Chapter 3
Beneficial Effects of *Trichoderma* on Plant–Pathogen Interactions: Understanding Mechanisms Underlying Genes

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Abstract *Trichoderma* is a genus of asexually reproducing filamentous fungi found in various ecosystems. It is among the utmost prevalent fungal genera commercially obtainable as a plant growth-promoting fungi (PGPF) and biocontrol agent. The biocontrol actions of *Trichoderma* are centered on the stimulation of various mechanisms such as competition for nutrients and space, mycoparasitism, alteration of the ecological conditions, antibiosis, and plant defensive mechanisms. Therefore, these fungi are commercially used in biocontrol of plant pathogens substituting the synthetic pesticides. The beneficial organism's genes and/or its products contain metabolites that reduce the harmful effects of plant pathogens and promote progressive responses in the plant. Certain genes have significant roles in the biocontrol process and are known as the biocontrol genes. These genes signal the secretion of enzymes and proteins that damage the plant pathogens. Some *Trichoderma* genes are also helpful in the control of different plant pathogens. In addition, *Trichoderma* produces plant growth-promoting molecules that stimulate growth and development of the plant. Within the rhizosphere, the conversation and recognition of signaling molecules by *Trichoderma* and plants may alter the physiological and biochemical characteristics of the plants as well as the biocontrol agent. A detailed realization of the molecular mechanisms underlying biocontrol would benefit from developing

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Trichoderma strains with superior biocontrol properties. In this chapter, we summarize the interactions of *Trichoderma* with host plants and plant pathogens at the molecular level.

Keywords *Trichoderma* spp. · Biocontrol mechanisms · Antibiosis · Mycoparasitism · Induced systemic resistance · Secondary metabolites · Biocontrol genes

3.1 Introduction

The population of the world will reach around 9.1 billion people in 2050 which would need rising of total food production by some 70% (FAO 2009). The ever-increasing use of chemical inputs cause numerous harmful outcomes, development of resistance among pathogens, and their nontarget environmental effects (Sheikh et al. 2013). The pesticide consumption also increases year by year as 45.39 thousand tons of pesticides were consumed in the recent years (Krishijagran 2015). The number of biotic and abiotic stress causes yield losses up to a large extent. Biotic stress includes fungi, bacteria, viruses, nematodes, weeds, and insects which cause yield loss up to 42% and these pose the main danger to agriculture, food production, and supply (Agrios 2009; Kashyap et al. 2017; Sharma et al. 2017). Pesticide resistance and environment threat due to injudicious use of synthetic pesticides for disease control, hence, sustainable and ecofriendly approaches are new alternatives as a biological control in agriculture. The biological control, an eco-friendly approach, includes the use of particular microorganisms to control target phytopathogens and action on parasites, predators or pathogenic agents in controlling or maintaining the population density of another organism at a level lower than that would be present in their absence (Chernin and Chet 2002).

Plant-associated microorganisms are capable to stimulate plant growth by improving bio fertilization, bioremediation, production of phytohormones, and reducing biotic as well as abiotic stress (Mendes et al. 2011; Kumar et al. 2014; Babychan and Simon 2017) (Fig. 3.1). As a biocontrol agent, *Trichoderma* promotes ISR in plants, improves the uptake of nutrients by plants, improves growth and development of roots, promotes plant growth, and enhances crop productivity, increases biotic and abiotic stress resistance and soil remediation (Contreras-Cornejo et al. 2016; Waghunde et al. 2016; Kyriacou and Rouphael 2018). *Trichoderma* spp. is possibly the most commonly used microorganism for agricultural crop development (Rouphael et al. 2017). Root colonization by *Trichoderma* spp. leads to important metabolic variations in the plant and hormonal modifications, as well as phenolic compounds, soluble sugars, photosynthetic rate, amino acids, transpiration, and amount of water content (Zeilinger et al. 2016).

Trichoderma spp. and their metabolites secreted within the rhizosphere influence the growth rate and nutrition of the plant, ISR, and control the phytopathogens (Zeilinger et al. 2016). The mechanisms of biocontrol include competition for space,

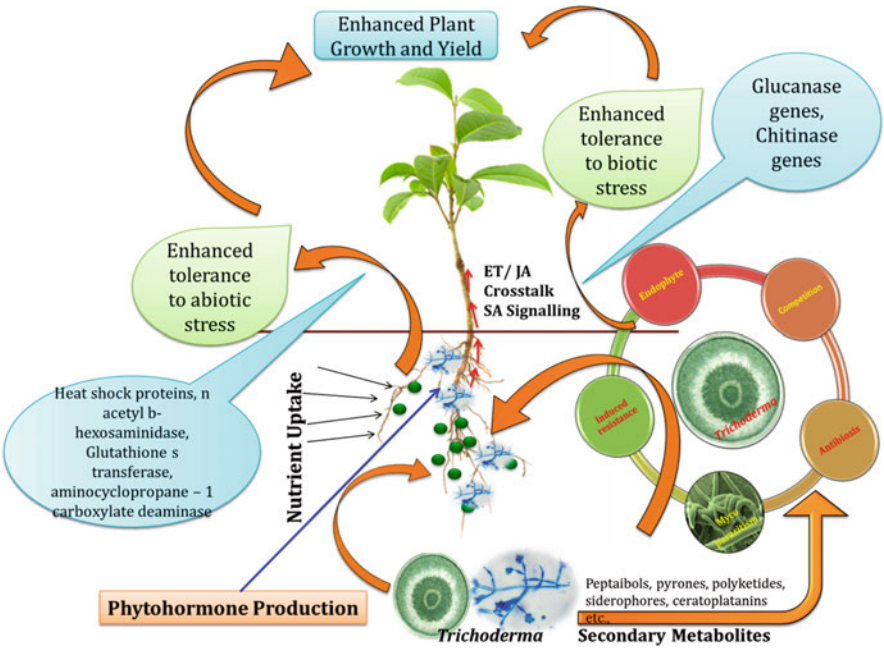

Fig. 3.1 Molecular mechanisms of *Trichoderma* species

resources, nutrients and synthesis, and production of antibiotics and extracellular degrading enzymes such as chitinase, β-1, 3-glucanase that target and break down cell wall of the pathogen resulting in its parasitization (Rai et al. 2016b). *Trichoderma* is an extensively studied genus that presently comprises more than 200 molecularly distinct species (Atanasova et al. 2013a). It is a free-living or saprophytic in soil, rhizosphere, and cellulosic materials; green spored ascomycete fungus with a worldwide distribution (Mukherjee et al. 2013; Waghunde et al. 2016). Members of the genus *Trichoderma* usually parasitize other fungi, saprophytically grow on wood, bark, and other substrates found in soil, interact with animals, plants, marine sponges and antagonistically kill other microbes (Kubicek et al. 2011; Holzlechner et al. 2016). Currently, *Trichoderma* spp. are the most effective bio-control agents used with about 60% of the recorded bio fungicides all over the world being *Trichoderma* based (Verma et al. 2007) and used as formulations due to their unique plant protecting abilities (Sharma et al. 2015; Oros and Naár 2017). In India, only around 250 bio fungicide products are accessible for field use and have a very meager portion compared to chemical fungicide. Numerous species of *Trichoderma* such as *T. atroviride*, *T. asperellum*, *T. harzianum, T. virens*, *T. hamatum*, *T. asperelloides*, and *T. gamsii* are established as potential biological control agents in plant protection and many effective strains have been registered for commercial use in agriculture (Lorito et al. 2010).

In present years, enormous reports have contributed to unraveling the molecular basis of the plant–*Trichoderma* interaction and the resultant positive effects to host plants. The genome size is usually small and with a haploid nucleus. The expected genome sizes and the chromosome numbers of *Trichoderma* spp. array from 3 to 39 Mb and from 3 to 7, respectively. Genes involved in biocontrol play a key role in regulating some signals which result in the production of certain enzymes or proteins that inhibit pathogens, plant growth promotion and therefore they are designated biocontrol genes (Nicolás et al. 2014). Genomic studies reveal that *Trichoderma* spp. contains various valuable genes that help deliver resistance to biotic and abiotic conditions, a range of expression patterns, allows these fungi applicable as biocontrol agents in plant growth promotional activities (Samolski et al. 2012). The genetics of fungal biocontrol agents have been prepared mostly with the genus *Trichoderma* (Mukherjee et al. 2012a; Reithner et al. 2014). The recent genome sequencing projects for *Trichoderma* spp. have targeted seven *Trichoderma* spp. such as *T. atroviride*, *T. reesei*, *T. virens*, *T. harzianum*, *T. asperellum*, *T. longibrachiatum*, and *T. citrinoviride* (Srivastava et al. 2014; Baroncelli et al. 2016; Rai et al. 2016a). Interestingly, *T. atroviride* and *T. viren* genomes are 36.1 and 38.8 Mbp, respectively, which is larger than that of *T. reesei* with a size of 34.1 Mbp and also have more than 2000 additional anticipated genes, while *T. reesei* has 500 distinctive ones compared to *T. atroviride* and *T. virens* (Table 3.1). The aim of the present chapter focuses on the beneficial effects of *Trichoderma* in plant–pathogen interactions and an in-depth understanding of the molecular mechanisms involved.

3.2 Mycoparasitism

Mycoparasitism is a complex process involving a direct attack by fungal species on another (Harman 2000a, b). The consecutive events involved in this process comprise recognition, attack, penetration, and killing of the host fungus. Host recognition by the parasite leads to coiling and appressoria formation, secretion of hydrolytic enzymes aiding penetration of the hyphae, and killing of the host (Holzlechner et al. 2016). This process also includes the secretion of antimicrobial metabolites, finally the captivation and killing of the pathogen (Harman et al. 2004; Omann et al. 2012). Mycoparasitism of plant pathogens by *Trichoderma* spp. has been well investigated and extensively measured to be a main contributing feature to the biocontrol of a range of commercially significant diseases. It is mediated by physical penetration of the mycoparasite into the host hyphae with the aid of specialized structures called haustoria accompanied by the secretion of several degradative enzymes or bioactive metabolites crucial for the breakdown of host fungal structures and finally nutrient uptake from the host (Daguerre et al. 2014).

