soils from cool temperate to tropical climates (Domsch et al., 1980; Roiger et al., 1991). Saprophytic *Trichoderma* species were also recovered as mycelia from soil's top horizon (F and H), humid litter of deciduous and coniferous forests as well as from extreme environments such as

mangrove swamps, salt marshes, and estuarine sediments (Domsch et al., 1980; Widen and Abitbol, 1980). Knowledge on effects of ecological factors on *Trichoderma* species may lead to improve understanding of distribution, population dynamics, survival, and proliferation in soil and rhizosphere. Papavizas (1985) also found *Trichoderma* populations on plant root surfaces, decaying bark and on resting structure of soilborne fungi such as sclerotia or other fungal propagules.

However, soil colonization, composition, biomass, and biological activity of *Trichoderma* species are influenced by ecological parameters such as moisture and temperature of soil, atmosphere, pH, OM, nutrient content, and plant types (Domsch et al., 1980). *Trichoderma* species have been reported to grow in a wide range of soil temperatures varying from 0°C to as high as 40°C favoring *T. viride* and *T. polysporum* in cool temperature regions, whereas *T. harzianum* in warm tropical soils (Klein and Eveleigh, 1998). In an extensive study by researchers (Zehra et al., 2017a), variation in temperature attributed to the existence of *Trichoderma* species in particular niches by affecting growth, metabolic activity, enzyme production, and production of volatile antibiotics. The reduction of soil moisture or increase in soil temperature greatly hampered the establishment of *Trichoderma* colonies in soils by reducing the hyphal growth, germination, and spore production (Clarkson et al., 2004).

In the past, a few studies also concluded that *T. pseudokoningii* and *T. hamatum* are adapted to excessive soil moisture conditions, whereas *T. koningii* and *T. hamatum* are widely distributed in diverse climatic conditions. In general, the optimum growth and development of *Trichoderma* have been reported not only in pH condition ranging from 3.5 to 5.6 but also extended to extreme pH up to 2.1 in several studies (Ghazanfar et al., 2018). In addition, soil carbon dioxide (CO_2) atmospheric content also affects growth of *Trichoderma* by affecting soil pH upon combining with water to form weak acid, that is, carbonic acid, which readily dissociates into H^+ ions and HCO_3^-, thus, decreasing soil pH (Killham, 1994). Dix and Webster (1995) also revealed that, under high soil CO_2 concentration, basic substrates positively affect the growth of *Trichoderma* species, by influencing the availability of ions and nutrients in soil through salt solubilization in soil solution. Survivability of *Trichoderma* species in soil after application is basically mediated by hyphae, aggregate, or mycelial fragments, resting structure such as chlamydospores and conidia (Papavizas et al., 1984). Persistence of conidia lasted up to 110–113 days without any amendments or decreased initially, then stabilized up to $1/10^{th}$ of original population in soil for 24 months (Papavizas and Lumsden, 1982; Abbas et al., 2022).

Mode of action of *Trichoderma*

Trichoderma species operated through mixed mode of action involving more than one mechanism for antagonistic interaction and suppression of plant pathogens either through direct mechanisms *viz.*, mycoparasitism, competition, and antibiosis or complex indirect interaction by stimulating induced systemic resistance (ISR), solubilization and sequestration of nutrients, nutrient uptake, and enhancement of plant growth (Figure 2). *Trichoderma* species have been known for their prolific production of extracellular enzymes, proteins, fungitoxic compounds, antibiotics, and defense-related substances in addition to their ability to enhance shoot and root growth

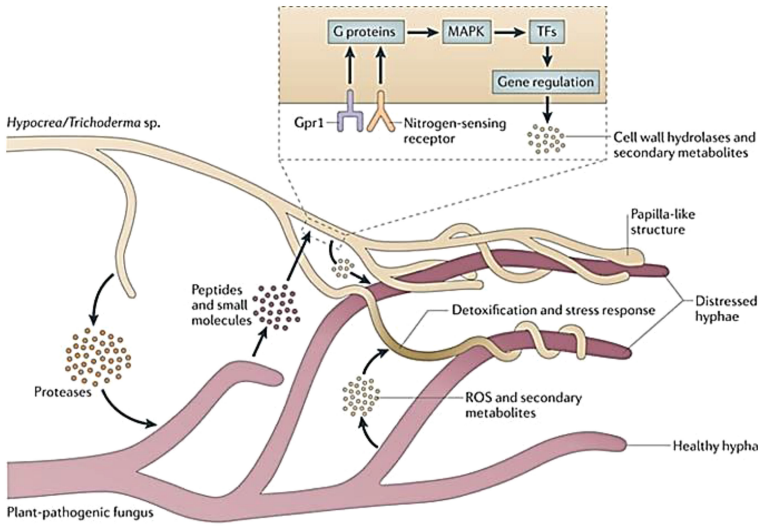

FIGURE 2
Mycoparasitism of *Trichoderma* spp. within the soil community (adopted from Druzhinina et al., 2011).

(Dutta and Das, 1999a), nutrient uptake, resistance to abiotic stresses, and crop productivity (Howell, 2003).

Mycoparasitism

Plant pathogenic fungi are sensitive to *Trichoderma* species through direct physical contact, and such biocontrol activity is called mycoparasitism (Figure 3; Dix and Webster, 1995; Druzhinina et al., 2011). However, the concept of mycoparasitism *via* mycoparasitism by *Trichoderma* dates back to demonstration of parasitism of *Rhizoctonia solani* by *T. virens* in mitigating citrus seedling disease by Weindling (1932). Earlier reports of direct parasitism of *Pythium ultimum* and *Sclerotium rolfsii* by *Trichoderma* species also provide evidence of its mycoparasitic ability (Papavizas, 1985). Dix and Webster (1995) suggested that mycoparasitism occurs as the direct mode of antagonism as a sequential process involving three steps, including chemotrophic growth, coiling and interaction of hyphae, and release of lytic enzymes. The mycoparasitic interaction is usually mediated by host-derived chemicals that are detected by *Trichoderma* species through specific signaling mechanisms mediating recognition via diffusible signals such as oligochitins, inducing enzyme secretion, namely, exochitinases, endochitinases, and 1,4-β-*N*-acetylglucosaminidases, extracellular β-(1,3)-glucanases, proteases, and lipases (Viterbo and Horwitz, 2010). Upon establishment of contact, *Trichoderma* attaches to the fungal cell through formation of papillae/appressoria-like structures, causing mycoparasitic coiling around the target fungus mediated by hydrophobin-like proteins and a lectin complex from the cell wall of *Trichoderma* and target pathogen (Figure 3), respectively (Howell, 2003). The secretion of particular lytic enzymes from the cell wall of *Trichoderma viz.*, glucanases, chitinases, pectinases, and peptaibol antibiotics induced a cascade of physiological changes within the target fungus facilitating flow of nutrients to the mycoparasite and degeneration of target fungus (Howell, 2003). Mycoparasitic ability of *Trichoderma* species have been studied against various soilborne pathogens, such as *Fusarium oxysporum*, *F. solani*, *R. solani*, *S. sclerotiorum*, *S. rolfsii*, and *Colletotrichum capsici* in our earlier studies (Dutta and Das, 1999a; Dutta and Das, 2002; Dutta and Das, 2009; Dutta et al., 2018; Dutta et al., 2020).

