Chapter 13
Trichoderma as Biostimulant: Factors Responsible for Plant Growth Promotion

Nibha Gupta

Abstract *Trichoderma* has detonated as biostimulant and mycofungicide for improvement of economically important plants of different agriculture, forestry, horticulture sectors, in regard to their protection against abiotic and biotic stress as well as proper growth, development, and productivity. *Trichoderma* plays a vital role by enhancing and modifying the root surface so that plants can do better nutrient uptake and mobilize minerals fast. It can enhance the mineral content in the vicinity of the rhizosphere through solubilization of bound forms, significantly facilitating the plant growth by releasing growth hormones. It is evident that *Trichoderma* induces systemic resistance in plants against various pathogens with the help of various volatile and nonvolatile metabolites, siderohores, enzymes, antioxidants, and polysaccharides. On the one hand, the fungus creates rhizosphere competence, and on the other hand, efficiently eases the unfavorable effect of various environmental stress through antioxidant production and physiological modulation in plants. Recently, molecular and biochemical dialogs between *Trichoderma* and host plants have been studied thoroughly and envisaged the significance of gene–gene interaction corroborate with protein–protein interaction among them. Though the *Trichoderma* and genesis of its benefits have been studied, described, and cited comprehensively, the content of the chapter emphasizes the molecular, physiological, biochemical, and morphological interaction of *Trichoderma* and enlighten the compact and composed picture of its direct and indirect benefit to the host plants.

Keywords *Trichoderma* · Secondary metabolism · Antagonism · Biofungicide

N. Gupta (✉)
Plant Pathology and Microbiology Division, Regional Plant Resource Centre, Bhubaneswar, Odisha, India

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13.1 Introduction

The widely accepted definition of plant biostimulant is that the “plant biostimulant is applied to improve crop production and nutritional quality of agri food products. They are used in agricultural management practices aimed at reducing chemical input, increasing productivity and recovering natural equilibrium in agro ecosystem (EBIC 2013; du Jardin 2015). ”The plant stimulants like organic and inorganic natural substances and beneficial microbes are being used for the growth promotion of economically important plants and proved sustainable and eco-friendly. A plant biostimulant is any substance or microorganism applied to plants with the aim to enhance nutrition efficiency, abiotic stress tolerance, and/or crop quality traits, regardless of its nutrients content. Commercial products containing mixtures of such substances and/or microorganisms are also designated as plant stimulants (du Jardin 2015). Plant biostimulants can be categorized into two categories, i.e., biochemical which includes humic and fulvic acids, protein hydrolysates and other N-containing compounds, seaweed extracts and botanicals, chitosan and other biopolymers, and inorganic compounds; whereas biological stimulants involve the role of obligate symbiont mycorrhiza, endosymbionts, and plant growth-promoting rhizobacteria (Colla et al. 2014; Deliopoulos et al. 2010; Hadwiger 2013; Halpern et al. 2015; Katiyar et al. 2015; Khan et al. 2009; Pilon-Smits et al. 2009; Shanmugaiah et al. 2009).

Trichoderma is free-living, green spored ascomycetes, opportunist, avirulent plant symbiont, ubiquitous habitants of soil, water, rhizosphere, and phyllosphere in tropical and temperate environment (Harman et al. 2004b; Howell 2003). It is more prevalent due to its attacking nature on other fungi. Though free living, they occasionally form endophytic associations with plant roots and may provide a range of benefits to their hosts (Colla et al. 2014; Cummings et al. 2016; Hermosa et al. 2012; Shoresh et al. 2010). The fungus is mycoparasite, antagonize other fungi, and utilize their nutrients. *Trichoderma* has gained importance as a microbial plant biostimulant in agriculture and horticulture due to its diverse applications as potential biological disease control agents, source of enzymes and health care medicines, and useful for bioremediation (Cristea et al. 2017; Woo et al. 2014). It is also present as one of the components in various biopesticides, biofertilizers, growth promoters, and biostimulants of commercial nature (Fiorentino et al. 2018; López-Bucio et al. 2015; Rao et al. 2016).