The remote detection is partly because of the consecutive expression of several fungi toxic pathogenesis-related proteins or hydrolytic enzymes or cell wall degrading enzymes (CWDEs), such as chitinases, glucanases, and proteases

Table 3.1 *Trichoderma* biocontrol genes and their mechanisms

Trichoderma species	Genes/elicitors	Pathogen	Mechanism	Reference(s)
T. arundinaceum	BcBOT	*Botrytis cinerea*	Biocontrol activity	Malmierca et al. (2016)
T. aggressivum	*zhd*	*F. graminearum*, *F. culmorum*	Zearalenone lactonohydrolase activity	Popiel et al. (2014)
T. arundinaceum	*tri4*	*B. cinerea*, *R. solani*	Biocontrol activity and induction of plant defense-related genes	Malmierca et al. (2012)
T. asperelloides	*chit36*	*Alternaria radicina*, *B. cinerea*, and *Alternaria dauci*	Enhanced tolerance	Baranski and Klocke (2008)
T. asperelloides	*chit36* + *excy1*	*B. cinerea*	Enhanced tolerance to salinity and heavy-metal stresses	Brotman et al. (2012)
T. asperelloides	*TasSwo*	*B. cinerea and P. syringae*	Stimulating local defense responses in cucumber roots and leaves and affording local protection	Brotman et al. (2008)
T. asperellum	*TasHyd1*	*P. syringae*	Biocontrol activity	Viterbo and Chet (2006)
T. asperellum	*TaACCD*		Enhanced tolerance to salt stress	Zhang et al. (2016)
T. atrovide	*tmk1*	*B. cinerea*, *R. solani*	Mycoparasitism and plant protection	Reithner et al. (2007)
T. atrovide	*lae1*	*A. solani*, *B. cinerea* *Alternaria alternata*	Regulation of asexual development and mycoparasitism	Karimi-Aghcheh et al. (2013)
T. atrovide	*Xyr1*	*B. cinerea*, *Phytophthora capsici*, *R. solani*	Induction of systemic resistance in plants	Reithner et al. (2014)
T. atroviride	*chit42 (ech-42*, *ThEn-42*, *Tv-ech1*, *chi1*, *harchit)*	*Rhizoctonia solani*, *Alternaria solani*, *Botrytis cinerea and Alternaria alternata*	*Induced the resistance* and enhanced bio-control activity	Lorito et al. 1998

(continued)

Table 3.1 (continued)

Trichoderma species	Genes/elicitors	Pathogen	Mechanism	Reference(s)
T. atroviride	*chit42 (ech-42, ThEn-42, Tv-ech1, chi1, harchit)*	*Venturia inaequalis*	Increased resistance and reduced plant vigor	Bolar et al. (2001)
T. atroviride	*chit42 (ech-42, ThEn-42, Tv-ech1, chi1, harchit)*	*Penicillium digitatum*	Released endochitinase	Brants and Earle (2001)
T. atroviride	*chit42 (ech-42, ThEn-42, Tv-ech1, chi1, harchit)*	*Alternaria brassicicola*	Increased resistance	Mora and Earle (2001)
T. atroviride	*chit42 (ech-42, ThEn-42, Tv-ech1, chi1, harchit)*	*Phoma tracheiphila and B. cinerea*	Enhanced resistance	Gentile et al. (2007)
T. atroviride	*gluc78*	*Sclerospora graminicola*	Improved resistance	O'Kennedy et al. (2011)
T. atroviride	*chit42 + nag70*	*V. inaequalis*	Increased resistance to reduced plant vigor	Bolar et al. (2001)
T. atroviride	*chit42 + nag70*	*V. inaequalis*	Increased resistance	Schäfer et al. (2012)
T. atroviride	*chit42 + nag70 + gluc78*	*R. solani*, *Magnaporthe grisea.*	Overexpression of the glucanase alone provokes fatal influence on plant growth	Liu et al. (2004)
T. atroviride	*chit42 + (1,3-1,4)-β-glucanase*	*R. solani*	Mycorrhizal colonization not affected, enhanced to tolerance	Kogel et al. (2010)
T. atroviride	*prb l*	*R. solani*, *Pythium ultimum. Botrytis cinerea*	Glucose gene insertion, enhances the ISR activity	Brunner et al. (2005)
T. atroviride	*Gpr1*	*B. cinerea*, *R. solani*, *S. sclerotiorum*	Antagonistic interaction	Omann et al. (2012)
T. atroviride	*Pks4*	*Alternaria alternata*, *R. solani*, *Sclerotinia sclerotiorum*	Pigmentation and stress resistance and in protection against toxins	Atanasova et al. (2013a)
T. atroviride	*Taabc2*	*Beauveria bassiana*, *B. cinerea*, *Fusarium* spp., *P. ultimum*, *R. solani*	ABC transporter membrane pump in the interaction with different plant–pathogenic fungi	Ruocco et al. (2009)

T. atroviride	*nag1*	*B. cinerea*	Carbon starvation is antagonized via a BrlA-like cis-acting element	Brunner et al. (2003)
T. atroviride	*Tga3*	*B. cinerea*	Signal transduction	Zeilinger et al. (2005)
T. atroviride	Tanshinone I and Tanshinone IIA		Promoted growth and tanshinone biosynthesis	Ming et al. (2013)
T. atroviride P1	*Gluc78*	*Pythium and Phytophthora*	Cell wall degradation	Donzelli et al. (2001)
T. Brevicompactum T. arundinaceum	*tri14*, *tri12*, *tri11*, *tri10*, *tri3*, *tri4*, *and tri6*		Trichodermin biosynthesis with strong antifungal activity	Xuping Shentu et al. (2018)
T. brevicompactum IBT40841	*tri5*	*S. cerevisiae*, *Kluyveromyces marxianus*, *Candida albicans*, *C. glabrata*, *C. tropicalis and Aspergillus fumigates.*	Production of trichodermin and antifungal activity and increases biocontrol activity	Tijerino et al. (2011)
T. gamsii T6085		*Fusarium* spp.	Biocontrol activity	Baroncelli et al. (2016)
T. hamatum	*chit42 and prb1*	*Sclerotinia sclerotiorum*	Mycoparasitic activity	Steyaert et al. (2004)
T. hamatum LU593	Monooxygenase	*S. sclerotiorum*, *S. minor and S. cepivorum*	Antagonist activity against and enhanced biocontrol activity	Carpenter et al. (2008)
T. harzianum	*prb1 and ech42*	*Sclerotium rolfsii* and *Rhizoctonia solani*	Parasitic activity and regulation of hydrolytic enzymes	Cortes et al. (1998)
T. harzianum	*Ech42*	*Botrytis cinerea and R. solani*	Biocontrol activity	Woo et al. (1999)
T. harzianum	*Tri5*	*Fusarium* spp.	Increases the virulence	Gallo et al. (2004)
T. harzianum	*chit42 (ech-42*, *ThEn-42*, *Tv-ech1*, *chi1*, *harchit)*	*A. alternata*	Enhanced resistance	Saiprasad et al. (2009)
T. harzianum	*agn13.1*	*B. cinerea*	Significant resistance	Calo et al. (2006)

(continued)

Table 3.1 (continued)

Trichoderma species	Genes/elicitors	Pathogen	Mechanism	Reference(s)
T. harzianum	*bgn13.1*	*C. acutatum*	Enhanced tolerance	Mercado et al. (2007)
T. harzianum	*chit42 + chit33*	*R. solani*, *Pseudomonas syringae*	Enhanced tolerance to salt and heavy-metal stresses	Dana et al. (2006)
T. harzianum	*chit42 + harcho*	*C. sublineolum*	Increased resistance	Kosambo-Ayoo et al. (2011)
T. harzianum	*chit42 + harcho*	*Erysiphe graminis f.sp. tritici*	Enhanced resistance	Rana et al. (2012)
T. harzianum	*chit42 + StSy + Cu,Zn-SOD*	*Mycosphaerella fijiensis and B. cinerea*	Increased tolerance	Vishnevetsky et al. (2011)
T. harzianum	*Thmfs1*	*A. niger*, *B. cinerea*, *F. oxysporum*, *G. saubinetii*, *R. solani*	Biocontrol activity	Liu et al. (2012)
T. harzianum	*nox1*	*P. ultimum*	Production of reactive oxygen species to specific biocontrol activity	Montero-Barrientos et al. (2011)
T. harzianum	*bgn13.1*		Enhanced tolerance to crown rot diseases but interferes with plant growth	Mercado et al. (2015)
T. harzianum	*qid74*	*R. solani*	Increased plant biomass through an efficient use of NPK and micronutrients and mycoparasitic activity	Samolski et al. (2012)
T. harzianum	*Epl-1*	*S. sclerotiorum*	Involved in mycoparasitism, resistance induction, and self-cell wall protection	Gomes et al. (2015)
T. harzianum	Trichodiene	*Botrytis cinerea*	Induce systemic resistance in plants against stress	Malmierca et al. (2015)
T. harzianum	Harzianolide	*Sclerotinia sclerotiorum*	Plant growth regulator and systemic resistance elicitor	Cai et al. (2015)

T. harzianum	*Sm1*	*Biotic/abiotic stress*	Elicitor for triggering of plant defense	Freitas et al. (2014)
T. harzianum	*AOC3*, *PDF1.2* and *ERF2* genes	*Sclerotinia sclerotiarum*	Induced Systemic Resistance	Alkooranee et al. (2017)
T. harzianum	PAL1, *chit1*, β1,3-Glucanase, PR- 1, LOX 1 gene	*Fusarium oxysporum f. sp. radicis cucumerinum Botrytis cinerea*	Induced systemic resistance	Alizadeh et al. (2013)
T. harzianum CECT 2413	*ThPTR2*	*B. cinerea*	Enhances mycoparasitic activity and induces peptide transportation	Vizcaino et al. (2006)
T. harzianum CECT 2413	*Thctf1*	*R. solani*, *F. oxysporum and B. cinerea*	Antifungal activity and production of 6-pentyl-2H-pyran-2 and enhanced bio-control activity	Rubio et al. (2009)
T. harzianum CECT 2413	*exc1 and exc2*, *chit42 and chit33 gene*, *prb1 and bgn13.1*	*F. oxysporum*	Mycoparasitic activity against and enhanced biocontrol activity and Expression of this gene helps in regulation of hydrolytic enzymes	Lopez-Mondejar et al. (2011)
T. harzianum Rifai	*qid74*	*R. solani*	Antagonism activity and mycoparasitic activity	Rosado et al. (2007)
T. harzianum T34	*ThPG1*	*R. solani and P. ultimum*	Secretion of plant cell wall degrading enzymes and enhanced biocontrol activity	Moran-Diez et al. (2009)
T. longibrachiatum	*Egl1*	*Pythium ultimum*	Enhanced biocontrol activity	Migheli et al. (1998)
T. longibrachiatum	*Hytlo1*		Established a mutually beneficial interaction with the colonized plant	Ruocco et al. (2015)
T. reesei	*gna3*	*P. ultimum*	Production of cell wall-degrading enzymes and mycoparasitism activity	Silva et al. (2009)
T. reesei	*pks4*	*A. alternata*, *R. solani*, *S. sclerotiorum*	pigmentation and stress resistance and in protection against toxins	Atanasova et al. (2013a)
T. virens	*TmkA*	*S. rolfsii and R. solani*	Shows increased biocontrol activity	Viterbo et al. (2005)

(continued)

Table 3.1 (continued)