Antibiosis

Weindling (1934) proposed the concept of "lethal principle" describing influence of certain lethal factors excreted by *T. lingorum* in soil inhibiting growth and development of *R. solani* and *S. americana* displayed a paradigm shift toward involvement of lethal factors apart from mycoparasitism in biocontrol activity. In 1941, the factor causing the "lethal principle" was identified as gliotoxin, secreted by *Gliocladium virens* (Now *T. virens*). Later, in 1983, Howell and Stipanovic (1983) reported another antibiotic, that is, gliovirin secreted from *T. virens* known for potential inhibitory effect against *Phytophthora* species and *Pythium ultimum*. The phenomenon of antibiosis, utilized by *Trichoderma*, produces low-molecular weight, diffusible, specific compounds, or an antibiotic possessing antifungal and antibacterial properties. Depending upon the biochemical nature, antibiotics act as metabolic inhibitors or block protein synthesis (translational pathways), penetrate host cells, inhibit cell wall synthesis, growth, uptake of

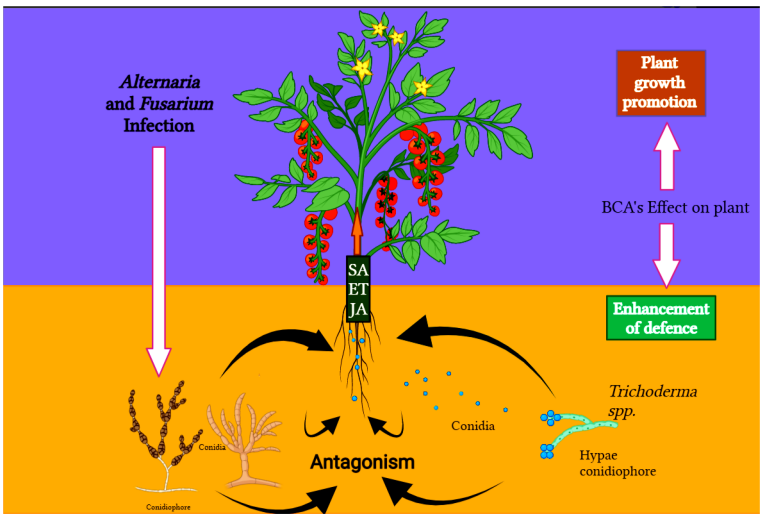

FIGURE 3
Plant-pathogen-antagonist tri-trophic interaction, how *Trichoderma* species can modulate the molecular signaling in the challenge between the *Fusarium* and *Alternaria* and the host (tomato).

nutrients, sporulation, and metabolite production by target pathogen.

Various species of *Trichoderma* are known for producing a diverse range of secondary metabolites (SMs) including polyketides, pyrones, oxygen heterocyclic compounds, polypeptides, terpenoids, and derivatives of fatty acids and amino acids (Table 2). The emission of coconut odor in case of few strains of *T. viride* and *T. hamatum* might be due to release of volatile 6-pentyl-α-pyrone, whereas, pigment-related compounds include anthroquinones such as chrysophanol (1,8-dihydroxy-3-methyl-9,10-anthroquinone), paschybasin (1,8-dihydroxy-3-methyl-9,10-anthroquinone), and emodin (1,6,8-trihydroxy-3-methyl-9,10-anthroquinone). Some metabolites attributed to mycotoxic properties of *Trichoderma* include trichothecenes (e.g., trichodermin, which impairs plant growth), cyclic peptides (e.g., suzukacillin, lipophilic alamethicin, trichopolyns, trichotoxins, and trichorianine, which attack the cell membrane of bacteria and eukaryotes promoting lysis), and isocyanide (e.g., trichoviridin). The volatile and non-volatile metabolites produced by various species of *Trichoderma* are described under separate section. In our recent study, cell-free culture filtrate of *T. pseudokoningii* showed efficacy against *C. capsici*, *S. sclerotiorum*, *R. solani*, and *F. oxysporum* due to release of extracellular SMs (Dutta et al., 2018).

Competition

Competition is one of the classical biocontrol mechanisms utilized by the genus *Trichoderma*, indirectly eliminating pathogens *via* reduction of food source and niche exclusion (Lorito et al., 1996; Elad et al., 2000). Corke and Hunter (1979) provided the first evidence of competition exerted by *Trichoderma* as a basis of biocontrol against *Chrondrostereum purpureum*, the silver leaf pathogen of plum trees. Sivan and Chet (1989) determined expression of antagonism by different *Trichoderma* species against *F. oxysporum* by exhibiting competition for carbon. *Trichoderma* species have been regarded as most aggressive competitors due to their ability to extensively proliferate in soil, competing for nutrients, space, water, or oxygen and capacity to mobilise soil nutrients as compared with other soil fungi. Such competitive ability enhanced by exerting resistance against a variety of toxins or antimicrobial compounds produced by other microorganisms due to the presence of ATP-binding cassettes transporters. Reports of *T. harzianum* CECT 2413 producing *Gtt1* gene encoding for high-affinity glucose transporter expressed at very low glucose concentration and *T. virens* producing *TvInv* encoding for intracellular invertase for sucrose hydrolysis provided evidence for nutrient competition similar to the scenario of competence among microorganisms (Benitez et al., 2004).

TABLE 2 Different types of secondary metabolites produced by *Trichoderma* species.

Secondary metabolites	Compounds	Species name	Functions	Target pathogens
Pyrones	6-pentyl-2H-pyran-2-one	*T. viride*, *T. atroviridae*, *T. harzianum*, *T. koningii*	Antifungal activity	–
Koninginins	Complex pyranes (Koningins A, B, D, E, and G)	*T. harzianum*, *T. koningii*, *T. aureoviride*		*Gaeumannomyces graminis*var. *tritici*, *R. solani*, *P. innamon*, *F. oxysporum*, *Pythium*
Viridins	Steroidal metabolite viridin	*T. koningii*, *T. viride*, *T. virens*		*F. caeruleum*, *P. expansum*, *A. niger*
Nitrogen Heterocyclic Compounds	Harzianopyridone (Harzianic acid & Pyrrolidindione ring)	*T. harzianum*	Antibiotic activity	*R. solani*, *G. graminis* var. *tritici*, *P. ultimum*
Azaphilones	Highly oxygenated bicyclic core & chiral quaternary center	*T. harzianum*T22	Growth inhibition	*R. solani*, *P. ultimum*, *G. graminis* var. *tritici*
Butenolides, Hydroxy-Lactones	Harzianolide, Butenolides, dehydro-harzianolide	*T. harzianum*	Antifungal	*P. ultimum*, *R. solani*
Isocyano Metabolites	Dermadin	*T. koningii*, *T. viride*, *T. hamatum*	Antibiotic	*Phytopthora* spp.
Diketo-piperazines	Gliotoxin (Q strains) & gliovirin (P strains)	*T. virens*		*P. ultimum* (P strains) *R. solani* (Q strains)
Peptaibols	A-aminoisobutyric acid & isovaline	*T. harzianum*	Inhibits β-glucan synthase	–

Information compiled from: Dunne et al. (1996).

Rhizosphere competence

The term "Rhizosphere" was coined for the first time for *Trichoderma* strains by Ahmad and Baker (1987) who attributed the capability of *Trichoderma* to colonize root surfaces to a depth greater than 2 cm (Chao et al., 1986), proliferate in developing rhizosphere to a concentration exceeding initial population on seed coat (Papavizas, 1982) and compete with other microorganisms for nutrients secreted by roots in rhizospheric soil. Seed treatment with *T. harzianum* rhizosphere competent strain T-95 of barley, cucumber, pea, radish, and tomato was implicated in reduced damping-off disease incidence caused by *Pythium ultimum* due to the absence of fungal units in up to 8 cm of root segment as compared with 3,000 CFU/g rhizosphere soil in case of untreated seeds (Ahmad and Baker, 1987). The colonization of roots by *Trichoderma* species is mediated by attachment of the fungus to roots *via* appressoria-like structures (class I hydrophobin encoded by gene TasHyd1), whereas penetration is achieved by release of protease and cellulolytic enzymes (Brotman et al., 2008). Recent study showed that rhizosphere competence by *Trichoderma* strains is governed by extensive communication *via* exchange and perception of signaling molecules, that is, deposition of fungal elicitors, auxin-like metabolites, and proteinaceous compounds released by *Trichoderma* are perceived by plants rhizosphere (Garnica-Vegara et al., 2015).

Studies by McLean et al. (2005) also determined that proliferation of *T. atroviride* C52 in onion rhizosphere and rhizoplane are dependent on the type of formulation used to introduce the fungus into the soil. Results indicated higher fungal concentration of 10^5 cfu/g soil was maintained through pellet formulation with reduced incidence of *Sclerotium cepivorum* as compared to solid-substrate and seed-coating formulations maintaining 10^4 and 10^1 CFU/g soil, respectively. Similarly, *T. viride* as cob-based formulation, when applied in the form of seed coat and soil treatment, imparted enhanced plant growth performance of mungbean, pea, and pigeon pea through better rhizosphere competence and reduced disease incidence of *Fusarium* in *Cajanus* sp. by 86.00% was also document by Pappu (2018).

Induced resistance

Induction of local and systemic resistance as indirect mechanism by *Trichoderma* species have been reported for both monocots and dicots involving recognition of the fungus by plants through ISR and systemic acquired resistance (SAR) against many phytopathogens (Harman et al., 2004). The response is mediated by phytohormones *viz.*, jasmonic acid (JA), and ethylene (ET) as closest analogue of induced resistance activated by rhizobacteria (Van loon, 2007) and induction of pathogenesis-related (PR) genes expression mediated by salicylic acid (SA), triggered by biotrophic and hemi-biotrophic pathogens. The first demonstration of induced resistance by *Trichoderma* was reported by Bigirimana et al. (1997) against *Colletotrichum lindemuthianum* and *Botrytis cinerea*, causing foliage diseases of beans.