The prime factors behind plant growth promotion are categorized into three groups: (1) metabolite production (antibiotics, HCN, siderophores), (2) biostimulating phytohormone production (auxin, cytokinin, gibberaline), (3) biofertilizing potential through mineral solubilization or nitrogen fixation, and (4) bioprotection through bioactive secondary metabolites, antibiotics, siderophores (Hermosa et al. 2012; Puyam 2016; Van Loon 2007). The plant growth promotion is directly exhibited in terms of increased seed germination, in above- and below-ground plant parts, chlorophyll content and yield size and/or number of flowers and/or fruits (Mendoza-Mendoza et al. 2018). Indirectly, the modification of root increase in absorption area, thereby improving the nutrient uptake and transport attributed to increase in biomass (Samolski et al. 2012). *Trichoderma* is endowed with these plant growth-promoting properties and significantly facilitates plant growth and development through numerous mechanisms including solubilization of soil nutrients increasing the nutrient efficacy and recycling releasing plant growth stimulatory agent and induced systemic resistance (Adams et al. 2007; Cai et al. 2013; Cornejo et al. 2009; Kapri and Tewari 2011; Li et al. 2015; Singh et al. 2015; Vinale et al. 2006).

The fungus is also very competent, interactive, and effective when co-inoculated with other beneficial microbes of agriculture importance (Colla et al. 2015; Kumar et al. 2009; Rani et al. 1998a, b; Singh and Kumar 2013; Vázquez et al. 2000; Zhuang et al. 2019). On account of plant growth promotion and development, *Trichoderma* is now being a major component of commercial biofertilizer products that contain microbial consortium beneficial for different crops for protecting seeds and strengthening seedlings, development of good root formation and establishment, and finally fully grown crop. *Trichoderma* is eco-friendly, leaves no chemical residue, reduces chemical fungicides, crop losses, and increases yields, is compatible with many crops and antagonistic toward many pathogenic fungi, cost-effective production and usage. It is evident that *Trichoderma* extends other indirect and multifarious benefits to different plant groups besides protection from plant pathogens (Sala et al. 2007; Singh et al. 2004). *Trichoderma* inhabits at the root and rhizosphere helps in decomposition and absorption of native organic materials. It can utilize wide-spectrum substrates and confer tough competition to other microbial rhizospheric associates. It elicits systemic resistance against pathogens. Root colonization by *Trichoderma* enhances plant root growth and nutrient and water uptake, increasing resistance to drought and crop productivity. The factors responsible for the intrinsic biological properties of *Trichoderma* that stimulate the positive effects on plant growth and development, enhancing their growth potential and nutritional uptake, fertilizer use efficiency, seed germination phenomenon, and stress tolerance are being reviewed here.

13.1.1 Modification in Rhizosphere and Roots

Rhizosphere is a composite system, acts as a plant–soil interface, is enriched with minerals, metabolites, gaseous compounds, and considered as a habitat of the microbiome, a variety of microorganisms belonging to nonsymbiotic and free-living, symbiotic, entophytic, parasitic, commensal group. Incidence of microbiome of different morphotypes, their biological properties and functions certainly depend upon the associated plant species, soil types and quality, ecological niche, and microhabitat. Externally added chemical fertilizers, pesticides, and biofertilizers also influence the biological role and functions of the existing microbiome either negatively or positively (Berendsen et al. 2012; Li et al. 2015; Fiorentino et al. 2018; Vázquez et al. 2000). It may affect the eukaryotic and prokaryotic population differently depending upon the host plants, habitat, and seasons under which applications are being carried out. It is known that varied crops and their metabolites are the prime components and can strongly affect soil microbial communities and dynamics (Larkin 2008).

Trichoderma is gaining importance due to its high activity in the edaphic, phyllosphere, and rhizosphere environment and has been very successfully used as mycofungicides, biofertilizers, and plant growth promoters. Their ability to colonize and grow in association with plant roots known as "Rhizosphere competence" is also one of the potential factors behind their role in plant growth promotion (Kaewchai et al. 2009). They are excellent competitors in the rhizosphere, have a capacity to modify the rhizosphere, are tolerant or resistant to soil stress or unfavorable conditions. They compete for the exudates produced by seedling, thereby restricting the growth of phytopathogens (Howell 2003). Root exudates of plants sometimes stimulate and attract *Trichoderma* and other microbial rhizosphere associates thereby helping in plant growth development and promotion under stress conditions also (Kandasamy et al. 2010; Lombardi et al. 2018). *Trichoderma* also plays an important role as decomposers, indirectly supporting root hair growth and allowing plants to take up more water and nutrient available distantly as their roots grow deeper into the soil.

Rhizospheric microflora are mostly influenced by root and soil composition and they establish beneficial interaction at the biochemical, physiological, or molecular level with co-microbiota of pathogenic nature or else affect the root architecture (Harman 2006; Hermosa et al. 2012). The carbon sources released through root exudates stimulate the growth and proliferation of several microbes including *Trichoderma* sp. which colonizes the root system and induces beneficial effects in plants (More et al. 2013; Fernandez et al. 2017; Vargas et al. 2009). Some *Trichoderma* strains do have rhizosphere competence and show a direct effect on plants, enhance their growth potential and nutrient uptake, fertilizer use efficiency, percentage and rate of seed germination, and stimulation of plant defense against biotic and abiotic stress (Shoresh et al. 2010).