Trichoderma species	Genes/elicitors	Pathogen	Mechanism	Reference(s)
T. virens	*TgaA*, *TgaB*	*S. rolfsii and R. solani*	Increases virulence in the plant–pathogenic interactions.	Mukherjee et al. (2004)
T. virens	*tvsp1*	*R. solani*	Biocontrol activity	Pozo et al. (2004)
T. virens	*Tac1*	*R .solani*, *S. rolfsii*, *Pythium* spp. *R. solani and P. ultimum*	Mycoparasitism and production of secondary metabolism	Mukherjee et al. (2007)
T. virens	*chit42 (ech-42*, *ThEn-42*, *Tv-ech1*, *chi1*, *harchit)*	*A. alternate*, *R. solani*	Increased resistance	Emani et al. (2003)
T. virens	*chit42 (ech-42*, *ThEn-42*, *Tv-ech1*, *chi1*, *harchit)*	*R. solani*	Enhanced resistance	Shah et al. (2009)
T. virens	*chit42 (ech-42*, *ThEn-42*, *Tv-ech1*, *chi1*, *harchit)*	*B. cinerea and Sclerotinia sclerotiorum*, *A. alternata*	Enhanced tolerance	Shah et al. (2009)
T. virens	*pacC*	*R. solani*, *S. rolfsii*	Antifungal activity	Trushina et al. (2013)
T. virens	*Vel1*	*P. ultimum*, *R. solani*	Morphogenesis and biocontrol properties	Mukherjee and Kenerley (2010)
T. virens	*pks4*	*A. alternata*, *R. solani*, *S. sclerotiorum*	Pigmentation and stress resistance and in protection against toxins	Atanasova et al. (2013a)
T. virens	*GliC gliI*, *gliF*	*P. ultimum*, *R. solani*	Mycoparasitism	Atanasova et al. (2013b)
T. virens	*gliK*	*P. ultimum*, *R. solani*	Mycoparasitism	Atanasova et al. (2013b)
T. virens	*gliM*	*P. ultimum*, *R. solani*	Mycoparasitism	Atanasova et al. (2013b)

T. virens	*ppt1*	*A. solani*, *B. cinerea*, *F. oxysporum*, *Fusarium* spp., *Phytophthora capsici*, *R. solani*, *S. cepivorum*, *S. rolfsii*	Secondary metabolism and induction of plant defense responses	Velázquez-Robledo et al. (2011)
T. virens	*Psy1*	*R. solani*	Biocontrol activity	Wilhite et al. (2001)
T. virens	4-phosphopantetheinyl transferase	*R. solani*	Biocontrol activity	Velázquez-Robledo et al. (2011)
T. virens	*ech42*	*Alternaria*	Enhanced tolerance	Kamble et al. (2016)
T. virens	*Sm2*	*Cochliobolus heterostrophus*	Important for plant protection	Gaderer et al. (2015)
T. virens	*tac1*	*R. solani and P. ultimum*	Mycoparasitic activity	Abbas et al. (2017)
T. virens IMI 304061	*TmkA*	*R. solani*	Induction of plant systemic resistance and biocontrol activity	Viterbo et al. (2005)
T. viride	*Xyn2/Eix*	*B. cinerea*	Elicits ET biosynthesis and hypersensitive response	Rotblat et al. (2002)

(Harman et al. 2004). Approximately 30% of the dry weight of the fungal cell is attributed to the presence of chitin, β-1, 3-glucans, and α-1, 3/1, 4-glucans. The biosynthesis of CWDEs is implicated in mycoparasitism which is regulated mainly at the transcriptional level and accountable genes are present as single-copy genes. Overall 20–30 genes, proteins, and other metabolites have a direct involvement in this communication. Morphological modifications and transformation to improve the copy number of these genes have been employed to overproduce these enzymes (Lu et al. 2004). The functions of different CWDEs in the course of mycoparasitism by *Trichoderma* spp. using a gene for gene approach and future studies will help in a better understanding of the process (Daguerre et al. 2014).

Since many of the lytic enzymes secreted by biocontrol agents are encoded by a single gene, it is considered to be a straightforward technique to isolate some of these genes and then transfer them to other biocontrol agents. The CWDEs are extracellular proteins with low molecular weight and high stability. Several forms or isozymes of a particular enzyme may be secreted that vary in size, regulation, and capacity to break down the cell walls of phytopathogens (Vos et al. 2015). Over 1100 *Trichoderma* spp. have been described containing 75 molecularly defined mycoparasitic against different plant pathogenic fungi (Druzhinina et al. 2011). Volatile secondary metabolites have also been implicated in mycoparasitism by *Trichoderma* spp. (Stoppacher et al. 2010).

3.3 Chitinases

Chitinases are among the most significant lytic enzymes produced by *Trichoderma*, which complete lysis of walls of fungal mycelia or conidia of phytopathogens. These chitinases are hydrolases that break down one of the major constituents of the fungal cell wall, chitin, a polymer composed of repeating units of *N*-acetyl-D-glucos-2-amine, linked by β-1, 4 glycosidic bonds (Bhattacharya et al. 2007). These are separated into β-*N*-Acetylhexosaminidases (GlcNAcases), endochitinases, and exochitinases. Endochitinases degrade chitin at interior sites releasing chitotriose, chitotetraose, and chitobiose. Exochitinases are further divided into chitobiosidases and *N*-acetyl-β-glucosaminidases (Prakash et al. 2010). Chitobiose, chitotriose, and chitotetraose are degraded into *N*-acetylglucosamine monomers by GlcNAcases in a similar manner to exochitinase. Genetic alteration of plant species with mycoparasitic genes from *Trichoderma* spp. signifies an advanced method of disease resistance. There are perhaps at least 30 chitinases alone, each with different genes and protein composition. Chitinase gene has been transmitted to several crops for developing fungal disease resistance. More specifically, De la Cruz et al. (1992) cloned *chit33* chitinase gene from *Sclerotinia sclerotiorum* and cloned *ech42* chitinase gene from *T. harzianum* (Garcia et al. 1994). A relative investigation of chitinases exposed that *Trichoderma* genomes harbor around 20 and 36 different genes encoding chitinases. The chitinolytic capability in *Trichoderma* is associated with varied chitinase genes including *ech42*, *chi33*, *nag1*, *chi18-13*, where these

diverse enzymes could confer advanced mycoparasitic action against phytopathogens (Seidl et al. 2005).

Based on the previous investigations, the presence of fungal cell walls or colloidal chitin, as well as carbon starvation, induce the genes encoding endochitinase 42 (*ech42*), endochitinase 33 (*chit33*) and *N*-acetyl-β-D-glucosaminidase (*nag1*) (Peterbauer et al. 1996; Margolles-Clark et al. 1996). The expression of *ech42*, related to light-induced spore germination was suppressed by carbon catabolites (Lorito et al. 1996); whereas *N*-acetyl-β-D-glucosamine (GlcNAc) induced the transcription of *nag1* (exochitinase) (Peterbauer et al. 1996). Effective transformation and expression of several endochitinase genes, for example, *chit42* and *chit33* from *T. harzianum* have improved fungal tolerance in crops such as *Brassica juncea*, potato, apple, broccoli, rice, carrot, and lemon (Kamble et al. 2016; Lorito et al. 1998; Bolar et al. 2001; Mora and Earle 2001; Liu et al. 2004; Baranski et al. 2008; Distefano et al. 2008). Transgenic tomato plants overexpressing *chi194*, a wheat chitinase gene, under the control of maize ubiquitin 1 promoter have been reported (Girhepuje and Shinde 2011). Mishra et al. (2016) reported the transfer of a *Trichoderma* endochitinase gene into a guava plant (*Psidium guajava*). The gene, *ech42* in *T. harzianum*, encoding endochitinase was studied and cloned into pAN7-1 vector. The antifungal action was established against *B. cinerea* and *R. solani* pathogens using the wild type and disruptant strains (Woo et al. 1999). Genes *chit42* and *chit33* coding chitinase in *T. harizianum* play a key role in the mycoparasitic action against the phytopathogens, particularly *F. oxysporum* (Mondejar et al. 2011). The co-transformation of apple with nag70 (*nag1*) and *ech42* resulted in a synergistic rise in biocontrol activity against *Venturia inequalis* (Bolar et al. 2001). A dramatic increase in disease resistance of potato and tobacco against *A. alternata*, *A. solani*, *B. cinerea*, and *R. solani* was observed with the combination of *T. harzianum* and *T. atroviride* endochitinase *ech42*.

3.4 Glucanases

Glucanases are another class of cell wall degrading enzymes with a key role in mycoparasitism. Glucans are glucose polysaccharides that cross link chitin or chitosan polymers. Based on the chemical bonding among glucose subunits there are two types of glucans. β-glucans are defined by β-(1, 3) or β-(1, 6) bonds and afford rigidity to the cell wall. α-glucans are considered by α-(1, 3) and/or α-(1, 4) bonds and function as a part of the matrix. The second most plentiful polymer in fungal cell walls is β-1, 3-glucan (Latge 2007) with β-1, 6- branches, which are broken down by β-1, 3-glucanases. In the genomes of *Trichoderma* spp., genes encoding this class of enzymes are over represented when compared to other related fungi (Kubicek et al. 2011; Geraldine et al. 2013; Vos et al. 2015). β-1, 6-glucanases have been identified in the area of contact between *Trichoderma* spp. and its prey. In *T. harzianum* CECT 2413, the overexpression of *Bgn16.3* encoding β-1, 6-glucanase resulted in a more effective biocontrol agent with growth-inhibitory action on

B. cinerea, *R. solani*, and *Phytophthora citrophthora* (Montero et al. 2007). The *Bgn16.2* showed antifungal activities individually or in combination with other chitinases resulting in impairing the growth of *B. cinerea* and *Gibberella fujikuroi* (De la Cruz and Llobell 1999). Strains of *T. harzianum* and *T. virens* overproducing β-1, 6-glucanases were more effective in the biocontrol of *R. solani*, *B. cinerea* (Ihrmark et al. 2010), and *P. ultimum* (Djonovic et al. 2006).

Inhibition of spore germination or the growth of phytopathogens by β-1, 3-glucanases is in synergistic cooperation with chitinases (El-Katatny et al. 2001) as well as antibiotics (Harman et al. 2004). Numerous β-1, 3-glucanases have been identified, but only a few genes have been cloned; those are *lam1.3* (Cohen-Kupiec et al. 1999) from *T. harzianum*, *bgn13.1* (Benitez et al. 1998) and *glu78* (Donzelli et al. 2001) from *T. atroviride*, and *Tv-bgn1* and *Tv-bgn2* from *T. virens* (Kim et al. 2002). Increased biocontrol of *T. virens* against *R. solani*, *P. ultimum*, and *R. oryzae* was reported using co-overexpression of two β -glucanases *Bgn2* and *Bgn3* genes (Djonovic et al. 2007). Overexpression of *bgn13.1* in transformants has been described as inhibitory to the growth of *B. cinerea*, *R. solani*, and *P. citrophthora*. Transformant T28, with maximum *bgn13.1* glucanase activity in repressing as well as inducing situations, displayed strong suppression of pathogens. Expression and secretion of endo-β-1, 3-glucanase, *bgn13.1* in *T. harzianum* was noticed when grown on fungal plant pathogen cell walls (De la Cruz et al. 1995). The *Gluc78* from *T. atroviride* P1 revealed strong antimicrobial action against an array of fungi and oomycetes including *Pythium* and *Phytophthora*; the activity was in synergy with other enzymes. *Tv-bgn1* and *Tv-bgn2*, these glucanases have been identified and cloned (Donzelli et al. 2001). In *T. atroviride gluc78* gene coding for an antifungal glucan 1, 3-β-glucosidase was identified, cloned, and sequenced. The pGEM-T vector was used for cloning *gluc78* gene and the expression study carried out against the phytopathogens *R. solani* and *P. ultimum* (Donzelli et al. 2001).