The concept was further supported by Yedidia et al. (1999) who studied induced resistance by *T. harzianum* against cucumber seedling disease. Indirect evidence of plant ISR by *Trichoderma* was first described by (Calderon et al., 1993) through induction of hypersensitive response (HR) and phytoalexin synthesis by *T. viride* cellulase in grapevine cell cultures. Later, Chang et al. (1997) demonstrated the capability of heat-stable mycelial extracts of *T. longibrachiatum* to induce disease resistance against *Phytophthora parasitica* by induction of higher level of *PR-1b* and *PR-5* in tobacco, *Nicotiana tabacum* (Chang et al., 1997). In addition, reports on soil inoculation with *T. harzianum*T39 imparted resistance to leaves of bean plants, that is, parts spatially separated from the site of inoculation against *B. cinerea* and *C. lindemuthianum* have also been documented (Bigirimana et al., 1997; De Meyer et al., 1998).

Nutrient solubilization and sequestration

The ability of *Trichoderma* species to enhance plant growth and productivity was determined by utilization of indirect mechanism mediated by solubilization of mineral nutrients available in limited amounts for plants in soil, involving chelation and reduction (Harman et al., 2004). Earlier evidence on solubilization of various plant nutrients such as rock phosphate, Cu^{2+}, Fe^{3+}, Zn^{2+}, and Mn^{4+} ions by *T. harzianum* T22 was documented by Altomare et al. (1999), possibly due to production of diffusible metabolites capable of reducing Fe (III) and Cu (II) due to the formation of Fe (II)-Na_2-2,9-batho- and Cu(I)-Na_2-2,9- dimethyl-4,7-diphenyl-1,10-phenanthrolinedisulfonic acid complexes. Brotman et al. (2012) described nitrogen use efficiency of *T. asperelloides* T203 through increased amino acid content in colonized plants by allocating, re-used nitrogen, and increased nitrogen uptake as major determinants of transported nitrogen in plants.

A reduction of soil pH, caused by biosynthesis and release of organic acids, such as gluconic, citric, and fumaric acids, facilitates *Trichoderma's* mobilization of immobile nutrients, including phosphates, iron, magnesium, and manganese (Vinale et al., 2008). Jalal et al. (1986) identified Fe-chelating complex, that is, siderophores produced by *T. virens* are derivatives of hydroxymate nature classified under three families *viz.*, fusarinines, coprogens, and ferrichrome, which play key role in binding insoluble iron (Fe^{3+}), transforms it into a soluble form (Fe^{2+}) making it available to plants. In addition, the formation of siderophore-iron complex by *Trichoderma* species participates in depletion of Fe sources from soil inhibiting growth of phytopathogenic fungi (Wallner et al., 2009). Siderophore production also played role in conidial germination of *T. atroviride* (Velazquez-Robledo et al., 2011),

competitiveness of *T. asperellum*, and suppression of *F. oxysporum* f.sp. *lycopersici* (Segarra et al., 2010).

Inactivation of pathogen's enzymes

Fungal cell walls are composed of polysaccharides, lipids, proteins, β-glucans, and 90% of chitin. In contrast, cell walls of oomycetes consist of cellulose. Production of hydrolytic enzymes viz., chitinase, glucanase, N-acetylglucosaminidase, and protease by *Trichoderma* sp. causes the breakdown down of polysaccharides, chitin, and β-glucans, which are responsible for rigidity and integrity of fungal cells, and are attributed to successful mycoparasitic relationships. In recent literature, dual culture experiments between *Trichoderma* and *R. solani* Heflish et al., (2021) unravelled the presence of a diffusible molecule before direct contact, determined to activate transcription of cell wall degrading enzymes (CWDEs) encoding genes. However, under secretome analysis conducted for direct confrontation of *T. harzianum* EST 323 against *R. solani* through two-dimensional gels (2-DE) and liquid chromatography mass spectrometry (LC-MS/MS), seven CWDEs (viz., xylanase, chitinase, β-1,6-glucanase, β-1,3-glucanase, mannose, and protease) were identified (Tseng et al., 2008).

In similar studies, proteomic analysis confirmed a critical role of CWDEs produced by *T. harzianum* in antagonism by deactivating mycelia of *B. cinerea*, indicating cell walls as the primary target during mycoparasitism (Yang et al., 2009). Several studies identified virulent genes encoding for CWDEs *viz.*, *Eng18B* a gene encoding for typical glycoside hydrolase family enzyme by *T. atroviride*, *Nag1*, and *ech42* gene encoding for *N*-acetyl-glucosaminidase and endochitinase, respectively, by *Trichoderma* species (Kulling et al., 2000). Recently, the concept of enzyme biosynthesis merged with production with antibiotics unravelled a synergistic mechanism of biological control in *T. harzianum* through a combination endochitinase, gliotoxin, and peptabiols resulted in a detrimental effect on conidial germination and hyphal elongation of *B. cinerea* (Gu et al., 2020).

Trichoderma species: Chemical profile

Trichoderma species are notable for having the ability to grow rapidly, exploit diverse substrates, and resist harmful chemicals. Among soilborne fungal communities, they are dominant. *Trichoderma* produce a broad range of biologically active compounds that are among the most fascinating and important properties of the organism. In particular, plant defense responses can be mediated by proteins, peptides, and low-molecular-weight compounds produced by *Trichoderma* species (Reino et al., 2008). Compounds with low molecular weights include aromatic compounds and polyketides such as butenolides and pyrones, isocyanate metabolites, and volatile terpenes. It produces volatile (such as ET, alcohols, hydrogen cyanide, ketones, and aldehydes) and non-volatile (such as peptides) compounds that inhibit microbial growth. Reino et al. (2008) have shown that *Trichoderma* species can produce a number of volatile (such as pyrones and sesquiterpenes) and non-volatile (such as peptaibols) metabolites. Here are a few examples of the volatile organic compounds (VOCs) and other metabolites released by different species of *Trichoderma*.

VOCs and their role in control of plant pathogens

Trichoderma are well-known for their VOCs that make them of interest to the scientific community. Natural products, or SMs, are among these compounds. Often, these compounds do unknown or obscure things in the producing organism that are vital to humankind. Some of these VOCs are beneficial to society, such as ones for medical, industrial, and agricultural purposes. Numerous reports suggest that some VOCs possess antibacterial and immunosuppressive properties as well as phytotoxic and mycotoxin properties. VOCs are low-molecular-weight organic compounds with substantive vapor pressure under ambient conditions. They have diverse chemical structures such as alcohols, ketones, mono- and sesquiterpenes, esters, lactones, or C_8 compounds (Korpi et al., 2009; Siddiquee et al., 2012). Chemical ecologists explain VOCs as semiochemicals that attract and deter insect pests and other invertebrates.

VOCs derived from fungi are used for biological control of plant pathogens in agriculture. Moreover, these VOC mixtures have been studied for their ability to promote plant growth. Food companies use the same biological control properties to reduce fungal spoilage of food commodities in postharvest, which is called "mycofumigation." The potential role of fungal VOCs has recently been examined. The genus *Trichoderma* is well-known for its production of volatile compounds with potential biological activity. VOC is usually defined as normal saturated hydrocarbons (C7-C30), cyclopentane, cyclohexane, alcohol, fatty acid, sulfur-containing compounds, esters, simple and benzine derivatives, hydroxy, or amino compounds. A compound's production differs based on (1) its specific molecular structure, (2) its strain and species, (3) its presence of microbes, and (4) the balance between its biosynthesis and biotransformation rates (Vinale et al., 2008, 2010). The important VOCs derived from *Trichoderma* are shown in Table 3.