Trichoderma is now considered as multi-tasked endophytic fungi of the host roots, as they are capable of residing in the root intracellular space, penetrating and colonizing the plant roots, especially intracellular space (Harman et al. 2004a; Harman 2011; Yedidia et al. 2001). The interaction of cysteine-rich cell wall protein is responsible for fungal adherence which has a vital role in lateral growth, air formation, and elongation. Such a phenomenon also imparts enhancing the root surface, indirectly helping in nutrient uptake and translocation in the shoots, thereby helping in enhancement in plant biomass and growth. As an example, *T. harzianum* is a most effective fungus and is able to colonize roots of most of the plant species, improve the rooting process, helpful in the establishment of plants in nursery conditions and thereby enhances the growth of several vegetables and floriculture crops (Chagas et al. 2017; MacKenzie and Starman 1995). Its inoculation influences the modification of root structure and stimulates the lateral root development in associated plants (Bjorkman et al. 1998; Cornejo et al. 2009). *Trichoderma* spp. produce and modulate hormonal signals in order to facilitate the colonization of roots' growth which, in turn, facilitates colonization by increasing the available surface area. The fungus produces auxins (indol 3 acetic ac (IAA), Indol-3-acetaldehyde (IAAld), Indol-3-ethanol (IEt.) (Casimiro et al. 2001; Reed et al. 1998). Manipulation of root system architecture (RSA) which involves the growth of lateral (LR) and adventitious root and root hairs (RH) formation is one important factor to regulate the effects of biotic and abiotic factors on plant growth and yield (Casimiro et al. 2003; Cornejo et al. 2014; López-Bucio et al. 2003, 2005). Such type of root growth-promoting behavior of *Trichoderma* has already been established under laboratory and field experiments done on various crop plants (Bal and Altintas 2006; Naseby et al. 2000; Yadav et al. 2009).

13.1.2 Bioaccumulation of Useful Metabolites in Rhizosphere System

Trichoderma spp. confer enhancement of growth and development of host plants and other biological associates. The fungus acts as a protective shield against adverse conditions like disease state, environmental conditions like high temperature, cold, drought, metals, acidic, salt, and alkaline conditions. These stress environments are managed by various metabolic processes and their product including enzymes, secondary metabolites, bioleaching, and mineral solubilization (Keller et al. 2005; Keller 2019; Manganiello et al. 2018).

Plant–microbe interaction is governed through communicating signals exerted by biomolecules (secondary metabolites like peptides, peptaibols, pyrones, siderophores, and volatile and nonvolatile metabolites) produced by rhizosphere inhabitants (Vinale et al. 2008a, b; Woo et al. 2014). *Trichoderma* also produces a variety of compound and metabolites which has a different function and potential application in different agriculture, biotechnology, and health care sectors (Singh et al. 2004). *Trichoderma* spp. produces over 250 metabolic products including cell wall degrading enzymes, peptides, secondary metabolites, and other proteins (Lombardi et al. 2018; Salwan et al. 2019; Sarrocco et al. 2009; Harman et al. 2004a; Sivasithamparam and Ghisalberti 1998; Vinale et al. 2009a, b, 2014). The plant growth-promoting effects are attributed to the role of *Trichoderma* alone and/or synergistic effect of other microbial associates and their induced metabolism which exhibited in the form of protection against plant pathogens, mineral solubilization capability, production of siderophores and secondary metabolites (Cornejo et al. 2014; Vieira et al. 2017). Besides plant growth-promoting activity, numerous evidence are available on the involvement of secondary metabolites in the antagonistic activity of *Trichoderma* against a considerable number of plant pathogens (Chet 1990; Kleifeld and Chet 1992; Inbar et al. 1994; Vinale et al. 2009a, b; Zeilinger et al. 2016).

13.1.3 Siderophores

Iron acts as a cofactor of numerous enzymes and an essential nutrient for the growth of plants and other microorganisms. In the aerobic environment (with oxygen and neutral pH), iron exists mainly as Fe3+ and tends to form insoluble ferric oxide, making it unavailable for root absorption and microbial growth (Miethke 2013). Fungal siderophores have been involved in transporting and storage of iron, competing for iron in natural soil, indirectly suppressing the plant pathogen by limiting the metabolism of iron to plants. *Trichoderma* secretes siderophore, an iron-chelating compound which binds with insoluble iron (FeIII) and converts to the soluble form (FeII) for plant absorption and inhibits the growth of plant pathogens by depriving them of iron sources (Howell 2003).