T. asperellum α-1, 3-glucanase *agn13.2* and *T. harzianum* β-1, 6-glucanase *bgn16.2* have been reported with antifungal activity against *B. cinerea* (Sanz et al. 2005). Three α-1, 6-glucanases have been isolated from *T. harzianum* 2413 strain (Elad et al. 2000). *T. longibrachiatum* transformants exhibiting overexpression of β-1, 4-endoglucanase gene *egl1* showed biocontrol activity against *P. ultimum* in cucumber. Among 31 *T. harzianum* isolates, five of them *T*30, *T*31, *T*32, *T*57, and *T*78 encoded genes for *N*-acetyl-β-D-glucosaminidase (*exc1 and exc2*), chitinase (*chit42* and *chit33*), protease (*prb1*), and β-glucanase (*bgn 13.1*) which were cloned and expressed. These genes are critical in the mycoparasitic activity against the phytopathogenic fungi particularly *F. oxysporum* (Lopez-Mondejar et al. 2011). The adenalyte-cyclase encoding gene in *T. virens* termed as *tac1* gene was isolated and cloned and its role in mycoparasitic activity against *R. solani* and *P. ultimum* has been studied (Mukherjee et al. 2007). The *qid74*gene identified in *T. harzianum* CECT 2413 plays a significant role in cell protection and offers adherence to hydrophobic exteriors aiding the fungus in mycoparasitic activity against *R. solani* (Rosado et al. 2007). A gene *Taabc2* cloned from *T. atroviride* has a crucial role in ATP binding cassette (ABC) transporter in cell membrane pump that benefits in the

mycoparasitic activity against *R. solani*, *B. cinerea*, and *P. ultimum* (Ruocco et al. 2009).

The *tag83* gene encoding exo-β-1, 3-glucanase enzyme was identified from *T. asperellum* and the expression of this gene exhibited parasitic activity against pathogens such as *R. solani* (Marcello et al. 2010). Two different types of β-1, 3 and β-1, 6 glucanase genes such as *TvBgn2* and *TvBgn3* transformants were expressed from *T. virens*. These genes secrete CWDEs that helps in the biocontrol activity. The glucose repressor gene *creI* from *T. harzianum* was isolated and characterized, and cloned using *pTZ57R/T* plasmid vector followed by transformation into *E. coli* DH10B and its role in the expression of cellulase and xylanase were studied (Saadia et al. 2008). Cellulase and xylanase are the major type of enzymes that involve in the cell wall degradation of the phytopathogens.

3.5 Proteases

Fungal proteases also play an important role in cell wall degradation and cleavage of peptide bonds in proteins (Haggag et al. 2006). Certain proteases secreted by *Trichoderma* spp. may be involved in the inactivation of extracellular enzymes produced by phytopathogenic fungi. Numerous studies substantiate the role of extracellular proteases in improved biocontrol efficiency of *T. virens*, *T. harzianum*, *T. asperellum*, *T. flavus* against pathogenic fungi and oomycetes such as *R. solani*, *F. oxysporum*, *B. cinerea*, *S. sclerotiorumor*, *P. ultimum*. The maximum mycoparasitic protease genes cloned so far is from *Trichoderma* spp. genes. The genes encode numerous serine proteases with subtilisin-like, chymotrypsin- or elastase-like, and trypsin-like activity and aspartic proteases. *T. virens Tvsp1* and *T. atroviride Prb1* are serine proteases (Pozo et al. 2004), while *T. asperellum TaAsp* and *T. harzianum* Sa76 are aspartic proteases (Yang et al. 2013). A novel serine protease gene from *T. harzianum* named *SL41* has been cloned and expressed effectively in *S. cerevisiae*. The cDNA of *Sl41* gene was sequenced and it was cloned in pMD18-T vector and was inserted into *E. coli* DH5-α (Liu et al. 2009). Numerous genes coding proteases and oligopeptide transporters are expressed earlier and during contact with the prey in different *Trichoderma* species (Seidl et al. 2009). A richness of genes encoding subtilisin-like serine proteases was also detected in a study of expressed sequence tags (ESTs) accumulated through the commencement of contact between *T. atroviridis* and its fungal preys *Rhizoctonia solani* and *S. sclerotiorum* (Seidl et al. 2009). The Protease *pra1* from *T. harzianum* isolate has an affinity for fungal cell walls (Elad et al. 2000) and this gene displays great potential in increasing biocontrol capacity, as serine proteases are active against oomycetes (Howell 2003). The alkaline protease *Prb1* from *T. harzianum* IMI 206040 strain has also been established to play a significant role in biological control efficiency (Benitez et al. 1998) and the *T. harzianum Prb1* gene transformants exhibited upto fivefold increase in the biocontrol effectiveness in the control of *R. solani.*

3.6 Mechanisms of Signal Transduction

Downstream transduction of signals, produced at the receptor sites, is necessary for further expression of genes in the host plants. Three significant signal transduction pathways are recognized in *Trichoderma* spp. that increase the expression of genes involved in biocontrol and mycoparasitism. Signal transduction pathways eliciting the genes involved in mycoparasitism have been deliberated in depth and contain heterotrimeric G-protein signaling, mitogen-activated protein kinase (MAPK) cascades, and the cAMP pathways (Zeilinger and Omann 2007). Adenylate cyclase and G-protein coupled receptors *Trichoderma* spp. are critical for the secretion of extracellular CWDE, production of antifungal metabolites, and development of infection Cyclic adenosine monophosphate (cAMP) is a significant regulator of structures. A positive trigger in the activity of adenylate cyclase by G-protein α-subunits *Tga3* and *Gna3* consequently improved mycoparasitism (Daguerre et al. 2014). Heterotrimeric G proteins contain a, b, and ɣ subunits are involved in transducing signals from transmembrane G protein-coupled receptors to a variability of intracellular targets. Depending on the system, Ga or Gbɣ transduces the signal by stimulating effectors such as adenylate cyclase or the MAPK cascade (Kaziro et al. 1991).

Cyclic adenosine monophosphate (cAMP) is a significant regulator of development, growth, and pathogenicity in filamentous fungi (Liebmann et al. 2003). The cAMP mediated signaling is a significant pathway in fungi in controlling the diversity, virulence, sexual development, nutritional status, stress, transcription, and cell cycle development (Kronstad et al. 1998). In most fungi, the adenylate cyclase activity is under the control of subunits of heterotrimeric G-proteins. The cAMP usually stimulates a cAMP-dependent protein kinase (PKA) that is composed of two regulatory and two catalytic subunits (Dickman and Yarden 1999), and the gene expression is regulated by means of phosphorylation of transcription factors. Lin et al. (2012) investigated the association of anthraquinone secondary metabolites emodin and pachybasin in the self regulation of coiling in *T. harzianum.* The addition of both of these *T. harzianum* derived metabolites improved the number of coils of the mycoparasite around hyphae of *R. solani* and resulted via stimulation of cAMP production. The detailed investigation of two genes in the heterotrimeric G protein signaling pathway such as the class I G-α subunits *Tga1* of *T. atroviride* and *TgaA* of *T. virens*, as well as the class III G-α subunits *Tga3* of *T. atroviride* and *Gna3* of *T. reesei*, have confirmed the functions of these genes are associated with biocontrol activity. The gene *Tga1* was reported crucial in the production of antifungal metabolites and regulation of coiling around the pathogenic hyphae (Rocha-Ramírez et al. 2002; Zeilinger et al. 2005). *TgaA* has a host-specific connection associated with the activity of MAP kinases while *Tga3* was found to be noteworthy for biocontrol activities.

Mitogen-activated protein kinase pathways transduce a great range of signals, containing those connected with pathogenesis. MAPK pathways signify one of the most prominent signal transduction systems in fungi. Numerous MAPKs convoluted in fungal mycoparasitism have been identified in *Trichoderma* spp. which harbor

MAPKKK, MAPKK, and MAPK signaling pathways, the three MAPK cascades which might act in mycoparasitism and biocontrol activity (Reithner et al. 2007; Kumar et al. 2010). The MAPKs in *Trichoderma* belong to the family of yeast and fungal extracellular related kinases (YERK1); other MAPKs include Pmk1 from *M. grisea*, *Fmk1* from *F. oxysporum*, *Bmp1* from *B. cinerea* or Ubc3/Kpp2 from *U. maydis*. The three MAPKs genes in the *Trichoderma* genome encode the so-called virulence MAPK (*TmkA/Tvk1*) ortholog of the pathogenicity related MAPKs of phytopathogens, the cell integrity kinase (*TmkB*), and the osmoregulatory MAPK (*Hog1*).

The expression levels of mycoparasitism-related genes (MGRs) in the MAP kinase encoding gene mutant of a *Trichoderma* strain raised during mycoparasitism when in direct contact with *R. solani*. The regulation of MGRs in *T. virens* is very complex; however, they share common elements including *Tvk1* like other fungi (Mendoza-Mendoza et al. 2003). The MAPK from *T. atroviride* (*Tmk1*) on characterization showed 98% similarity to *T. virens TmkA/Tvk1* (Reithner et al. 2007). *Δtmk1* mutants showed a reduction in radial growth and the conidiation was light-independent. The direct plate confrontation analyses against the pathogens *R. solani* and *B. cinerea* as hosts revealed that *T. atroviride Tmk1*—similar to *T. virens TmkA*—affected the host specificity as *Δtmk1* mutants had the ability to parasitize *R. solani* whereas they failed to attack *B. cinerea*. The *TmkA* mitogen-activated protein kinase from *T. Virens* is known to cause mycoparasitic activity to *R. solani* and *S. rolsfii* (Mukherjee et al. 2003). MAP kinase cascade connecting MPK4, MPK3, MPK11, and MPK6 and additional genes containing Ca^{2+} reliant proteinase kinases are triggered to found PTI (Bethke et al. 2012).