Table 3 revealed that the major compounds produced by *Trichoderma* species include gliotoxin, gliovirin, glisoprenin, viridin, 6-pentyl-α-pyrone, hepteledic acid, koninginins, trichodermamides, peptaibols, anthraquinones, polypeptides, terpenoids, polyketides, trichodermaides, trichothecenes, harzialactones, compounds derived from alpha-amino acids, and azaphilones (Vey et al., 2001; Reino et al., 2008). Liu et al. (2009) reported that crysophanol, pachybasin, ω-

hydroxypachybasin, emodin, 1, 7-dihydroxy-3-hydroxymethyl-9,10-anthraquinone, and 1,5-dihydroxy-3-hydroxymethyl-9,10-anthraquinone showed potential bioactivity against several plant pathogens. In addition, pchybasin and emodin play major roles in the biocontrol mechanism of *Trichoderma* mycoparasitic coils through cAMP signaling (Lin et al., 2012). A novel compound, cerinolactone, extracted from *T. cerinum* together with three known butenolides containing harzianolide, 3,4-dialkylfuran-2(5*H*)-one nucleus, T39butenolide, and dehydroharzianolide, both compounds exhibited activities against *B. cinerea*, *R. solani*, and *P. ultimum* (Vinale et al., 2012). *T. harzianum* ETS 323 exhibits a stimulatory effect and an antagonistic action on *R. solani* by a novel compound of l-amino oxidase (Th-LAAO). Considering these results, *T. harzianum* is a good biocontrol agent due to its ability to provide insight into the function of l-amino acid oxidase (Yang et al., 2011). Due to these beneficial effects, *T. asperellum*, *T. atroviride*, and *T. harzianum* strains have been used as plant protection agents in agriculture to control molds (Verma et al., 2007).

Mycoparasitism and interaction of *Trichoderma* with plants are mediated by VOCs (Vinale et al., 2008). Few research investigations addressed the effect of various culture media on the volatile types produced by *Trichoderma* (Wheatley et al., 1997) or the function properties of some of these volatiles (Nemčovič et al., 2008). There have been reports of multiple *Trichoderma* species producing VOCs as shown in Table 3 (Stoppacher et al., 2010). VOCs form intermediates and end products of diverse metabolic pathways and include ketones, alcohols, esters, lactones, mono- and sesquiterpenes, and some C_8 compounds (Korpi et al., 2009; Siddiquee et al., 2012). These compounds are relatively nonpolar and have high vapor pressures. The compounds with high molecular weight are polar, such as peptaibols.

To determine whether these compounds are significant during the life cycles of their producing species properly, controlled studies are needed. Nevertheless, observing fungal ecology may lead to the development of strategies that have proven effective for the discovery of novel bioactive fungal compounds. The use of biocontrol tactics is one example. Historically, *Trichoderma* species have been used as biological control agents since the 1930s, and numerous field experiments have proven that applications of *Trichoderma* species promote plant growth while limiting pathogen growth. Thus, due to production of VOCs, *Trichoderma* species are effective biofungicides, as they degrade other pathogenic fungi enzymatically, produce antimicrobial compounds that kill pathogenic fungi, and compete with them for nutrients and space.

Non-volatile metabolites and their role in control of plant pathogens

SMs produced by *Trichoderma* species have a variety of biological activities. There have been a number of reviews published about *Trichoderma* metabolites. These reviews focus on structure, biological activity, or fungal origin. An overview of some of the most important non-volatile compounds in *Trichoderma* has been provided in Table 3. Seventeen compounds were isolated from the endophytic fungus *Trichoderma* sp. Xy24: ergosterol, trichodimerol, cyclonerodiol, and trichoacorenol (Zhang, 2015); 10,11-dihydroxy-cyclonerodiol, trichocage B, harzianone, 14-hydroxy-trichoacorenol; ergokonin B, (9R,10R)-dihydro-harzianone, and methyl stearate (Zhang et al., 2014), trichoacorenol B, harzianelactone, cyclonerodiol B, and trichoacorenol C (Zhang et al., 2016). *Trichoderma harzianum* and *T. longibrachiatum* that contain tetracyclic scaffolds, harziandione, have been described as potential microbial biocontrol agents against *C. lagenarium* and *F. oxysporum* (Miao et al., 2012). There is a potential antagonistic action of *T. saturnisporum* owing to the presence of cerebroside A, sorbicillin B, bisvertinolone, and saturnispol A–D (Meng et al., 2017). The presence of 5-hydroxyvertinolide, bislongiquinolide (Andrade et al., 1997), and Ergokonin A (Vicente et al., 2001) in *T. longibrachiatum* also demonstrated antagonistic activity. Likewise, the antagonistic effect of *T. harzianum* was also attributed to non-volatile metabolites such as ergosterol, harzianolide, endoperoxide, and 3-indol acetic acid.

Compatibility studies

Inorganic pesticides (insecticides, fungicides, and herbicides) and fertilizers have played vital role in supplementing plant nutrients and curbing biotic stresses. The utilization of bioformulations as part of integrated plant disease management strategies involved combination of cultural, physical, chemical, and biological means. Dutta et al. (2017) studied compatibility of *T. pseudokoningii* with selective fertilizers, insecticides, fungicides, herbicides, and organic stickers. Researchers found that all the tested pesticides inhibited the growth of *T. pseudokoningii*, with the exception of thiamethonaus 25% WG at 0.125% and ritha at the highest test dose found compatible. Urea and MOP were found to be compatible, whereas SSP and CAN inhibited growth. These variations in inhibitory potential are attributed to inherent variations in chemical ingredients within the fungus' cellular components. In another study, *T. viride* also showed compatibility with insecticide (imidacloprid), fungicides (mancozeb, tebuconazole, pencycuron, and propineb), and herbicides (imazathafir, 2, 4-D sodium salt, and oxyfluorfen) (Madhavi et al., 2011). In a recent study, Singh et al. (2019) tested compatibility of *Trichoderma* species with nematicides such as carbofuran, aldicarb, phorate, and thionazin and found compatibility with carbofuran and phorate for management of root knot nematode in rice. *Trichoderma viride* and *T. harzianum* were also found compatible with azoxystrobin and metalaxyl, respectively (Shashikumar et al., 2019).

TABLE 3 Volatile and non-volatile metabolites identified from *Trichoderma* species.

Species name	Non-volatile metabolites	References	VOC	Reference
T. arundinaceum	Prealamethicin F50, alamethicin II, alamethicin F50, atroviridin J	Chavez et al. (2017)	Harzianum A	Malmierca et al. (2012)
T. asperellum	Trichodermaerin, aspereline G	Chen et al. (2013); Chantrapromma et al. (2014)		
	6-Amyl alpha-pyrone	Yang et al. (2014)		
	Dechlorotrichodenone C	Song et al. (2018)		
T. hamatum			Isonitrin A	Baldwin et al. (1991)
			Viridiol	Wipf and Kerekes (2003)
	Harziandione	Liang (2016)		
T. koningiopsis	Trikoningin KB I	McMullin et al. (2017)		
	Konginginin A -M	Chen et al. (2015)		
	Lutidonecarboxylic acid, cyclonertriolisoechinulin A, echinuline, cyclopenol 3-o-methylviridicatin	Shi (2018)		
T. citrinoviride	Ergosterol endoperoxide	Liang (2016)	Citrantifidiene (hexa-1,3-dienyl ester of acetic acid), citrantifidiol (cyclohexane-1,3-diol)	Evidente et al. (2008)
T. harzianum	Ergosterol endoperoxide, harzianolide, trichoharzianin, 3-indol acetic acid	Liang (2016), Vinale et al. (2008)	Harzianum A	Nielsen et al. (2005)
	β-sitosterol	Ahluwalia et al. (2015)	Harziphilone	Reino et al. (2008)
			Hexadecanoic acid, hexatriacontane, indane	Siddiquee et al. (2012)
T. longibrachiatum	β-sitosterol	Tarus et al. (2003)	Harzianone, harziane diterpene	Miao et al. (2012)
	Cerevisterol ergosterol peroxide, squalene sorbicillin	Ji et al. (2014)	Bisvertinolone	Abe et al. (1998a)
	Ergokonin A	Vicente et al. (2001)		
	5-Hydroxyvertinolide	Andrade et al. (1997)		
	Bislongiquinolide	Andrade et al. (1997)		
T. viride	Bislongiquinolide	Ahmed et al. (2009)	Trichodermin	Nielsen et al. (2005)
	Trichodecenins, trichorovins, trichocellins	Fujta et al. (1994)	Viridenepoxydiol, Viridepyronone	Evidente et al. (2006; 2003)
	Trichorovin I and II,	Wada et al. (1995)		
T. polysporum	Valinotricin, cyclonerodiol oxide	Fujita et al. (1984)	Emodin Ergosterol	Fujita et al. (1984)
T. atroviride	Atrichodermone A-D, trichodermone A 1,3-dione-5,5-dimethylcyclohexane	Kandasamy et al. (2018)	Chloroform, Cinnamic acid, Diterpene B, C, D, E, Limonene, Toluene	Nemcovic et al. (2008)
	40-(4,5-Dimethyl-1,3-dioxolan-2-yl) methylphenol, 30-hydroxybutan-20-yl) 5-oxopyrrolidine-2-carboxylate, troviridetide	Lu et al. (2012)	Ethylbenzene Iso-menthone, Isopentyl acetate, Menthone, Nerolidol, α-curcumene, β-bisabolene	Polizzi et al. (2011)
			α-Terpinene, α-phellandrene, α-terpinolene, ϒ-terpinene	Stoppacher et al. (2010)
T. polysporum	Trichosporin Bs	Lida et al. (1993)		