13.1.4 Volatile Compounds

Trichoderma produces volatile organic compounds (VoC) which are of low molecular mass, low boiling point, low polarity, and chemically these are hydrocarbon, aromatic, amine thiols and terpenes and now reported to mediate the plant growth and development in agricultural crops (Bitas et al. 2013; Hung et al. 2013; Junker and Tholl 2013; Korpi et al. 2009; Lee et al. 2015; Lee et al. 2016; Lemfack et al. 2014; Schulz and Dickschat 2007; Vinale et al. 2008b). The production of VoC is not only species-specific but also influenced by soil habitat, soil nutritional content, microbial composition, biomass, and environmental conditions (Insam and Seewald 2010; Lee et al. 2015; McNeal and Herbert 2009). Meena et al. (2017) reported the positive response of volatile compounds from *T. harzianum* for *Alternaria alternata*. As indicated, an auxin-like effect was observed in etiolated stems treated with harzianolide and 6-pentyl-a-pyrone, the major VOCs produced by different *Trichoderma* strains (Vinale et al. 2008a). This compound is important for multiple actions involving fungal mycelium growth inhibition, germination of spores, and pigmentation of plant pathogenic fungi (Salwan et al. 2019).

Many *Trichoderma* species are known as biofungicides and biofertilizers and helpful in crop growth enhancement. *Trichoderma* spp. are producers of many small metabolites having antimicrobial and anticancer properties (Cordovez et al. 2018; Tukhbatova et al. 2014). Nonvolatile metabolites from *Trichoderma* are summarized by Meng-Fei et al. (2019). He described 329 nonvolatile compounds from 20 known species and other unidentified species. Fungi produce a vast range of secondary metabolites and they are known for their capacity to secrete high levels of enzyme, antibiotics, vitamin, polysaccharide, and organic acids (Meyer 2008). Many reports are coming up on the antimicrobial compounds isolated from *Trichoderma* (Li et al. 2016). Zhang et al. (2019) reviewed novel and bioactive metabolites from endophytes including *Trichoderma* sp. They isolated two new isocoumarin and many other compounds having antibacterial activity.

13.1.5 Plant Growth Regulator

Fungi produce a variety of essential phytohormone and natural growth inducers like gibberellic acid and auxin which are crucial in maintaining normal growth and metabolic activity (Cornejo et al. 2009; Hermosa et al. 2012). Such fungi have a critical impact on the physiological status and adaptation of host plants that they colonize. IAA stimulates the higher production of longer roots with root hairs and root laterals which are finally involved in nutrient uptake. It also regulates the cell elongation and numbers which ultimately result in better growth and development. *Trichoderma* spp. are also reported to synthesize and produce IAA and exhibit plant growth promotion efficacy in many agricultural crops in field conditions (Guey et al. 2018; Kumar et al. 2017; França et al. 2017). The hormonal signal perceived by roots resultantly grow well, indirectly enhances nutrient and water uptake and ultimately plant growth. *Trichoderma* species, especially *T. virens* and *T. atroviride*, exhibited characteristic auxin-related phenotype that promoted the root growth, enhanced nutrient and water uptake, and finally increased biomass production (Kumar et al. 2017; Maria et al. 2017).

13.2 Alleviation of Abiotic Stress

13.2.1 Impact on Physiological Response of Plants

An alternative strategy to improve plant tolerance to stress is the use of plant growth-promoting microbes. *Trichoderma* species is a multitasker and rhizospheric salient biocomponent having beneficial effects on plant growth and enhancing resistance to both biotic and abiotic stress. They are known to produce different kinds of enzymes, elicit defense response**,** a fine metabolic regulation, thereby qualifying to combat the environmental changes and nutrient limitations (Mastouri et al. 2010; Schuster and Schmoll 2010; Singh et al. 2014).

The growth-promoting properties of *Trichoderma* inoculations on radish, pepper, cucumber, tomato, rice, wheat, etc. were demonstrated well (Baker et al. 1984; Chang et al. 1986; Harman 2000). It was thought to be due to increased root development and crop yield, the proliferation of secondary roots, and seedling biomass and foliar area. However, recent literature says it is due to the different physiological mechanisms responsible for the enhancement in plant growth (Doni et al. 2014). Application of *Trichoderma* increased photosynthetic rate, stomatal conductance, water use efficiency, transpiration, internal CO_2 content catalase and superoxide dismutase activities, proline content in treated plants grown in stress environment (Yasmeen and Siddiqui 2017). Mastouri et al. (2010) observed that the treatment of seed with *T. harzianum* accelerates seed germination, increases seedling vigor and ameliorates, water, osmotic, salinity, chilling and heat stress by inducing physiological protection in plants against oxidative damage. Ripa et al. (2019)

assessed the plant growth-promoting and abiotic stress tolerance property of wheat endophytic fungi including *Trichoderma* strains which exhibited salt, heavy metal and drought tolerance at a high level and also exhibited resistance to all tested antibiotic.