3.7 Competition

Starvation is a general cause of death of soilborne microorganisms (Benitez et al. 2004), so competition for limited nutrients is especially significant in the biocontrol of phytopathogens. Competition is the phenomenon in which the introduced biocontrol agent, i.e., *Trichoderma* and the pathogen compete for the obtainability of nutrients and space (Hjeljord et al. 2000). In most of the filamentous fungi, iron and carbon are two vital elements, essential for viability. This process could be connected also to the production of organic acids, such as gluconic, citric, and fumaric acids, which reduce soil pH and allow the solubilization of phosphates, micronutrients, and mineral cations like iron, manganese, and magnesium (Vinale et al. 2008a). The *Trichoderma* spp. displays natural resistance to fungicides, herbicides, and phenolic compounds and various toxic chemicals. *Trichoderma* spp. can, therefore, grow quickly and influence pathogens with the production of metabolic compounds that inhibit spore germination of the pathogen (fungistasis), cause death of the pathogen (antibiosis), or alter the conditions of the rhizosphere (Benitez et al. 2004). The disease inhibition activity of *Trichoderma* spp. is exerted either directly by obstructing growth and development of soilborne pathogens

through competition for nutrients or excretion of antibiotics in the rhizosphere (Bakker et al. 2007; Sultana et al. 2009) or indirectly by stimulating a plant-mediated systemic resistance (van Wees et al. 2008). In their investigation, Lehner et al. (2013) describe the detection of around 12–14 siderophores in *T. atroviride*, *T. asperellum*, *T. gamsii*, *T. hamatum*, *T. virens*, *T. harzianum*, *T. polysporum*, and *T. reesei* by isotope-based screening using dimerum acid, coprogren, fusigen, fusarinine A, and the intracellular siderophore ferricrocin being produced by all species (Lehner et al. 2013).

3.8 Competition for Nutrients

Iron acts as a cofactor of several enzymes and an essential nutrient for the growth of plants and other microorganisms. Iron attainment is a significant component of microbial competition, particularly within the rhizosphere, where there is intense microbial activity. The biocontrol agent *Trichoderma* spp. may show rapid growth or utilize the available food source more efficiently in comparison to the phytopathogens, thereby suppressing the pathogen growth and taking over. This process is termed as competition for nutrients. The ability of *Trichoderma* spp. to scavenge iron from the environment makes it unavailable for the competing pathogens. Certain *Trichoderma* isolates produce highly efficient siderophores, iron-chelating compounds which bind with insoluble iron (FeIII) and converted to soluble form (FeII) for plant absorption and stop the growth of phytopathogens by depriving them of iron sources (Benitez et al. 2004). *Trichoderma* spp. are known to produce extracellular siderophores of the fusigen and coprogen family. Several *Trichoderma* spp., such as *T. viride*, *T. harzianum*, and *T. lignorum* are well-known siderophore producers better than the pathogenic strains of *Fusarium* such as *F. solani* and *F. oxysporum* (Dutta et al. 2006).

Competition for iron has been found to be among the critical factors in the antagonism of *T. asperellum* against *F. oxysporum* and may as well be beneficial for plants due to the iron solubilizing activity (Segarra et al. 2010). *T. virens* and *T. reesei* harbor an extra putative gene cluster for siderophore production (Mukherjee et al. 2012b). *T. virens* and *T. reesei* harbor two putative gene clusters covering an NRPS as the core member, whose orthologs (*SidD* and *NPS6*) are known to be intricate in siderophore production (Kubicek et al. 2011). During iron deprived situations, the synthesis of these iron scavenging siderophores are under the impact of HapX protein that specifically binds to CCAAT binding complex (CBC) (Thon et al. 2010). *T. harzianum* CECT 2413 strain encodes a high-affinity glucose transporter (Gtt1) and interestingly the Gtt1 gene is only expressed during very low glucose concentrations similar to the development of competence among microorganisms (Benitez et al. 2004). *Gtt1*, a high-affinity glucose transporter of the mycoparasitic fungus *T. harzianum*, has been characterized (Delgado-Jarana et al. 2003). Vargas et al. (2009) reported an intracellular invertase *TvInv* from *T. virens*

that is involved in sucrose hydrolysis signifying the plant-derived sucrose as a vital nutritional resource to *Trichoderma*.

3.9 Competition for Root Colonization

From the standpoint of microbes, surfaces of living plants and soils are often nutrient-limited environments. Colonization of the root tissue is generally confined to the penetration of the first or second layers of cells and to the intercellular spaces (Brotman et al. 2008). Proteins of *Trichoderma* spp. involved in root colonization can act as MAMPs (Lorito et al. 2010; Ruocco et al. 2015). For example, swollenin, a protein encoded by *TasSwo* gene, induces defence responses in cucumber roots and leaves affording local defense against plant pathogens (Brotman et al. 2008) and endopolygalacturonases endoPGs produced by *Trichoderma* spp. aid in root penetration and constitute a preeliciting role in ISR (Baroncelli et al. 2015). Further, root penetration is accomplished via the secretion of cellulolytic, hemicellulolytic, and proteolytic enzymes (Viterbo et al. 2004).

Hydrophobins and expansin-like proteins (Brotman et al. 2008; Ruocco et al. 2015) are essential for the adherence to the root surface by *Trichoderma* spp. and in cell wall development, respectively. These are small secreted proteins that have a distinctive domain of eight cysteine residues at conserved positions. Hydrophobins were primarily separated into class I and class II hydrophobins according to their hydropathy patterns and solubility (Linder et al. 2005). *T. asperellum* harbors the *TasHyd1* hydrophobin gene, which has been revealed to support in plant root colonization, enabling the attachment of hyphal filaments to hydrophobic root surfaces (Viterbo and Chet 2006; Guzmán-Guzmán et al. 2017). Among the three hydrophobin genes *Hyd1*, *Hyd2*, and *Hyd3* recently identified in the fungus, only *Hyd3* is implicated in root colonization by *C. rosea* (Dubey et al. 2014). Hydrophobins in phytopathogenic fungi are necessary to anchor fungal cells to host plant surfaces and they could play a similar role in biocontrol agents such as *T. asperellum* and *C. rosea*.

Plant lytic enzymes involve actively in root colonization, similar to endopolygalacturonase *ThPG1* from *T. harzianum* and expansin-like proteins capable of recognizing cellulose swollenin *TasSwo* have also been revealed to be involved in plant root colonization (Moran-Diez et al. 2009). In *T. asperellum*, xylanases *Abf1* and *Abf2* along with proteases *PapA* and *PapB* are secreted in response to cucumber root attachment (Viterbo et al. 2004). The role of xylanases in plant root colonization by *Trichoderma* is not directly confirmed but these enzymes are upregulated during *Trichoderma*–plant interactions. Biochemically diverse microbe-associated molecular patterns (MAMPs) have been identified in *Trichoderma* (Shoresh et al. 2010), including the ceratoplatanin protein *SM1/Epl1* (Frischmann et al. 2013), ethylene-inducing xylanase (Ron and Avni 2004), and Swollenin protein from *T. asperellum*. *Epl1* has been defined with the ability to generate defense responses in plants (Salas-Marina et al. 2015; Ramada et al. 2016). The *SM1* is induced and expressed not just

during plant interactions but also in the absence of a plant and further promotes the expression of genes related to pathogenesis and hypersensitive reactions (Djonovic et al. 2007).

3.10 Production of Antibiotics and Secondary Metabolites

Antibiosis occurs during microbial interactions and involves low molecular weight diffusible secondary metabolites (SMs) or antibiotics produced by *Trichoderma* strains that are detrimental for the growth of plant pathogen (Benitez et al. 2004; Viterbo et al. 2007). Fungal antibiosis is associated with the production of antibiotics and/or hydrolytic enzymes and secondary metabolites related to possible competition for nutrients in the rhizosphere and microbial antagonism (Harman et al. 2004). Antibiotics and secondary metabolites produced by *Trichoderma* spp. are crucial in their biocontrol activity (Ajitha and Lakshmedevi 2010). Secondary metabolites including antibiotics are not directly involved in the natural growth, development, or reproduction of the fungus. They are chemically dissimilar from natural compounds and may play important roles in the defense response, competition against other microorganisms, symbiosis, metal transport, differentiation, and stimulation or inhibition of spore formation and germination, etc. (Reino et al. 2008).

Based upon analytical studies, from the genus *Trichoderma* about 180 secondary metabolites (natural products) have been identified, representing various classes of chemical compounds and with the structures of more than 100 compounds described (Reino et al. 2008). Several molecules involved in the suppression of numerous soilborne plant pathogens have been described (Benitez et al. 2004). The communication between *Trichoderma* and their plant hosts is established by complex chemical interaction comprising volatile and diffusible secondary metabolites, small peptides, and/or antibiotics, which affect root growth, branching, and absorptive capacity (Lopez-Bucio et al. 2015). *Trichoderma* spp. produces several secondary metabolites, antibacterial and antifungal antibiotics which comprise volatile and nonvolatile toxic metabolites such as harzianic acid, alamethicins, tricholin, peptaibols, 6-*n*-pentyl-6H-pyran-2-one (6PP/6-PAP), formic aldehyde, acetaldehydes gliotoxin, viridian, Terpenoids, harzianopyridone, harziandione, massoilactone, viridin, gliovirin, glisoprenins, trichodermin, heptelidic acid, epipolythiodioxopi perazines (ETPs) (Gajera et al. 2013; Hermosa et al. 2014; Strakowska et al. 2014).

Various genes are components of large biosynthetic gene clusters harboring those encoding core enzymes such as polyketide synthases (PKSs), nonribosomal peptide synthetases (NRPSs), accessory enzymes and genes for transporters and transcription features (Bansal and Mukherjee 2016a). Genomes of some more mycotrophic species including *T. asperellum*, *T. parareesei*, *T. harzianum*, *T. gamsii*, and the opportunistic human pathogens *T. longibrachiatum* and *T. citrinoviride* were subsequently added to the public databases (Baroncelli et al. 2016). The hydrolytic enzymes along with antibiotics results in an advanced intensity of antagonism than

that achieved by either mechanism singly (Monte 2001). Synergetic effects between an endochitinase from *T. harzianum* and gliotoxin and that of hydrolytic enzymes and peptaibols on conidial germination of *B. cinerea* have been reported (Howell 2003). A peptaibol synthetase from *T. virens* has recently been identified and the corresponding gene, which has been cloned, will facilitate studies of this compound and its contribution to biocontrol.

The genes involved in secondary metabolite biosynthesis in *Trichoderma* are present as clusters that can span more than 10 kb, with a few exceptions (Lo et al. 2012). These clusters encode the enzyme complexes such as the NRPS or PKS that comprise of various domains and modules with distinct activities (Strieker et al. 2010). The synthesis of the structural backbone of these unique secondary metabolites by PKS and NRPS utilizes building blocks such as malonyl groups and amino acids or their derivatives (Brakhage and Schroeckh 2011). The genes crucial in the biocontrol mechanisms of *Trichoderma* are of great value. The vast prospective of *Trichoderma* spp. to produce an array of diverse metabolites is reflected in the genomes of the species. Secondary metabolite genes of *Trichoderma* are organized just about the signature genes which encode NRPSs, PKSs, and terpene synthases, which define the biosynthetic pathways and clusters (Osbourn 2010).