(Continued)

TABLE 3 Continued

Species name	Non-volatile metabolites	References	VOC	Reference
T. reesei	Harzialactone A, 3,6-dibenzylpiperazine-2,5-dione, 3-benzyl-8-hydroxyl-pyrrolopiperazine-2,5-dione	Sun et al. (2007)		
T. saturnisporum	Cerebroside A, sorbicillin B, bisvertinolone, saturnispol A-D	Meng et al. (2017)		
T. citrinoviride	Penicillenol B1, penicillenol B2	Hu et al. (2014)	Citrantifidiene, Citrantifidiol	Evidente et al. (2008)
	Citrostadienol, euphorbol, trichocitrin	Liang (2016)		
T. virens	Trichocarane A,14-hydroxy CAF-603 7-β-hydroxy CAF-603, chromone	Shi (2018)	Mevalonic acid	Phuwapraisirisan et al. (2006)
			Oleic ester	Lee et al. (1995a)
			Trichocaranes A, B, C and D	Macias et al. (2000)
			Trichodermamides A-B, Trichodermin	Garo et al. (2003)
			Viridin	Singh et al. (2005)
			Viridiol	Phuwapraisirisan et al. (2006)
T. gamsii	Trichoderone A, aspochalasin	Ding et al. (2012)		
T. koningii	Trichodermaketone C & D, koninginin A-F	Sawant et al. (1996)	6-Pentyl- α-pyrone, dermadin	Stoppacher et al. (2010)
	Trichokonin I-IV	Huang et al. (1995)	Ergokonin A B	Reichenbach et al. (1990)
			Gliotoxin	Haggag and Abo-Sedera (2005)
			Palmitic acid	Benoni et al. (1990)
			Trichodermamides A-D	Song et al. (2010)

In a view to improve the efficacy of *T. harzianum* application against phytopathogens and plant growth promotion, its compatibility was tested with biosynthesized (27.64 nm) and commercial grades (20 nm, Sigma-Aldrich, St. Louis, Missouri, United States) of silver (Ag) and chemically synthesized zinc oxide (ZnO, 20 nm) nanoparticles (NPs). In this context, Biswas and Dutta (2019) reported 100% compatibility of *T. harzianum* with commercial grade of AGNPs at 5,000 ppm and slightly lower of 98.94 and 90.00% in case of myco-AgNPs at 1,000 and 5,000 ppm, respectively. In contrast, inhibitory effect on growth of *T. harzianum* was observed under all the tested concentrations of ZnONPs. Recently, in a study by Upamanya et al. (2020), compatible reactions of *T. harzianum* and *T. asperellum* were also tested with fungal entomopathogens *viz.*, *Beauveria bassiana s.l.*, and *Metarhizium anisopliae s.l.* (recently named as *M. robertsii*) for development of microbial consortia. Under standard co-culture conditions, combination-I (*B. bassiana s.l.* + *T. harzianum*, *M. anisopliae s.l.* + *T. harzianum*, *B. bassiana s.l.* + *M. anisopliae s.l.* + *T. harzianum*) and combination-II (*T. asperellum* + *B. bassiana s.l.*, *T. asperellum* + *M. anisopliae s.l.*, *T. asperellum* + *B. bassiana s.l.* + *M. anisopliae s.l.*) gave compatible reaction. Mixed culture showed mutual growth and overlapping among test microbial biocontrol agents, due to lack of production of SMs by individual organism against another, while growing in the same media.

Mass culture, growth, and formulation of *Trichoderma*

The development of potential *Trichoderma* species as successful microbial biocontrol agents and its effective commercial application depends on production of viable propagules, mass production, formulation strategies, and optimized delivery systems. Fungal spores of *Trichoderma* as active ingredient are formulated using different organic and inorganic carriers (diluents and surfactant), through solid or liquid state fermentation to improve physical characteristics, increase shelf life, and protect against adverse environmental conditions. Different kinds of *Trichoderma* propagules used in formulation includes hyphae, chlamydospores, and conidia, of which both conidia and chlamydospore are highly preferred means due to their ability to withstand adverse environmental conditions as compared with hyphae due to lack of resistance toward dehydration (Howell, 2003).

Under solid state formulation, *Trichoderma* species are commonly multiplied on boiled rice, sorghum seeds, rice saw dust, wheat bran-saw dust, and agro-waste products such as peels of potato, brinjal, papaya, banana, spinach, guava, used tea leaves, sugarcane, and pea husk used as solid substrate or food base. Solid formulation types *viz.*, wet dust, dry pellets, granules, dry dust, and granules are adjuvated by using adhesive substances such as Arabic gum, carboxymethylcellulose (CMC), clays, compost, talc powder, and so forth. In a study by Dutta and Das (2009), the seed treatment of French bean (var. Contender) with talc-based formulation of *T. harzianum* in combination with methylcellulose and carbendazim was found significantly efficient and at par with seed treatment with carbendazim for the management of white mold rot of bean.

Liquid formulations were adopted for multiplication of fungal propagules in soluble materials *viz.*, broth cultures of potato dextrose broth (PDB), and agricultural substrates such as rice water, vegetables juices, and boiled dal. Fully grown mycelial mat along with supernatant imposed with submerged conidia are grounded homogenously and amended with several adjuvants such as carboxymethyl cellulose (CMC), Tween-80, mannitol, peptone, and oil. Sprayable/liquid formulations include soluble liquids (SLs), soluble powders (SPs), soluble granules (SGs), emulsifiable concentrates, and liquid suspension dispersed in water, that is, suspension concentrates (SCs) and aqueous suspension (AS). Das et al. (2006) tested efficacy of osmoticant (mannitol) amended PDB liquid formulation yielded higher biomass, sporulation, cfu, and dry weight of biomass followed by modified Richard's broth (MRB). In addition, talc-based formulation at 3:1 dose showed higher sporulation as compared with starch-based formulation at 1:1 dose with a shelf life of 60 and 30 days, respectively. However, seed treatment with bioformulation enriched with *T. harzianum* + talc + osmoticant assessed under field condition showed lowest stem rot disease index caused by *R. solani* with higher enhanced percent seed germination, plant vigour, and crop yield.

In North-Eastern region (NER) of India, several locally made liquid-based biopesticides from native strains of *Trichoderma* species were developed such as Org-Trichojal (*T. harzianum*) in Assam, UmTricho (*T. harzianum*), *UmTriv* (*T. viride*), and two *Trichoderma*-based microbial consortia, that is, UmTim *(T. harzianum* + *Metarhizium anisopliae s.l.*) and UmComb (*T. harzianum* + *Beauveria bassiana s.l.* + *M. anisopliae s.l.* + *Akanthomyces* (=*Lecanicillium*) *lecanii* + *Pseudomonas fluorescens*) in Meghalaya (Figure 4) and maintained by team workers at Central Agricultural University (Imphal), Umiam and Assam Agricultural University, Jorhat (Dutta et al., 2020; Dutta, 2020). The technology was used in preparation were standardized by Dutta et al. (2020) as mycelial mat centrifuged in PDB, amended with mannitol (osmoticant), sunflower oil (UV protector), Tween-80 (surfactant), CMC (cellulose-enrich), peptone (nitrogen supplier), and glycerol (preservative) with a shelf life of 180 days (Figure 4). Developed bioformulations have been locally accepted by farmers, KVKs, and institutes from the region as well as in different states of India and have been adopted in organic package of practices for cauliflower, cabbage, and spice crops of Assam. Seed treatment with *T. harzianum*–based bioformulation, that is, Org-Trichojal@ 5g/L of water + CMC @ 0.02% for 1h followed by shade dried for 2h prior to sowing has been recommended against soilborne disease such as damping off of cabbage and cauliflower. In spice crop cultivation, that is, bhoot jolokia, *Capsicum chinense* Jaqc, and seed treatment with *T. harzianum*–based bioformulation, *Org-Trichojal* was recommended at the rate of 5 ml/kg of seed against

FIGURE 4
Biopesticides developed from native strains of *Trichoderma* spp. *viz.*, **(A)** *Org-Trichojal* (*T. harzianum*) in Assam and **(B)** *UmTriv* (*T. viride*), **(C)** *UmTricho* (*T. harzianum*), and *Trichoderma*-based consortia, **(D)** *UmComb* and I **(E)** *UmTim* in Meghalaya of NER (Source: Dutta et al., 2020).