13.2.2 Nutritional Starvation

Competition for substrates is the most important factor for fungi as is competition for light in the case of the evolution of plants (Garrette 1956). Microbiome competition also causes nutritional starvation and ultimate defeat of weak associates (Benitez et al. 2004). In a similar way, the microorganisms growing in the vicinity of *Trichoderma* strains encounter the nutrient limitation and rhizospheric colonization. Root exudates and rhizosphere are rich sources of nutrients such as sugar, amino acids, iron, vitamins, organic acids, etc. Competition for carbon is an effective mode not only in *Trichoderma* but also in some other fungi such as strains of *Rhizoctonia solani* and *F. oxysporum* (Alabouvette et al. 2009; Sarrocco et al. 2009).

13.2.3 Salinity Tolerance

Salinity stress affects negatively on plant growth and causes ion toxicity, osmotic stress, oxidative stress, and nutrient deficiency which result in poor growth, reduction in yield, and nutritional deficiency (Chinnusamy et al. 2006). One of the phytohormone ethylenes and its direct precursor ACC is induced by salinity and many abiotic stressed imposed during host–pathogen interaction (Boller 1991; Gailīte et al. 2005). Indole acetic acid and ACC deaminase production by *Trichoderma* sp. was found to be an important factor behind enhanced tolerance toward salt stress when treated with wheat seedlings (Zhang et al. 2019). Besides GA and IAA, antioxidant compounds produced by these fungi especially *T. longibraciatum* are also known to alleviate the negative effects of salinity on many agricultural crops (Aban et al. 2017; Ahmad et al. 2010a, b; Mishra et al. 2015; Rawat et al. 2011). Application of *Trichoderma* in plants enhances the IAA levels reflected in the form of root development, enhanced level of abscisic acid, L proline, ascorbic acid and osmoprotective status, Na elimination through root exudates of plants under salt stress (Cornejo et al. 2014; Rawat et al. 2013). Stress tolerance is also induced due to the synthesis of phenol diacylglycerol, sterol esters, nonesterified fatty acid, and enzymatic antioxidants like SOD superoxide dismutase, catalase, peroxidase, ascorbate peroxidase glutathione reductase (Ahmad et al. 2015; Hashem et al. 2014).

Antioxidative defense mechanisms also play a vital role in mitigating salt stress in many plants. Prolonged salinity stress is responsible for oxidative stress that generates reactive oxygen species (ROS) deleterious to biological molecules (Ahmad et al.

2010a, b). *Trichoderma* induces resistance in host plants against NaCl stress through improved uptake of essential elements and modulation of osmolytes. Fu et al. (2017) studied the alleviation of the effect of *Trichoderma asperellum* on active oxygen production in maize seedling under saline-alkali stress condition. It has been reported that *Trichoderma harzianum*-inoculated plants restore the pigment content, enhances the proline content, plant growth, and development under stress conditions.

13.2.4 Drought Stress

Plant growth and development have also been affected by drought conditions. Plant growth-promoting microbes play a vital role in the alleviation of such stress in plants. Such microbial inoculants impart drought tolerance by producing various metabolites and hormones (Vurukonda et al. 2016). One of the responsible factors behind drought tolerance of plants under *Trichoderma* association is increased secondary metabolites and proline content. Under drought conditions, plant growth and physiological parameters decline as per the observation made on experimental tomato plants (AlwhibiMonaa et al. 2017). The *Trichoderma*-treated plants showed increased root and shoot growth and chlorophyll pigment under drought stress condition. Pectin and total protein content was also increased. An obvious increase in phenol and flavonoid content was observed. It also maintained a high level of growth regulators like indole acetic acid, indole butyric acid, and gibberellic acid under drought stress.

Trichoderma inoculations delayed the drought-induced physiological and biochemical changes in rice, wheat, and tomato (AlwhibiMonaa et al. 2017; Shukla et al. 2012, 2015; Rawat et al. 2016). The fungal treatment enhanced root growth, improved acquisition and storage of water in rice and phenolics, decreased stress-induced metabolites, delayed the stomatal conductance, net photosynthesis, proline, MDA and hydrogen peroxide content increase in phenolics. *Trichoderma* seed priming also reduces the accumulation of toxic reactive oxygen species (ROS) and resultantly root vigor enhances. The production of stress-related enzymes viz., superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), has been reported in rice under drought condition.