3.11 Non-ribosomal Peptide Synthases (NRPSs)

The genome of *Trichoderma* is a repertoire for secondary metabolite production, including both beneficial and a few toxic compounds, which have been well characterized and few novel (Mukherjee et al. 2012b). Polyketide synthases and NRPSs are two major classes of secondary metabolites (Baker et al. 2012). NRPSs are large modular enzymes involved in the synthesis of Nonribosomal peptides (Mukherjee et al. 2012c). NRPS enzymes are composed of a series of modules that behave like an assembly line, each incorporating one monomer into the peptide (Strieker et al. 2010). The monomers may be peptaibols or even compounds that are non-amino acids. The peptides may be structurally linear or cyclic, and often go through large chemical modifications (Strieker et al. 2010). Peptaibols fit into the antifungal armory of *Trichoderma* and are now reported to trigger the apoptotic death of the host. *Trichoderma* spp. synthesize NRPSs, the large multifunctional enzyme domains that assemble various compounds using a diverse precursors such as non-proteinogenic amino acids and hydroxy or carboxyl acids (Mukherjee et al. 2011; Shi et al. 2012). Genes encoding hydrolytic enzymes like chitinases and glucanases and those for SMs like NRPSs are concurrently expressed to destroy the plant pathogens (Kubicek et al. 2011). Numerous NRPSs implicated in the synthesis of peptaibols in *Trichoderma* spp. have been recognized (Mukherjee et al. 2011). However, the characterization of NRPSs from additional biological control agents is still lacking.

3.12 Peptaibols

Peptaibols are short-chain linear polypeptides that generally exhibit strong antimicrobial effects against bacteria and fungi, and act in synergy with CWDEs inhibiting the growth of fungal pathogens and rendering the plant resistant to phytopathogens (Mukherjee et al. 2011). Peptaibols produced largely by members of *Trichoderma* are peptides composed of α-aminoisobutyric acid and a C-terminal 1, 2-amino alcohol constituting the major group which is characterized by an acylated N-terminus and an amide-bound amino alcohol at the C-terminus (Degenkolb et al. 2008). About 1000 various peptaibiotics that have been recognized and categorized into numerous groups on the basis of their chemical constructions and these include lipoaminopeptides, lipopeptaibols, peptaibols, and cyclic peptaibiotics (Neumann et al. 2015).

Trichoderma spp. are usually considered as the richest source of peptaibols and over 80% of the entries in the Comprehensive Peptaibiotics Database can be assigned to this fungal genus with *T. viride*, *T. brevicompactum*, *T. virens*, *T. parceramosum/T. ghanense*, and *T. harzianum* being the most extensively studied species (Stoppacher et al. 2013; Neumann et al. 2015). The biocontrol activity of peptaibols originates from their capacity of membrane altering properties, formation of pores in lipid membranes, as well as induction systemic resistance in plants against pathogens attack (Mukherjee et al. 2011). Numerous NRPSs involved in the synthesis of peptaibols in *Trichoderma* spp. have been studied (Mukherjee et al. 2011). There are two peptaibol synthetases such as of 18 and 14 modules in *Trichoderma* genomes and more than 700 peptaibol sequences are known, generally of *Trichoderma* origin (Degenkolb et al. 2008).

The genome of ITEM 908 harbors three loci with sequences encoding the homologs of potential peptaibol synthetases in *T. virens* (Mukherjee et al. 2012b). The three genes named *tex1*, *tex2*, *and tex3* have been identified as paptaibol synthetases. *Tex1* is a long chain peptide (18–25 remains) peptaibol synthetase and it is involved in the synthesis of 18 residue peptaibols (Wiest et al. 2002). *Tex1* accumulates an 18-residue peptaibol (trichovirin II) and by using *Dtex1* mutants trichovirin II type peptaibols revealed to activate induced resistance in hosts (Viterbo et al. 2007). Peptaibols of class 11, 14, and 18mer potentially inhibit pathogens including *A. solani*, *P. capsici*, *R. solani*, *S. rolfsii*, and *S. cepivorum* (Velázquez-Robledo et al. 2011). The three *Trichoderma* genomes discovered the presence of only 7, 14, and 18–20 module peptaibol synthetases (Degenkolb et al. 2012). Recently, the short peptaibol synthetase gene *tex2* has been delivered for the association of 11 and 14 modules peptaibols by a single NRPS *Tex2* of *T. virens* (Mukherjee et al. 2011; Reithner et al. 2011), later confirmed in *T. reesei* (Etxebeste et al. 2010). The *T. virens Tex2* was revealed to synthesize a total of 88 peptaibols belonging to 11 and 14-residue groups. The peptaibol trichokonin VI of *T. pseudokoningii* SMF2 was revealed to induce an extensive apoptotic programmed cell death in *F. oxysporum* (Shi et al. 2012). The *tex3*, homologous to *tex1* has seven complete modules arranged in a linear fashion (Mukherjee et al. 2012c) and

homologs of all of these three genes in the genome of *T. atrobrunneum* ITEM908. Exogenous treatments of *Trichoderma* peptaibols in tobacco plants elicited a defense response by multiple defenses signaling pathways and resulting in increased resistance to the tobacco mosaic virus (Benitez et al. 2004; Luo et al. 2010; Holzlechner et al. 2016). The non-ribosomally synthesized peptaibols act as potential signature molecules forming the basis of mass spectrometry-based, species-specific monitoring approaches, as the peptaibiome of particular *Trichoderma* spp. is unique from that of closely related species (Marik et al. 2017).

3.13 Gliotoxin and Gliovirin

Gliotoxin and gliovirin are Epipolythiodioxopiperazines (ETPs), a class of peptides (Patron et al. 2007). The ETPs characterized by a diketopiperazine ring with a disulfide bridge derived from a cyclic peptide, produced by *Trichoderma* (Błaszczyk et al. 2014) and the genes for its biosynthesis in *T. virens* have been identified (Vargas et al. 2014). Gliotoxin belongs to the nonribosomal peptides (Patron et al. 2007). Gliotoxin derives from cyclic dipeptides that arise by the condensation of two α-amino acids and is produced biosynthetically from L-phenylalanine and L-serine via the cyclic dipeptide. The gliotoxin is produced by Q strains of *T. virens* whereas another ETP, gliovirin, is exclusively produced by the P strains of *T. virens*, both of which have potential antimicrobial activity (Scharf et al. 2016). Gliotoxin has attracted great attention for its function in the biocontrol of soilborne pathogens (Howell 2006). The *T. virens* veA ortholog *vel1* regulates gliotoxin biosynthesis, biocontrol activity, and many other secondary metabolism-related genes (Mukherjee and Kenerley 2010; Mukherjee et al. 2013). The gliotoxin genes clusters *gliZ*, *gliJ*, *gliA*, and *gliT* identified in the *T. virens* Q strain genome have a powerful role in the biocontrol of soilborne plant pathogens (Howell 2006).

3.14 Siderophores

The fungal siderophores, fusarinines, coprogens, and ferrichromes belong to the group of hydroxamate siderophores that share the structural unit N5-acyl-N5-hydroxyornithine (Renshaw et al. 2002; Lehner et al. 2013). Isotope assisted screening revealed an average 12-14 siderophores produced by *T. asperellum*, *T. atroviride*, *T. gamsii*, *T. harzianum*, *T. hamatum*, *T. virens*, *T. polysporum*, and *T. reesei* with dimerum acid, coprogren, fusarinine A, fusigen, and the intracellular siderophore ferricrocin (Lehner et al. 2013). Genome sequencing of *Trichoderma* spp. have revealed a single gene for ferricrocin synthesis, belonging to a secondary metabolism gene cluster (Kubicek et al. 2011). In *Trichoderma* spp. three NRPSs linked to siderophore biosynthesis have been known in different gene clusters (Mukherjee et al. 2013; Zeilinger et al. 2016). The genome of ITEM 908 harbors

homologs of the aldehyde dehydrogenase (g626), the oxidoreductase (g625), the NRPS (g624), the ornithine monooxygenase (g623), and the transcription factor (g622). The second gene cluster comprises *NPS6*, a key enzyme that is accountable for extracellular siderophore production in *T. virens* (Mukherjee et al. 2013).

T. virens and *T. reesei* each contain two putative gene clusters having an NRPS as the core member, whose orthologs (*SidD* and *NPS6*) having potential in siderophore synthesis (Kubicek et al. 2011; Mukherjee et al. 2012c). *T. harzianum* produced the maximum number of siderophores, while, *T. reesei* biosynthesized one *cis*-fusarinine as the main siderophore and three others that were present only in *T. harzianum*.

3.15 6-Pentyl Pyrone (6-PP)/Pyrones

A volatile compound, 6-Pentyl pyrone (6-PP) with the unique coconut aroma, was produced by *Trichoderma* spp. (Vinale et al. 2008a, b). This compound fits into the chemically diverse class of low molecular weight metabolites with a high vapor pressure at room temperature and low water solubility grouped as volatile organic compounds (VOCs). Pyrones are derivative from fatty acids and the biosynthesis of 6-PP has been studied in *T. atroviride* by using [U-14C] and [1-14C] linoleic acid. *T. atroviride* exhibited an upregulation of the lipoxygenase gene thought to be involved in 6-PP biosynthesis and in *T. arundinaceum*, growth in co-culture with *B. cinerea* led to enhance expression levels of the "tri" biosynthetic genes (Malmierca et al. 2015). A lipoxygenase gene specific to *T. atroviride* may be involved in the biosynthetic pathway for the production of 6-PP but no useful characterization has yet been achieved (Kubicek et al. 2011).

A transcription factor gene called *Thctf1* was isolated from *T. harzianum* and involves in the synthesis of 6-pentyl-2H-pyran-2-one (6-PP) and displays antifungal activity against *R. solani*, *B. cinerea*, and *S. rolfsii*. The sequences were studied using the Laser gene package and cloned using pGEM-T vector (Rubio et al. 2009). Pyrones have been identified from numerous *T. harzianum* strains that are antagonistic to *G. graminis* var. *tritici* and *F. moniliforme*. The 6-PP secreted by *T. harzianum* potentially degrades mycotoxins including fusaric acid (FA) and additionally inhibits the mycelial growth of *F. moniliforme* (El-Hasan et al. 2008). Various *Trichoderma* spp. such as *T. viride*, *T. atroviride*, *T. harzianum*, *T. koningii* are able to produce the volatile antibiotic 6-PP which is antagonistic to *B. cinerea*, *R. solani* and *F. oxysporum* (Reino et al. 2008). The PR-1 gene was induced by 6-PP and harzianopyridone at 1 mg/l in canola cotyledons, indicating the initiation of an SA-dependent SAR response. At the same time, a chitinase PR-3 gene related to JA-dependent defense was induced by an equal amount of 6-PP, harzianopyridone or azaphilone (Viterbo et al. 2010). Recent studies revealed that *T. atroviride* produced 6-PP promoting plant growth and regulating the root architecture, preventing primary root growth and inducing lateral root formation (Garnica-Vergara et al. 2015).