R. solani and *Fusarium* spp. Commercial formulations of *Trichoderma* species available worldwide and in India are listed in Table 4.

Genetic manipulation

Genetic manipulation of *Trichoderma* species has been achieved by different techniques including protoplast-mediated transformation (PMT), electroporation, biolistic transformation, and *Agrobacterium*-mediated transformation (AMT) leading to alteration of fungal cell by insertion of genetic material into genome. Penttila et al. (1987) first successfully attempted introduction of DNA in prototrophic strain *T. reesei* along with *arg*B gene as auxotrophic marker and *smd*S as dominant marker from *Aspergillus nidulans* by polyethylene glycol (PEG)/$CaCl_2$–mediated protoplast transformation technique. Auxotrophic marker genes enable high transformation efficiency, whereas dominant marker genes confer properties *viz.*, antibiotic resistance, nutrition utilization, for example, nitrogen or carbon, allowing transformed cells to thrive as compared with non-transformed cells. Several examples of dominant marker genes include acetamide (acrylamide) as nitrogen source encoded by *amdS* gene of *A. nidulans*, invertase *suc*Agene of *A. niger* using sucrose as carbon source, and pyrithiamine (*ptrA*)–resistant gene of *A. oryzae* have been expressed in *T. reesei* (Berges et al., 1993; Kubodera et al., 2002). Later, transfer of *Trichoderma* genes in plants was first successfully demonstrated by Lorito et al. (1998) in tobacco and potato plants expressing 42 kDaendochitinase gene *chit42*, conferred high resistance against *A. alternata*, *A. solani*, *B. cinerea*, and *R. solani.*

Chitinases genes elevated defense response by involving greater induction of ROS through expression of defense-related genes, PR enzymes, and terpenoid biosynthesis. Numerous studies demonstrated the expression of potential defense genes of *Trichoderma* sp. in plants through genetic transformation techniques have successfully conferred enhanced resistance to phytopathogenic fungi and bacteria (Table 5). Recently, marker-free transgenics of *Trichoderma*

TABLE 4 Commercial formulation of *Trichoderma* species.

Commercial products	*Trichoderma* strains	Manufactured by	Country
Antagon TV	*T. viride*	Green tech Agro-products	India
Anatgon	*Trichoderma* spp.	DeCeuster Meststoffen N.V. (DCM)	Belgium
Biocon	*T. viride*	Tocklai Experimental Station, Tea Research Association	India
Bioguard	*T. viride*	Krishi Rasayan Export Pvt. Ltd.	India
Bip T	*T. viride*		Poland
Binab T	*T. harzianum, T. polysporum*	BINAB Bio-Innovation AB; Henry Doubleday Research Association	Sweden, UK
Bioderma	*T. viride+ T. harzianum*	Biotech International Ltd.	India
Bio Fit	*T. viride*	Ajay Biotech Ltd.	India
Defense SF	*T. viride*	Wockhardt Life Science Ltd.	India
Eco fit	*T. viride*	Hoechst Schering Agro Evo Ltd.	India
Ecoderma	*T. viride+ T. harzianum*	Morgo Biocontrol Pvt. Ltd.	India
Funginil	*T. viride*	Crop Health Bioproduct Research Centre, Ghaziabad	India
Gliostar	*T. virens*	GBPUAT, Pantnagar	India
Monitor	*Trichoderma* spp.	Agricultural and Biotech Pvt. Ltd.	India
Plant biocontrol agent-1	*T. harzianum*	GBPUAT,	India
Plant shield	*T. harzianum*	Bioworks, Inc.	USA
PromotPlusWPPromotPlusDD	*T. koningii, T. harzianum*	Tan Quy	Vietnam
Trichostar	*T. harzianum*	Green tech Agro-products	India
Trichoguard	*T. viride*	Anu Biotech Int. Ltd.	India
Tricho-X	*T. viride*	Excel Industries Ltd.	India
Org-Trichojal	*T. harzianum*	Assam Agricultural University	India
UmTricho	*T. harzianum*	CPGS-AS, Central Agricultural University	India
UmTriv	*T. viride*		
UmTim (Consortia)	*T. harzianum+ M. anisopliae s.l.*		
UmComb (Consortia)	*T. harzianum + Beauveria bassiana s.l. + Metarhizium anisopliae s.l. + A. lecanii*		

Information compiled from: Puyam (2016); Dutta et al. (2020); Dutta (2020).

TABLE 5 Genetic manipulation using *Trichoderma* spp. in different crops conferred disease resistance.

Crop	Pathogen	*Trichoderma* species	Mechanism and activity
Onion roots	*Sclerotium cepivorum*	*T. koningii*	Hyphae penetrated into infected epidermal and cortical tissue of root, destroyed pathogen hyphae *via.*, production of endo- and exo-chitinases
Cotton seedlings	*R. solani*	*T. virens* Gv29-8	Over-expression of gene cht42, encoding for chitinase showed enhanced biocontrol activity and reduced cotton seedling disease
Bean leaves	*B. cinerea*	*T. harzianum*	Chitinase activity (ech42) reduced disease symptoms
			Proteases inactivate hydrolytic enzymes produced by *B. cinerea*, break down into peptide chains or constituent amino acids, thus destroy their capacity to incite diseases
Tobacco, Potato, Tomato	*Alternaria alternata, A. solani, B. cinerea, R. solani*	*T. harzianum* P1	Transfer and expression of 42 kDa gene encoding for endochitinase*chit42* demonstrated high-level, broad-spectrum resistance
Apple	*Venturia inaequalis*	*T. atroviride* P1	Transgenics expressing *chit42* gene encoding both endo- and exo-chitinases showed reduced growth but enhanced resistance
Broccoli	*Alternaria brassicola*	*Trichoderma* sp.	Expression of *chit42* gene increased resistance
Tobacco	Fungal and bacterial pathogens	*T. harzianum*	Overexpression of two endochitinases (*Chit33* and *Chit42*) conferred broad resistance: synergistic effect
Femminello siracusano lemon	*Phomatracheiphila*	*T. harzianum*(*chit42*)	Foliar protein extracts from *chit42* introduced lemon inhibited conidial germination and fungal growth
	B. cinerea		Smaller lesion area, enhanced transcript levels of ROS and ISR-related genes
Rice	*Rhizoctonia solani*	*T. virens*	Expression of *cht42* gene accumulated *cht42* transcript and chitinase activity showed 62.00% reduction in sheath blight disease index
Tomato	*Meloidogyne incognita*, root knot nematode	*T. harzianum* T-203	Genes encoding protease enzyme drastically reduced root galling and penetrate egg masses
Cucumber	*Pythium ultimum*	*T. longibrachiatum*CECT2606	Transformants with over-expression of gene encoding β-1,4-endoglucanase effective in biocontrol

Information compiled from: Howell (2003), Schuster and Schmoll (2010), Olmedo-Monfil and Casas-Flores (2014), Contreras-Cornejo et al. (2016).

spp. were also generated *via* marker removal, recycling, and reusing for another transformation, through excision of marker genes mediated by native homologous recombination (HR) machinery or by heterologous site-specific recombinases. Sequential deletions using different cassettes comprising the excision of marker genes *viz.*, direct-repeat-mediated HR for removal of pyr*4* gene (Hartl and Seiboth, 2005) and site-specific Cre recombinase for removal of *xyn1* promoter (Steiger et al., 2011) were reported in *T. reesei*. In addition, split-marker systems for successful gene deletions were also used in *T. virens* and *T. atroviride* (Trushina et al., 2013). Knockout strategies involving RNA interference (RNAi) gene silencing was also used to silence *cel6a* (cellobiohydrolase 2) gene expression in *T. reesei* (Brody and Maiyuram, 2009).