During *Trichoderma* and host plant association and interaction, the proteome and transcriptome of host plant change due to the fungal metabolite and colonization. Thus, the fungi reprogram plant gene expression resulting in alleviation of plant response to their environment (Bae et al. 2011). Alleviation of damage by reactive oxygen species (ROS) water use efficiency and secretion of phytohormonal analog are the three mechanisms employed by the fungi in enhancing plant growth under drought stress. It has been assumed that since the interaction between the plant and the fungus happens largely at the rhizosphere, such mechanism is probably connected to an increase in water absorption effectiveness due to the increased root capacity and hence increased water absorption (Mastouri et al. 2012).

13.2.5 Heat and Cold Tolerance

Low temperature is a major environmental factor limiting plant growth and development in high altitudes. In response to cold stress, plants regulate their physiological, biochemical, and molecular phenomenon like cell membrane permeability, photosynthesis, water absorption, and content and osmoregulation. *Trichoderma* also moderates the low-temperature stress in plants and efficiently alleviate the adverse effects of cold stress leading to enhancement in photosynthetic and growth rates (Ghorbanpour et al. 2018). Reduction in lipid peroxidation rate and electrolyte leakage and an increase in leaf water content and proline accumulation could also be observed as an effect of *Trichoderma* applications. Some *Trichoderma* spp. are isolated from glacial sites of the Indian Himalayan region and reported to be cold-tolerant antifungal strains (Ghildiyal and Pandey 2008). Such types of fungal inoculants as biological agents are useful for field applications in colder regions. Poosapati et al. (2014) studied high temperature-tolerant T isolate with antagonistic activity agent *Sclerotium rolfsii*. This strain was highly tolerant to heat showed at 52 C *T. asperellum*.

13.2.6 Metal Tolerance

Heavy metal contamination of soil and water has become an important environmental issue as it affects different microbiota drastically. Some filamentous fungi pave the way through bioremediation of heavy metal contamination. One of them is *Trichoderma* species which has shown tolerance to a range of toxicants and Cu, Cd, As, Zn heavy metal in vivo (Adams et al. 2007; Ezzi and Lynch 2005; Harman et al. 2004b; Hoseinzadeh et al. 2017; Karcprzak and Malina 2005; Maurya et al. 2019). Due to metal tolerance behavior, *Trichoderma* spp. became a dominant organism in some polluted environments and may play an important role in eco-friendly metal removal technology (Karcprzak and Malina 2005; Nongmaithem et al. 2016). *Trichoderma* cell wall revealed the presence of hydroxyl group and amide group that play a vital role in bioabsorption of heavy metals (Bishnoi et al. 2007). Such a metal tolerance trait of these fungal strains makes them effective cleaning agents of heavy metal polluted environments (Oladipo et al. 2018). Field application of these types of fungal strains has also exhibited a positive effect on translocation index and bioaccumulation factors besides enhancement in biomass and C, N. P, and solubility of heavy metal as compared to uninoculated plants (Nongmaithem et al. 2016). Babu et al. (2014) evaluated *Trichoderma virens*, a heavy metal-tolerant and plant growth-promoting fungus for remediation and bioenergy crop production on mining soil. The fungus tolerates heavy metal and reduces residual concentration in the soil thereby promoting phytostabilization in contaminated soil. The mycoremediation properties of *Trichoderma longibrachiatum* and its protective role for lead-induced oxidative stress in plants has also been studied (Devi et al. 2017). Bioremediation using efficient fungi like *Trichoderma virens*, *T. harzianum*, T. *saturnisporum*, and *T. gamsii* can help in eliminating heavy metal contaminants of wastewater in mining industries (Tansengco et al. 2018).

13.3 Enhancement in Mineral Solubilization and Uptake

Phosphorus is present in the soil in huge amounts but it a major plant growth-limiting nutrient because most of its amount is easily fixed in the soil in the form of insoluble phosphate. Other elements like Fe, Mn, Cu, and Zn which are very important in many physiological and metabolic processes are also not available in active forms. As a result, their deficiency affects the production, yield, and quality of agriculture production (Altomare et al. 1999; Lei and Zhang 2015; Lopaz et al. 2015). The mineral solubilization ability of *Trichoderma* is also one of the important biostimulating factors behind plant growth and development. Soil is a composite system of living and nonliving plethora of biological and nonbiological components including soluble and bound forms of different minerals (Rawat and Tewari 2005). Mineralization of different soluble and insoluble mineral is a dynamic process and greatly influenced by soil pH and extracellular secondary metabolites and enzymes which regulate the solubilization of minerals and uptake by plant system. It has been reported that *Trichoderma* solubilizes bound minerals through lowering the soil pH by releasing organic acid, gluconic acid, lactic acid, citric acid, tartaric acid, succinic acid, and fumaric acid extracellularly and allow the dissolution of phosphate as well as macro- and micronutrient, Fe, Mg, Mn, which are necessary for plant metabolism (Cao et al. 2008; Harman 2006). Besides, acidification of the surrounding media, *Trichoderma* solubilize minerals phytate, Fe2O3, CuO and metallic Zn through chelation by siderphores, reduce by ferric reduction, and hydrolysis by phytase (Li et al. 2015).