3.16 Polyketides

The polyketides are a structurally diverse group of secondary metabolites, produced by numerous organisms, including filamentous fungi, with antibiotic activity such as (tetracyclines, polyenes, and macrolides), the mycotoxins (aflatoxin, fusaric acid, and fumonisin), the pigments (bikaverin and fusarubin) as well as the statins (lovastatin and compactin) (Zeilinger et al. 2016). These groups of molecules are that have carbon skeletons made up of polyenes, polyphenols, macrolides, enediynes, and polyethers. Polyketides are synthesized via pathways catalyzed by a collection of enzymes called PKSs, which are great multi-enzyme protein complexes that function with a coordinated group of active sites.

Genomes of *Trichoderma* spp. are rich in PKS encoding genes, suggesting the significance polyketides in the biology and activity of the fungus. There are several PKS genes involved in biosynthetic pathways and the genomes of *T. virens* and *T. atroviride* comprise 18 PKSs and the genome of *T. reesei* encodes 11 PKSs (Baker et al. 2012). The PKS genes are found usually as clusters along with genes coding cytochrome P450 monooxygenases, short-chain reductases or epimerases (Schmoll et al. 2016). Phylogenomic analysis of PKS genes of *T. reesei*, *T. virens*, and *T. atroviride* showed that most of the PKSs belonged to the lovastatin/citrinine or fumonisins clades that were present as orthologues in all three species studied (Baker et al. 2012). Two *T. atroviride* PKS genes were found to be expressed when confronted *R. solani*, indicating its possible role in mycoparasitism (Mukherjee et al. 2012b, c). Similar *gliP* and other SMs associated genes, PKSs in *T. virens* are regulated by the velvet complex protein *Vel1* (Mukherjee and Kenerley 2010).

There are numerous fungal SMs of interest produced by NRPS–PKS hybrid enzymes that consist of a PKS fused to a single, or in some cases truncated NRPS module (Fisch 2013). These hybrid enzymes are encoded in the genomes of *T. atroviride*, *T. reesei*, and *T. virens* (Kubicek et al. 2011). The first *Trichoderma* genome to be sequenced was from *T. reesei* and that contained 2 NRPS-PKS hybrid-encoding genes and the genes encoding terpenoid synthases (12 genes), NRPS (8 genes), and PKS (11 genes) (Martinez et al. 2008). The genome of *T. atroviride* harbors genes for 14 NRPSs, 18 PKSs, a single NRPS-PKS hybrid, and 14 terpenoid synthase domains (Kubicek et al. 2011). The efficient investigation of the *T. virens* showed that *Tex13*, a hybrid enzyme PKS/NRPS, was involved in inducing phenylalanine ammonialyase, the defense-related gene in maize seedlings; further the induction of *Tex13* is more than 40-fold during interactions of *T. virens* with maize roots (Mukherjee et al. 2012c).

3.17 Terpenoids/Steroids

Terpenoids are the most versatile natural products on earth and comprise a group of volatile and non-volatile secondary metabolites. The assembly of numerous activated forms of five carbon compounds isopentenyl/isoprene (C_5H_8) units depending on the number of carbon atoms. Each class contains molecules that are linear and cyclic; terpene cyclases generate the cyclization. Terpenoids recognized from *Trichoderma* spp. include volatile terpenes, the tetracyclic diterpene harziandione, sesquiterpenes such as the trichothecenes trichodermin and *harzianum* A and the triterpene viridin (Stoppacher et al. 2010; Cardoza et al. 2011). Compounds such as trichodermin isolated from *T. polysporum*, *T. sporulosum*, *T. virens*, and *T. reesei*, *Harzianum* A from *T. harzianum* and mycotoxin T2 detected in cultures of *T. lignorum* are examples of trichothecenes with antifungal activity. Trichothecene is synthesized by certain fungal genera such as *harzianum* A and trichodermin from *T. arundinaceum* and *T. brevicompactum*, respectively (Cardoza et al. 2011). The terpenoid Trichodermin is an extremely fungi toxic as well as phytotoxic, trichothecene type toxin produced by *T. brevicompactum* (Yuan et al. 2016). The production of trichodermin in *T. brevicompactum* involves the *tri5* gene which has a significant role such that its overexpression increases trichodermin production as well as the antimicrobial activity (Tijerino et al. 2011). A nonphytotoxic trichothecene, Harzianum A is antagonistic to fungal plant pathogens and triggers the genes responsible for plant defense. The *tri* gene cluster involved in harzianumA synthesis was characterized in *T. arundinaceum* (Malmierca et al. 2013). The triterpene biosynthetic pathway is catalyzed by enzymes encoded by the *erg1*, *erg7*, and *erg9* genes that are also capable of synthesis of viridin, a well-known antifungal molecule. In *T. harzianum*, the overexpression of *erg1* enhanced its antifungal effects against *B. cinerea* and reduced the lesion size. However, the induction of salicylate related plant defense genes and root colonization ability of *T. harzianum* was reduced (Cardoza et al. 2014).

The trichothecenes, sesquiterpenes are a huge group of toxic SMs produced by a few fungal species (Woloshuk and Shim 2013). The *tri* gene cluster for trichothecene biosynthesis has previously been defined in *T. arundinaceum* and *T. brevicompactum* and is made up of orthologues of seven genes present in the *Fusarium tri* cluster (Cardoza et al. 2011). Trichothecenes are sesquiterpenoid epoxides initially formed through isomerization–cyclization of farnesyl pyrophosphate from the parent compound trichodiene. Trichodiene synthase, encoded by *tri5* gene is the key enzyme catalyzing this reaction. The genes involved in trichothecene biosynthesis including *Tri5* are all organized in a coordinately regulated gene cluster.

Terpenes were isolated from *T. lignorum* HKI 0257, a new sesquiterpenoid named lignoren. This compound has a santalene-like structure and displays a sensible antimicrobial activity against *B. subtilis*, *M. smegmatis*, *P. aeruginosa*, *S. salmonicolor*, and *Rhodotorula rubra* (Berg et al. 2004). A recent study reported that the *T. reesei* genome encodes 6 terpene synthases or cyclases, 7 in *T. atroviride*,

and 11 in *T. virens*, of which two, three, and six are part of biosynthetic gene clusters (Bansal and Mukherjee 2016b). Harzianic acid (HA), a nitrogen heterocyclic compound produced by *T. harzianum* has growth-promoting effect (Vinale et al. 2009) which acts as an antagonistic effect on fungal pathogens as reported in canola seedlings (Vinale et al. 2009). Also, they promote nutrients uptake and growth of plants by their ability to produce siderophores (Vinale et al. 2013).

3.18 Induced Systemic Resistance by *Trichoderma*

Induced systemic resistance is one of the most important mechanisms of biocontrol effects of *Trichoderma* (Harman 2006; Vinale et al. 2008a). Induction of metabolic changes in plants is brought about by several strains of *T. virens*, *T. asperellum*, *T. harzianum*, and *T. atroviride* that result in increased resistance to a wide range of plant pathogenic microorganisms. The colonization and induction of plant resistance by *Trichoderma* with some species is related to that elicited by rhizobacteria, which enhance the defense system but do not involve the production of pathogenesis-related proteins (PR proteins) (Harman et al. 2004). Induced resistance conferred to host plants by microorganisms are of two different kinds named induced systemic resistance (ISR) and systemic acquired resistance (SAR), which differ by the biochemical pathways involved (Birkenbihl et al. 2017). The SAR is triggered by previous exposure and infections by avirulent pathogens, whereas ISR is triggered by previous colonization of the rhizosphere by *Trichoderma* spp. SAR is a salicylic acid-dependent pathway, whereas ISR is salicylic acid independent (Hermosa et al. 2013; You et al. 2016; Birkenbihl et al. 2017). These defense pathways involve the evolution of pattern recognition receptors that specifically recognize microbe-based signals referred to as pathogen or microbe-associated molecular patterns (PAMPs or MAMPs) (Hermosa et al. 2012). The ability of *Trichoderma* spp. hyphae to release a variety of MAMPs for molecular recognition may contribute to signal cascade by signaling molecule within the plant such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Lorito et al. 2010).

In the interactions of *Trichoderma* with plants, different classes of metabolites may act as elicitors or so-called resistance inducers (Woo and Lorito 2007). These metabolites are usually proteins including enzymes (serine proteases, xylanases, chitinases, phenylalanine ammonia lyase, peroxidase, polyphenol oxidase, lipoxygenase, cellulases, and glucanases) (Shoresh et al. 2005), proteins as PR (pathogenesis-related protein), gene products resembling proteins encoded by avirulent genes, low molecular compounds released from cell walls of fungi or plants by fungal hydrolytic enzymes and phytoalexin accumulation in host plants (Tuão Gava and Pinto 2016). *Trichoderma* endochitinase can also increase defense, probably via induction of plant defense-related proteins. Expression of *T. atroviride* endochitinase *Ech42* displayed enhanced resistance toward *Fusarium* sp. infection (McIntyre et al. 2004). Expression of *T. harzianum* chitinase *Chit42* in tobacco and potato plants resulted in improved resistance to the foliar pathogens *A. alternata*,

A. solani, *B. cinerea*, and to the soilborne pathogen *R. solani* (Howell 2003). Similarly, effects were seen on the heterologous expression of *Chit42* in strawberry infected with *Colletotrichum* and with *Chit42* and a β-1, 6 glucanase in melon and tomato plants. *T. harzianum* efficiently increased the SA and JA contents in melon thus altering the plant responses against *F. oxysporum* (Martínez-Medina et al. 2010). Expression of fungal chitinases in plants with CBDs, such as *Chit42CBD*, which already has increased antifungal activity, may result in greater resistance against phytopathogens (Limon et al. 2004). *Eix* also acts as a fungal elicitor that regulates phytoalexin production and defense gene expression through calcineurin B-like protein-interacting protein kinases, OsCIPK14/15, in rice (Kurusu et al. 2010). *T. longibrachiatum* cellulases, *T. viride* xylanase *Xyn2/Eix*, *T. harzianum* endopolygalacturonase *ThPG1* generates a response in *Arabidopsis* (Moran-Diez et al. 2009).