Defense mechanism and their exploitation

The *Trichoderma* species, most commonly *T. atroviride*, *T. harzianum*, *T. virens*, *T. hamatum*, *T. asperellum*, and so forth, are progressively used as efficient microbial biocontrol agents due to their ability to activate local or systemic resistance in plants (Table 6). The concept of induced defense responses in plants by *Trichoderma* inoculation was first supported by the work of Yedidia et al. (1999), inoculated roots of 7-day-old cucumber seedlings with *T. harzianum* T-203 at 10^5 spores/ml. Roots and leaves of treated cucumber seedlings demonstrated initiation of plant defense, exerted increase in peroxidase activity, increase in chitinase, and deposition of callose-enriched appositions in inner surface of callose walls. Different strategies utilized by *Trichoderma* such as production of lytic enzymes, ABC transporter membrane pumps, diffusible or volatile and SMs compromising enzymatic and chemical weapons utilized by plant pathogens, make it efficient mycoparasite and antagonist. The defense mechanism of *Trichoderma* are triggered by regulatory mechanisms utilizing signal transduction pathways including heterotrimeric G-protein signaling, mitogen-activated protein kinase (MAPK) cascades, and cAMP pathway (Zeilinger and Omann, 2007).

Attempts made by Reithner et al. (2005) identified heterotrimeric G-protein signaling genes, that is, *TGA* of *T. virens*, *GNA3* of *T. reesei*, and *TGA1* and *TGA3* of *T. atroviride* belonging to classes I and III of adenylate cyclase inhibiting G-alpha subunits, played an important role in the regulation of antifungal metabolites and coiling around host hyphae. MAP-kinase TVK1 characterized in *T. asperellum*, *T. atroviride*, and *T. virens* mediated the transfer of information from sensors, regulate signaling mechanisms, cellular responses in plant roots, and increased biocontrol effectively against *R. solani*

TABLE 6 Defense mechanism induced by *Trichoderma* spp. in various crops against different pathogens.

Crop	*Trichoderma* sp.	Pathogens	Defense activities
Beans	*T. atroviride*		Early defense response, secondary metabolites induced intracellular Ca^{2+} variations
Cucumber	*T. asperellum*T203	*Pseudomonas syringae* pv. *lachrymans*	Activated MAPK, expression of *LOX1* (Lipoxygenase 1), *JA* (Jasmonic acid), *PAL1* (Phenylalanine ammonia lyase), *SA* (Salicyclic acid), *ETR1* (Ethylene receptor 1), *CTR1* (Constitutive triple Response 1), *ET* (Ethylene),
Cotton	*T. asperellum*T203	*Pseudomonas syringae* pv. *lachrymans*	PAL, hydroperoxide lyase (HPL), production of phytoalexins (phenolic secondary metabolites), terpenoids, increased peroxidase and chitinase activity
Tomato	*T. harzianum* strain	*Alternaria solani*	Local and systemic resistance; rhizosphere competent
Melon	*T. harzianum, T. longibrachiatum*	*Fusarium oxysporum*	SA and JA signaling pathway, cellulose activated ET and SA pathway, induced peroxidase and chitinase activities
Cotton, rice, *Arabidopsis thaliana*	*Trichoderma* sp.		*Trichoderma*-mediated immunity- reactive oxygen species (ROS), nitric oxide,
Cotton	*T. virens* (G-6, G-11, G6-5)	*R. solani*	Induced terpenoid synthesis *viz.* desoxyhemigossypol (dHG), hemigossypol (HG), gossypol (G)

(Mendoza-Mendoza et al., 2003). The perception of signals transmitted by *Trichoderma* in plants facilitated root colonization by swollenin and enhanced systemic resistance by ceratoplatanin family proteins, MAPK functions, indirectly leading to enhanced root proliferation, better growth and protection of plants. In a study, in model plant *A. thaliana*, root inoculation with *T. virens* and *T. atroviride* reported to increase the level of phytoalexin camalexin along with induction of PR-1a and *LOX2* SA-responsive gene expression (Contreras-Cornejo et al., 2011; Contreras-Cornejo et al., 2016). Similarly, in another study, root inoculation of *A. thaliana* with *T. asperelloides*T203 triggered rapid increase in the expression of transcription factors, that is, *WRKY18*, *WRKY40*, *WRKy60*, and *WRKY33* exerted positive role in JA-mediated defense (Brotman et al., 2013; Abbas et al., 2022).

Field and industrial applications

The pioneering work on *Trichoderma* species on their field application for disease management was initiated during 1970s, which reported success of several *Trichoderma* species *viz.*, *T. harzianum*, *T. hamatum*, and *T. viride* against *Pythium* spp., *F. oxysporum*, *R. solani*, and *Sclerotium rolfsii* (Roy, 1977). Since then, many researchers from the region have worked on improving the efficacy of *Trichoderma* as potential antagonists against many soilborne and foliar plant pathogens and protectors of plants, as shown in Table 7.

In 1976, the discovery of cellulase production efficiency of *T. reesei* QM6a by U.S. army during World War II (Reese, 1976) focused extensive research toward industrial application of enzymes, SMs, antibiotics and protein produced by *Trichoderma* spp. *T. reesei*, being potent cellulase producer were focused for improvement of enzyme cocktail efficiency resulting in the production of biofuel, that is, bioethanol from cellulosic waste material. Achievement of high level of cellulase and hemicellulase production on cellulose, xylan, plant polymers or lactose and high protein secretion capacity up to 100 g/L for 60.00% major cellulase Cel7a (CBHI) and 20.00% Cel6a (CBHII) attributed to agricultural or paper and pulp industry by-products (Buchert et al., 1998). Earlier evidences showed that the expression of heterologous protein by *T. reesei* was exploited for the production of calf chymosin followed by expression of immunologically active antibody fragments for production of several enzymes and proteins (Pentilla, 1998). Safe-scale industrial enzymes produced by *Trichoderma* species are used for brewing processes (β-glucanases), macerating enzymes in fruit juice production (hemicellulases, cellulases, and pectinases), feed additive for livestock farming (xylanases), baking, malting, grain alcohol production (cellulases), and food preservatives (Galante et al., 1998b).

In a study by Waiter et al. (2005), they reported that mutanase enzyme produced by *T. harzianum* can also be used in toothpaste for preventing accumulation of mutan in dental plaque. In wine industry, crude blend preparations of glycosidases and CWDEs produced by *T. reesei* are exploited in wine-making process for improving juice yield, flavor, clarification, filterability, facilitate liberation, and solubilization of phenolic compounds from seeds, skin, and flesh of grapes (Villanueva et al., 2000). Earlier, Perez-Gonzalez et al. (1993) also explored beneficial application of endo-β-1,4-glucanases and xylanases genes from *T. longibrachiatum* and *T. reesei* in wine making by developing recombinant yeast strains for improving free flow, different colors, intensity, stability while ageing, sensorial, and tasting capabilities in Pinot Noir and Ruby Cabernet. In addition, chemical such as 2,4,6-trichloroanisole

TABLE 7 Application of *Trichoderma* species as fungal biocontrol agents against various crop diseases.

