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Role of *Trichoderma* spp. in Biocontrol of Plant Diseases

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G. Hariharan, L. M. Rifnas, and K. Prasannath

Abstract

Crop losses incurred by major plant pathogens, fungi, bacteria, nematodes and viruses are in a surge. The detrimental impacts of current disease management practices create an urgent need to develop non-chemical and eco-friendly methods. Biological control or biocontrol of phytopathogens is a sustainable and sound approach to overwhelm various threats caused by the existing control measures. Among the biocontrol agents (BCAs), avirulent, filamentous mycoparasitic *Trichoderma* spp. are well-known for their agricultural application versatility. The host plant-*Trichoderma*-pathogen interaction plays a pivotal role in plant disease management. *Trichoderma* spp. network with plant pathogens via direct mechanisms of mycoparasitism, antibiosis and competition while indirectly inducing systemic disease resistance and promoting plant growth and yield when *Trichoderma*-plant interaction is switched on. The interactions support efficient biological disease control and overall crop recovery from various diseases and ultimately lead to successful crop production. *Trichoderma*-based BCAs offer significant contributions in the arena of plant protection and disease management. An array of *Trichoderma* spp. have proven effective against a broad range of plant pathogens by enhancing the plants' overall health and improving their yield. The biocontrol activity, plant-*Trichoderma* interactions and the efficacy could vary with the type of the pathogens, *Trichoderma* strain and host plant. Besides, the efficacy and stability of widely used and newly recognized strains of

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Trichoderma still need to be evaluated under different environmental conditions in the field for successful outcomes.

Keywords

Biocontrol · Host plant-*Trichoderma*-pathogen interaction · Plant diseases · Plant pathogens · *Trichoderma* spp.

3.1 Introduction

Fungal and bacterial pathogens are the primary cause of plant diseases, which can cause severe losses on crops every year. These losses can reduce food supplies and lead to inferior quality agricultural products, economic difficulties for plant growers and processors and, finally, increased prices of end products. To a broader extent, the improvement of the agriculture sector encountered the need to feed a rising human population. However, the increase in agricultural production has achieved a certain remarkable level in several countries (Bommarco et al. 2013). The increase in crop yield is widely related to improved plant pest and disease management methods, which include a clear understanding of the disease-causing organisms and the use of a broader range of different types of control strategies. There must be efficient and sustainable crop protection measures for a vast economic and ecological significance for global food production (Flood 2010). Climatic change, population growth and international trade are the challenges faced by future crop production practices (Chakraborty and Newton 2011; Sundström et al. 2014). The above challenges have already resulted in enhanced risks of establishment, distribution and transmission of plant pests and diseases (Cheatham et al. 2009; Barnwal et al. 2013), leading to undesirable effects on human health and the environment (Savary et al. 2017).

Most of the plant pathogens are specific to a particular group of plant species, and their effects are very much harmful when they attack an economically important crop. When cereal grains, especially rice and wheat, are affected by diseases, it may cause severe complications for the worldwide population's economy and nutritional status since both supply the majority of the world's daily dietary intake. Plant pathogens such as bacteria, virus and fungi infecting plants usually do not cause effects on human (Balique et al. 2015). Plant pathogens can affect human by decreasing the availability of food material by contaminating with toxic compounds. It is well-known that plant pathogens can reduce food availability by interacting not only with crop yield but also with the reduction of harvesting quality and nutritional values. It can lead to a lack of food supply to the entire world, and ultimately in worst cases, there are chances for starvation and death.

Globally, crop producers require chemical pesticides to control plant pathogens to sustain agricultural products' value and quality (Junaid et al. 2013). It was projected that 37% of crop loss was caused by insect pests and 12% was due to plant pathogens (Sharma et al. 2012). Controlling plant pathogens by chemical method is effective and convenient, but it has proven to be a threatening strategy to all life forms on

earth. The excessive and improper use of pesticides over the past years caused several environmental and health problems in addition to their expensive production costs for developing countries. Furthermore, the long-term use of chemical pesticides can lead to the advancement of specific organisms that can express resistance against chemical applications (Naher et al. 2014). Nowadays, the world pays attention to sustainable, secure and eco-friendly alternative options to control plant pathogens. The sustainable management of plant diseases aims to create an unfavourable environment for plant pathogens. Ultimately, the environment must suit healthy plants to ensure optimum crop yield through the efficient use of available natural resources (Zhan et al. 2015).