The *T. asperellum* swollenin *TasSwo* stimulates defense responses in cucumber roots and leaves and affords local protection against phytopathogens (Moran-Diez et al. 2009). *T. asperellum* produces the class I hydrophobin *TasHyd1*, which aids in root surface colonization, possibly by improving its attachment to the root surface and protecting the hyphal tips from plant defense compounds (Viterbo and Chet 2006). In oil palm plants the expression of defense gene chitinase was increased in plants treated with *T. harzianum* and *Ganoderma boninense* compared to those treated with *G. boninense* alone (Naher et al. 2012). In a study on cucumber plants, *T. asperellum* induced a systemic response of two defense-related genes encoding phenylalanine and hydroperoxidase lyase and systemic accumulation of phytoalexins against *P. syringae* pv. *lachrymans* (Yedidia et al. 2003). *T. asperellum* T203 modulated the expression of the genes *Lox1* (Lipoxygenase 1), a constituent of the JA biosynthetic pathway; PAL1, an element of the biosynthetic pathway for SA; and *Etr1* and *Ctr1*, both components of ET signaling (Shoresh et al. 2005). Contreras-Cornejo et al. (2011) who recommended that JA as an important factor in boosting plant immunity involved in defense responses elicited by *Trichoderma* in *Arabidopsis* against *B. cinerea*. Similar soil application of *T. viride* to tomato plants with *F. oxysporum* or *R. solani* resulted in an increase in the expression of JA-related *PDF1* and *PDF2* genes (Hafez et al. 2013).

Molecular confirmation exhibited that *A. thaliana* root colonization by *T. asperelloides* T203 activates a quick rise in the expression of transcription factors (WRKY18, WRKY40, WRKY60, and WRKY33) activating JA pathway responses and represses SA signaling. WRKY18, WRKY40, and WRKY60 are pathogen-induced and encode three structurally related WRKY proteins that exert a positive role in JA-mediated defense (Brotman et al. 2013). Mathys et al. (2012) reported that induced resistance in *Arabidopsis* roots treated with *T. hamatum* is regulated by JA and ET related genes. Additionally, the JA inducible genes lipoxygenase *(Lox1)* and phenylalanine ammonialyase (*Pal1*) and the ET-inducible genes ethylene receptor (*ETR1*) and constitutive triple response 1 (*CTR1*) were found to be induced both locally and systemically on treatment with *T. asperellum* T-203 spores alone. Tucci et al. (2011) observed that *Trichoderma* CF treatment triggered ISR through SA-dependent gene expression

Several SMs and proteins involved in mycoparasitism and antibiosis have been identified as ISR elicitors. Secondary metabolites like alamethicin and trichokinin (20mer peptaibol), 18mer peptaibol, 6-pentyl-a-pyrone, harzianolide, and harzianopyridone at high doses have antimicrobial effects but at low concentrations are ISR inducers (Vinale et al. 2014). Peptaibols produced by *Trichoderma* may act as elicitors of plant defense mechanisms against pathogens (Wiest et al. 2002). A peptaibol synthetase from *T. virens* was purified and the achieved cloning of the corresponding gene will facilitate an understanding of the role of this class of compounds in plant defense response. Application of alamethicin, a long sequence peptaibol with a 20-residue produced by *T. viride*, elicits JA and SA biosynthesis in lima bean in *Phaseolus lunatus* (lima bean) (Maischak et al. 2010) and *A. thaliana* hypersensitive reaction to pathogen attack (Rippa et al. 2010). The 18mer peptaibols from *T. virens* elicit systemic induced defense responses in cucumber against the leaf pathogen *P. syringae* (Viterbo et al. 2007; Luo et al. 2011).

Early defense responses triggered by SMs from *T. atroviride* induced intracellular Ca^{2+} variations in soybean cells (Navazio et al. 2007). The defense mechanisms plants and their developmental responses to *Trichoderma* share common components. This was evident when 1 ppm of 6-pentyl-a-pyrone, harzianolide, and harzianopyridone activated plant defense mechanisms and regulated plant growth in pea, tomato, and canola (Vinale et al. 2008b), suggesting that plants' *Epl-1* has been described as being able to trigger defense reactions in plants (Gomes et al. 2015; Ramada et al. 2016; Salas-Marina et al. 2015). Fernanda Blauth de Lima (2017) reported that, when challenged by the *Guignardia citricarpain* citrus black, *T. harzianum* T1A there was a decrease in the total amount of secreted proteins, particularly those involved in primary metabolism while the secretion of proteins related to fungal interaction increased. *T. harzianum* T1A secretes proteins related to the control of *G. citricarpa* and induction of plant resistance, even in the absence of pathogen challenge.

A PKS/NRPS hybrid enzyme involved in defense responses in maize was identified (Mukherjee et al. 2012c). Non-enzymatic proteins such as small cysteine-rich hydrophobin-like protein of the cerato-platanin (CP) family *Sm1* secreted by *T. virens* and *Epl1* secreted by *T. atroviride* trigger the activation of plant defense mechanisms and the induction of systemic resistance in cotton and maize (Seidl et al. 2006). In response to invasion by a pathogen, the *Sm1* of *T. virens* acts as an elicitor inducing the expression of CAD1-C gene encoding (+)-δ-cadinene synthase in cotton petioles which is the primary precursor for phytoalexin production (Djonovic et al. 2006; Yoshikuni et al. 2006). Induction of defense mechanisms in plants is also brought about by another group of proteins that are the products of avirulence-like (*Avr*) genes (Woo et al. 2006). The hydrophobin-like protein produced by T22 was identified to induce both enhanced root development and disease resistance (Ruocco et al. 2007). Early defense reactive oxygen species (ROS) such as H_2O_2 and nitric oxide also are associated in *Trichoderma*-mediated plant immunity in cotton, rice, and *A. thaliana* (Gupta et al. 2014; Contreras-Cornejo et al. 2014).

3.19 Stress Tolerances

The genus *Trichoderma* is able to inhabit and colonize diverse niches due to its metabolic versatility and tolerance to stress conditions. Among fungal biocontrol agents, *Trichoderma* spp. have gained much interest due to their high reproductive capacity, prolific producers of secondary metabolites, survived under unfavorable conditions, and ability to resist against plant pathogenic fungi (Contreras-Cornejo et al. 2016). *Trichoderma* spp. colonize plants and produce certain compounds (gibberellins, ethylene, auxins, plant enzymes, antioxidants) and phytoalexins and phenols that confer abiotic stresses tolerance and enhance the branching capacity of the root system (Brotman et al. 2013; Lopez-Bucio et al. 2015). Several recent studies report that *Trichoderma* induces tolerance against abiotic stresses and improves plant growth (Zeilinger et al. 2016; Yasmeen and Siddiqui 2017). *Trichoderma* spp. can also promote growth and induce resistance to a variety of abiotic stresses, including water deficit, temperature, salinity, and osmotic stress (Zelicourt et al. 2016).

Trichoderma spp. are significant for regulating numerous genes involved in plant defense against biotic and abiotic stresses and improving the plant basal metabolism (Domínguez et al. 2016). The genes responsible for resistance to salt or other stresses in *T. harzianum*, *ThHog1* (Delgado-Jarana et al. 2006), *Hsp70* (Montero-Barrientos et al. 2010) and Thkel1 (Hermosa et al. 2011) have been successively characterized. In an HSP24-carrying transgenic mutant of *S. cerevisiae*, the small heat shock protein *Hsp24* of *T. harzianum* was shown to enhance salt, heat, and drought tolerances (Liming et al. 2008). Cloning of *hsp70* gene in *pGEM-T* vector and its expression in different isolates of *T. harzianum* enhanced fungal resistance to heat and other stresses such as oxidative tolerances, osmotic and salt tolerance (Montero-Barrientos et al. 2010). The sequences were analyzed using DNA star package and aligned using CLUSTAL X algorithm. The genome of *T. reesei* revealed three genes for potential small heat shock proteins; in *T. atroviride* there were four genes and in *T. virens* five genes were present. All of them are homologs to *N. crassa Hsp30* (Plesofsky-Vig and Brambl 1995). *Hsp30* of *N. crassa* was found essential for carbon utilization at high temperatures (Plesofsky-Vig and Brambl 1995).

Montero-Barrientos et al. (2007) studied the response of the small heat shock protein *Hsp23* of *T. virens* T59 to high and low temperatures and reported the expression of *Hsp23* was improved on ethanol addition. The *Hsp23* gene when transferred to the biocontrol strain *T. harzianum* T34 resulted in higher biomass production in the mutant strains than in the wild type T34 strain along with improved thermotolerance (Bonaccorsi et al. 2006). The *Thkel1* gene encodes putative kelch-repeat proteins which modulate glucosidase activity and confer salt tolerance, enhance seed germination, and osmotic stress in *Arabidopsis* plants, probably due to the glucosidase activity and abscisic acid (ABA) level modulations (Hermosa et al. 2011). The vector used for cloning was pSIL-KEL and was transformed into *T. harzianum*. The *Thkel1* gene expression was studied by growing the fungus under various biotic and abiotic stress conditions (Hermosa et al. 2011).

Rana et al. (2012) reported that genes encoding an endochitinase (*chit42*) and a chitosanase (*harcho*) from *T. harzianum*, if co-transformed in wheat plants resulted in an increased tolerance to the powdery mildew pathogen (*Blumeria graminis* f.sp. *tritici*). Under conditions of water scarcity, *T. harzianum* T22 modulated the expression of genes that encoding enzymes that scavenge ROS, such as SOD, catalase, and ascorbate peroxidase, in both root and shoots of tomato plants (Shoresh et al. 2010; Mastouri et al. 2012). The highly conserved ribosomal protein subunits like *Rpl44* and *Rps3ae* are also promising candidates for enhanced tolerance in crop plants (Liang et al. 2015) and these genes are generally found downstream to those resistant pathways likely having a direct contribution to stress tolerance. Systemic induction of about 40 genes by *T. harzianum* 382 in tomato plants with functions related to biotic or abiotic stress, as well as RNA, DNA, and protein metabolism (Shoresh et al. 2010). About 205 differentially expressed proteins were identified, in roots and shoots of maize plants inoculated by *T. harzianum* T226. From *T. virens* glutathione transferase gene *TvGST* was cloned. The expression of this gene in transgenic plants showed tolerance to cadmium accumulation in plants thus acting as a cadmium tolerance gene (Dixit et al. 2011).

3.20 Hyphal Growth

In *T. reesei* the *TrCCD1* gene helps in hyphal growth, development of conidiospores, and production of carotenoid pigment, therefore improving biocontrol activity (Zhong et al. 2009). Chitinase degrade chitin, the linear homopolymer of β-1, 4-*N*-acetyl-D-glucosamine, which is the main cell wall constituent of plant pathogenic fungi thus inhibiting the in vitro germination and hyphal growth (Lorito et al. 1996). These genes find application in improving plant defense against fungal pathogens. Bae and Knudsen (2000) reported that the to monitor hyphal growth, activities, and existence of a *T. harzianum* strain, transformed strain ThzID1 with plasmids carrying the *gfp* (pTEFEGFP), *Gus* (pNOM102), and *hygB* (pAN7-2) genes. The mitotic stability of the cotransformants and their ability to colonize the inactive sclerotia of the plant pathogen *S. sclerotiorum* in soil were studied.

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