Crop	Disease	*Trichoderma* spp.	References
Knol-khol	*Sclerotium w*ilt and rot	*T. harzianum*	Singh et al. (1988)
Soybean	Stem rot (*R. solani*)	*T. harzianum*	Dutta and Das (1999a; 1999b), Dutta et al. (2000); Das et al. (2006)
Rice	Sheath blight (*R. solani*)	*Trichoderma*	Das et al. (1997); Das and Hazarika (2000)
Tomato	Collar rot (*Sclerotium rolfsii*)	*T. harzianum*	Dutta and Das (2002)
Potato	Black scurf (*R. solani*), Bacterial brown rot (*Fusarium, Phoma* spp.)	*T. viride*	Gogoi et al. (2007)
	S. sclerotiorum	*T. harzianum*	Mech (2004)
French bean	White mold (*S. sclerotiorum*); Root knot nematode	*T. harzianum*	Dutta et al. (2008); Dutta et al. (2020)
Beans	Damping-off (*Pythium aphanidermatum*)	*Trichoderma* spp. (T-105)	Kamala and Indira (2011)
Beans	Damping-off, Wilting (*R. solani, Fusarium* spp.)	*T. harzianum*	Kamala and Devi (2012)
Ginger	Rhizome rot (*F. oxysporum* f.sp. *zingiberi*)	*T. viride, T. harzianum*	Khatso and Tiameren Ao (2013)
Etlingera linguiformis	Leaf blight (*Curvularia lunata*var. *aeriai)*	*T. harzianum*	Kithan and Daiho (2014)
Tea gardens	*Pestalotia theae, Fusarium solani*		Naglot et al. (2015)
Tea	Red rust, Poria (*Poria hypobrunea*)	*T. harzianum. T. asperellum*	Dutta et al. (2016)
	Black rot (*Corticumtheae*)	*T. atroviride, T. citrin* (Aerospore)	Thoudam and Dutta (2012)
	Die back	*T. harzianum, T. viride*	Dutta et al. (2016)
Turmeric	Leaf spot (*Colletotrichum capsici*)	*T. harzianum*	Kangjam et al. (2017)
Carrot	*Sclerotinia* Rot (*S. sclerotiorum*)	*T. harzianum*+ chitosan (1%), zinc (0.25%), boron (0.5%)	Bora (2017)
Tomato	Wilt (*F. oxysporum* f.sp. *lycopersici)*	*T. harzianum*	(Zehera et al. 2017a; 2017b)
Lettuce	*R. solanacearum, F. oxysporum* f. sp. *lactucae*	*T. viride*	Khan et al. (2018)
Cowpea	Powdery mildew (*Erysiphe flexuosa*)	*T. harzianum*	(Omomowo et al. 2018)
Ghost pepper	Root rot *(R. solani)*	*Trichoderma* spp.	Koijam and Sinha (2018)
Tomato	Damping off (*Pythium* spp., *R. solani)*	*Trichoderma* spp. (T55, TR122, TR66, TR136)	Biam and Majumder (2019)
Banana	Fusarium wilt (*F. oxysporums*.sp. *cubense*)	*T. reesei* (RMF-13, 25), *T. harzianum* (RMF- 28)	Lalngaihawmi and Bhattacharya (2019)
Tomato	*Fusarium solani*	*T. hamatum*	Kareem and Matloob (2019)
Ground nut	*Colletotrichum* spp	*T. harzianum*	Dutta et al. (2021)
Tomato	Wilt (*F. oxysporum* f.sp. *lycopersici)*	*T. atroviride* and *T. longibrachiatum*	Sallam et al. (2019)
Tomato	Pythium damping off (*Pythium aphanidermatum)*	*T. harzianum* (Th), + *T. asperellum* (Ta), + *T. virens* (Tvs1), + *T. virens* (Tvs2) + *T. virens* (Tvs3)	(Elshahawy and Mohamedy2019)
Ivy gourd	Root knot nematode (*Meloidogyne incognita*)	*T. asperellum*	Sonowal et al. (2020)
Tomato	Wilt (*F. oxysporum* f.sp. *lycopersici)*	*T. harzianum*	Dubey et al. (2020)
Common bean	Root rot (*M. Phaseolina, R. solani*)	*T. atroviride*	El-Benawy et al. (2020)
Cucumber	*Powdery mildew (Podosphaera xanthii)*	*T. harzianum, T. viride*	Sarhan et al. (2020)
Soybean	Anthracnose (*Colletotrichum truncatum)*	*T. koningiopsis*	Silva et al. (2020)
Mungbean	Dry root rot (*M. phaseolina*)	*T. harzianum*	Swehla et al. (2020)
Tomato	Rhizoctonia wilt (*R. solani*)	*T. viride*	Aboelmagd (2021)
Tomato	Wilt (*F. oxysporum* f.sp. *lycopersici)*	*T. harzianum* *T. viride*	Jamil (2021)
Chickpea	Ascochyta blight (*Ascochyta rabiei)*	*T. hamatum* and *T. koningii*	Poveda (2021)
Mungbean	Dry root rot (*Macrophomina phaseolina*)	*T. harzianum*	Swehla et al. (2020)
Tomato	Pythium damping off (*P. aphanidermatum*)	*T. asperellum*	Kumhar et al. (2022)

(Continued)

TABLE 7 Continued

Crop	Disease	*Trichoderma* spp.	References
Potato	Early blight (*Alternaria solani*)	*Trichoderma* spp.	Metz and Hausladen (2022)
Onion	Purple blotch (*Alternaria porri*)	*T. asperellum*	Camacho-Luna et al. (2021)
Banana	Anthracnose (*Colletotrichum musae*)	*T. piluliferum*	Da Costa et al. (2021)
Tomato	Early blight (*Alternaria solani*)	*T. asperellum*	Ajiboye and Sobowale (2022)
Lettuce	Cercospora leaf spot (*C. lactucae-sativae*)	*T. asperellum*	Promwee and Intana (2022)

released by *T. longibrachiatum* and *T. viride* have been involved in cork taint and musty-off odors. In addition, the application of *Trichoderma* sp. in beer industry attributed to exploitation of cellulolytic enzymes and recombinant yeast (*Saccharomyces cerevisiae*) constructed from *egl*1 gene from *T. reesei* for glucan hydrolysis, reduction of β-glucan content, enhanced filterability and beer flavor (Faulds et al., 2008).

Challenges and solutions

Trichoderma species are effective biocontrol agents that can replace chemicals in agriculture. It is essential that microbial biocontrol agents succeed or fail as commercial products (Vurukonda et al., 2018). In order to be successful as a commercial product, it should fulfill farmer's needs such as repeated positive results, realistic prices, easy usage, and long shelf life (Murphy et al., 2018). Nevertheless, a bioproduct with microbial biocontrol agents and/or SMs has the specific problem that its viability decreases during storage as well as its effectiveness for controlling pathogens and pests (Vurukonda et al., 2018). Lack of understanding of biocontrol techniques can result in a reduction in application and requirement of the product. Thus, understanding the practical deployment of *Trichoderma* as microbial biocontrol agents for disease management in agriculture is crucial.

Despite this, it is urgent that communication between researchers and the farmers be improved for efficient biocontrol methods. Therefore, it is crucial to ensure that farmers are aware of the correct use of products for a specific pathogen (Dutta and Das, 2009). There have been many studies investigating *Trichoderma* as efficient microbial biocontrol agents. Most of these research investigations, however, were conducted in lab environments, and their applicability was evaluated in the field. Alternatively, some *Trichoderma* species may be friendly with particular host plants in a narrow range of environmental conditions. The biological efficacy of *Trichoderma* can be affected by changes in agricultural conditions, including soil OM, pH, nutrients, and moisture content (Murphy et al., 2018). An in-depth analysis of field trials will help to develop strains of *Trichoderma* that are friendly with the crops and environment, as most isolates of *Trichoderma* are unique to their hosts and environments. Therefore, it is best to identify the field-related problems, follow up on continuous *in vivo* and *in vitro* laboratory experiments, and find a solution for that particular problem related to *Trichoderma* antagonists against plant pathogens and diseases. It is anticipated that these products will be in higher demand in the future (Vurukonda et al., 2018).

Conclusions and future

In terms of managing plant diseases, *Trichoderma* species could be a viable alternative to synthetic fungicides. *Trichoderma* species is already widely used against plant diseases as a microbial biocontrol agent. To develop successful commercial products of *Trichoderma*, *in vitro* tests under standardized conditions are routinely conducted to screen potential isolates of the fungus. However, field trials under different environmental conditions must also be conducted. Ecological and physical parameters of microbial biocontrol agents along with their environmental effects should be investigated in field experiments. For the commercialization of *Trichoderma* and their use by farmers in remote areas who do not know about them, further research is vital, as this would significantly reduce economic and environmental costs. We may be able to achieve this by using novel molecular technologies such as metagenomics and statistical advances, as well as environmental dynamics. Future work could integrate screening with antagonistic ability validation in greenhouse and field trials, as well as the production of biomass after the commercialization of *Trichoderma* species required to protect global food security. The following are an outline of the broad future outlook.

- Phylogenetic diversity of the genus *Trichoderma* needs to be explored by understanding sexual development; the genetic basis of chlamydospore production and the identification of niche-related genes through combined expression analysis and functional genomics can provide a blue print of *Trichoderma* species.
- As an opportunistic mycoparasite, investigation on induction and regulation of enzyme expression responsible for improvement of biocontrol abilities and development on potential commercial bio-fungicides need to be focused.

- Applications of high-throughput screening of peptaibols produced by *Trichoderma* provide extended scope of research in bio-medical applications beyond agriculture.
- Effort should also be made to identify plant receptors for *Trichoderma* elicitors and effectors triggering defense mechanisms in order to reprogramme host's genetic machinery for understanding interaction of avirulent plant symbionts and host defense.
- Extensive studies regarding identification of diverse physiological traits to upgrade industrial application of *Trichoderma* for production of antibiotics, enzymes and biofuels as an alternative strategy.

Author contributions

PD: Original Draft Preparation review and edit, LD: review and edit, AP: Wrote existing crop management strategies, volatile and not volatile metabolites, challenges and future prospects, review and edit. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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