The mineral solubilization properties and activity of *Trichoderma* are species specific and environmentally regulated. *Trichoderma* produces organic acid to solubilize insoluble tricalcium phosphate at high pH stress whereas drought stress induces the production of alkaline phosphate enzymes. This beneficial activity of *Trichoderma* was evaluated and confirmed in many crop plants like rice, groundnut, tomato, etc. (Chagas et al. 2015; Singh et al. 2014; Shukla and Vyas 2014). Many species of *Trichoderma* are endowed with dual quality as hormone producer aided with mineral solubilizing potential makes them more useful mycopesticides for extensive commercial use in agriculture (Vinale et al. 2008b; Resende et al. 2014).

13.4 Enhancement in Plant Defense and Immune Stimulation

13.4.1 Mycoparasitism Related Metabolites

Trichoderma involves mycoparasitism for antagonistic behavior toward plant pathogens. The mycoparasitic event involves chemotropic growth, host recognition, coiling, and appressoria formation, secretion of hydrolytic enzymes like glucanases, chitinases and proteases, penetrations of the hyphae and lysis of the host cell (Harman et al. 2004a; Kumar et al. 2016). There are at least 20–30 genes, proteins, and other metabolites that are directly involved in this interaction. The functions of different glucanases and chitinases in the process of mycoparasitism are well studied from *Trichoderma* spp. using gene-for-gene experiments. Different types of *Trichoderma* produce mycoparasitin-related compounds. *T. harzianum* produces anthraquinone which enhances the number of coils. *Trichoderma atroviride*, *T. virens, T. reesei* produces ferricrocin a siderophors and key metabolite for iron chelation. There is a report on the inhibition of glucon biosynthesis by *T. longibrachiale*. Many *Trichoderma* species produce hydrolytic enzymes like glucanases, chitinases, endopolygalacturonase which hydrolase fungal cell wall (Daguerre et al. 2014).

13.4.2 Bioactive Metabolites

Trichoderma species are classified as microbial biological control agents “MBCA” (Woo et al. 2014). Numerous *Trichoderma* are successful MBCA of various plant pathogens. Initially, the biopesticidal properties of *Trichoderma* were considered as prime benefits, and eventually, these MBCAs are demonstrated to be effective biofertilizers, biostimulants, and bioenhancers of crop resistance to various biotic and abiotic stresses (Fontenelle et al. 2011). *Trichoderma* species are common in soil and root ecosystem, ubiquitous saprobes and have been tested as biological control agents against a wide range of pathogenic fungi like *Alternaria, Botrytis, Botryosphaeria, Dematophora, Fusarium, Lasiodiploidia, Rhizoctonia, Pythium, Phytophthora, Sclerotium*, and nematodes (Abdel Fattah et al. 2007; Manganiello et al. 2018; Singh et al. 2008). Various diseases controlled by *Trichoderma* spp. are sheath blight, bakanae, leaf blight, loose smut, wilt, root rot, ring rot, dieback, crown, black scurf, web blight of different crops like rice, wheat, chickpea, pigeon pea, apple, guava, chilli, tomato, potato, beans, etc. (Puyam 2016). Commercial formulation of *T. harzianum*, *T. polysporus, T koningii* is now available as brand names in aboard like Binab T, Plant Shield, Antagen, Promot plus, etc. In our country, most of the products are formulated from *T. viride* and *T. harzianum* on commercial productions like Antagen TV, Trichostar, Gliostar, Monitor, Birdene, Biofil, Ecofit, Trichoguard, Bicon, etc. (Puyam 2016).

Trichoderma is accredited with many biological control credentials like antibiosis, antagonisms, mycoparasitism, and induction of plant defense response. Rhizosphere interaction between plant and microbes involves communication between them through biomolecules synthesized inside and active extracellularly. The interactive host–microbe relationship establishes and is dependent upon their mutual molecular dialogs (Cornejo et al. 2014). Host plants have systemic acquire resistance or induced systemic resistance which is dependent upon the production of salicyclic acid, jasmonic acid, and ethylene (Meena et al. 2017; Yuan et al. 2019). The synthesis and production of signaling molecule like hydrogen peroxide, nitric oxide, and salicylic acid are activated by *Trichoderma* thereby inducing plant defense and mycoparasitism (Nawrocka et al. 2019). Such types of biocontrol activity is due to well-coordinated transcriptomic, proteomic, and metabolomic responses of plants in the presence of *Trichoderma* in its rhizosphere vicinity (Mukherjee et al. 2012). Production of phenolic compounds like hydroxyl benzoic acid, cinnamic acid, catechins, flavonols, flavones, flavanone also induces the systemic defense response (Nawrocka et al. 2019).

Trichoderma and its direct interaction with plant pathogens involve cell wall degrading substances including antibiotics (Benitez et al. 2004; Harman et al. 2004b; Kredics et al. 2001). *Trichoderma* produces a variety of antibiotics like trichokonins, glovinin, gliotoxin, viridian, pyrones, and reveal antibiosis against plant fungal pathogen (Howell 2003; Harman et al. 2004a). The beneficial interaction of *Trichoderma* with plants depends upon signal exchange among them and mediated by effector proteins known as hydrophobin that alter the host structure and help in the establishment of symbiotic relationship (Guzmán-G et al. 2017). To date 317 peptaibols are reported, and among them, 190 are synthesized by *Trichoderma* (Whitmore and Wallace 2004). These are characterized by the presence of unusual amino acid alpha aminoisobutyric acid isovalin, imino acid hydroxyproline (Chugh and Wallace 2001; Mukherjee et al. 2011). The production of cell wall degrading enzymes such as chitinase, cellulose protease, have a vital role in the inhibition of fungal pathogen and induced resistance of host plant system (El-Katathy et al. 2001; Gajera et al. 2012; Vinale et al. 2008b).

Trichoderma produces many antibiotics which have inhibitory action against many plant pathogens like *Rhizoctonia, Pythium, Gaeumannomyces, Candida, Penicillium, Aspergillus, Cryptococus, Sclerotium, Staphylococcus,* and *Mycena.* It is known that antimicrobial activity is species-specific and it produces specific metabolites against specific individual organisms. Besides antifungal properties, it produces protein inhibitors, antibacterial, antiviral, immunosuppressor compounds (Cornejo et al. 2014).

Trichoderma produces such types of compounds which alter the fungal growth of plant pathogen. Steroidal compounds viridian produced by *T. koningii, T. virens, T. viride* alter the spore germination of Botrytis, Colletotrichum, and Fusarium sp. Many *Trichoderma* sp. produces Trichothecene (Trichodermin) inhibiting the protein synthesis. *T. harzianum* produced by phenyl ethanol inhibits aflatoxin production by Aspergillus flavus. Disruption of cell wall cellulose is made by swollenin produced by *Trichoderma* (Andberg et al. 2015; Eibinger et al. 2016).

Fungal oligosaccharides are now focused on the biological management of crop diseases by elicitation of defense response (Boregowda et al. 2017). Crude oligosaccharide extracted from *Trichoderma* spp. enhanced the disease protection ability in pearl millet when they followed the seed priming process. Oligomers of chitin and glucan are fungal elicitors generated from the fungal cell wall and are measured as primary signals responsible for the initiation of plant resistance reactions. It is well known that several oligosaccharides of fungal cell wall components stimulate phytoalexin secretion and lignin and callose formation in plants (Kauss et al. 1989; Lattanzio et al. 2006).

13.5 Conclusions

Trichoderma resides mostly in soil and infrequently occurred as endophyte within host plants of agriculture, forestry, and horticulture importance. This fungus is also known as mycofungicide and endowed with many intrinsic properties like fast growth and development, inhibiting a broad spectrum of fungal disease, diversity of control mechanism, rhizosphere competence, tolerant or resistant to fungicides, stress tolerance, nutrient solubilization and mobilization and antagonism, etc. Such intrinsic nature of growth, biochemical, physiological, and metabolic behavior makes the fungus more beneficial for the growth and development of associated host plants. Factors responsible for the biostimulating characteristics of *Trichoderma* which includes morphological and microbial modification of host plants, bioaccumulation of metabolites, biotic and abiotic stress tolerance, nutrient solubilization, uptake and mobilization, biocontrol properties have been elaborated in detail. It is evident that the beneficial activity of *Trichoderma* is species-specific, and comprehensive search of this group of fungi from different ecological niche and agroclimatic zones is required as many more tropical regions remain to be unexplored in this regard.

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