Main aspects to be focused in sustainable management of plant disease are maintaining healthy soil, healthy planting or propagation materials, use of resistant crop cultivars, biological control methods, rapid diagnostic methods and forecasting models. Healthy soils have a significant effect on the density of plant pathogens, particularly concerning soil-borne pathogens (Janvier et al. 2007), the structure of beneficial microbiota and nutrition availability (Larkin 2015; Van Bruggen et al. 2016). Crop production and management practices have a significant impact on soil quality, leading to consequent effects on the incidence of diseases in soil. Hence, maintaining a healthy soil for soil beneficial microorganisms greatly influences plant disease management. The use of healthy propagation materials is the initial preventive measure to consider losses due to emerging plant pathogens. It can be a useful tool in the prevention of native or alien pathogens in cropping environment. Several strategies have been activated for few or more important crops to certify the health of propagation materials, including specific phytosanitary assays that estimate the possibility of pathogens present in the materials using biological and molecular strategies.

Importantly, biological methods such as microbicides are the best sustainable approach in profitable agricultural production (Shafi et al. 2017). Biocontrol agents (BCAs) are used for plant disease control with or without integrated manner with other chemicals as environmentally friendly and sustainable approaches. BCA refers to the use of some specific living microorganisms to suppress the growth of plant pathogens (Pal and Gardener 2006). In other words, biological control means using beneficial organisms, their genes or their products to suppress or reduce the harmful effects of plant pathogens (Junaid et al. 2013). It can be integrated into cultural and physical controls and reduced chemical usage for an efficient integrated pest management (IPM) system. Several BCAs have been identified, and those are available as bacterial agents for plant disease control, e.g. *Bacillus*, *Pseudomonas* and *Agrobacterium*, and as fungal agents, e.g. *Trichoderma*, *Aspergillus*, *Gliocladium*, *Candida*, *Ampelomyces* and *Coniothyrium* (Koumoutsis et al. 2004; Atehnkeng et al. 2008; Gilardi et al. 2008). Considering *Trichoderma* fungi, they have been proven to be a robust BCA in the biological control of several plant pathogens. Hence, this book chapter summarizes the biological significance of *Trichoderma* spp. and their crucial role in the control of plant pathogens.

3.2 An Introduction to *Trichoderma* spp.

Trichoderma is one of the major and well-known filamentous fungi that is widely spread in soil, plant materials, decomposing vegetative materials and wood (Gajera et al. 2013). It is believed as an outstanding biocontrol agent due to its unique characters, such as rapid multiplying ability, high spread and easiness in isolation and culture (Pandya et al. 2011). The control mechanism shown by *Trichoderma* spp. varies according to the type of fungus and environmental conditions, such as temperature, pH and nutrient concentration (Gajera et al. 2013). It is one of the easily adaptable biocontrol agents used to manage plant pathogenic fungi. The majority of *Trichoderma* spp. are free living in nature. It plays two vital major roles as decomposer and plant symbiont. As a decomposer, it makes nutrient readily available for plants and plays a significant role in the nitrogen and carbon cycle. In roots of a crop, it helps in biomass increase and root hair development. Because of more root hairs, the roots penetrate deeper into soil and take up more water and necessary nutrients, ultimately supporting plant growth and development. Hence, these fungi are used in increasing crop yield. Bio-fungicides based on *Trichoderma* are becoming successful applications in agriculture with more than 50 registered products worldwide. Those different formulations are produced in different countries and are distributed to farmers to get optimum growth and yield of various types of crops (Woo et al. 2014). At present, *Trichoderma* based bioproducts share about 60% of fungal BCAs, and there is an increasing trend in registered *Trichoderma*-based biocontrol agent products. *Trichoderma harzianum* is one of the active biocontrol agents used widely among the commercially available biofertilizers and biopesticides in the market (Vinale et al. 2006; Lorito et al. 2010).

Characteristics and mechanisms of *Trichoderma* spp. have more benefits for plants as they can improve plant growth, increase the solubilization of essential nutrients to plants, induce secondary metabolite production by plants, produce growth-enhancing compounds and stimulate plant defence against plant pathogens. The specific and advantageous mechanisms of *Trichoderma* confirm it as a suitable organism in biological control of plant diseases (Al-Ani 2018). The unique qualities of *Trichoderma* spp. are the most driving factor towards their continuous success in their plant pathogen control journey (Verma et al. 2007). It can antagonize a broad range of soil-borne plant pathogens in various types of crops (Monte 2001). This potential of *Trichoderma* spp. aids as the fundamental for an effective agent in biological control method (Chet 1993). This capacity to act against pathogenic organisms is used to produce biopesticides and other BCAs to control the spread of various pathogenic organisms in agriculture.

Trichoderma spp. consist of many filamentous fungal strains belonging to many various ecosystems. These fungi can function as parasites, antagonists and plant symbionts against several pathogenic microbes causing diseases in plants. *Trichoderma* is the most studied and commercially marketed fungal BCA in the forms of biopesticides, biofertilizers and soil amendments. Further, *Trichoderma* spp. are the abundantly and most frequently found microbes in root ecosystems (Harman et al. 2004a). It plays a key role in the health of the ecosystem since it has

been a component of mycoflora in nature and cultivating soil in all climatic zones (Klein and Eveleigh 1998). It has the ability to colonize above- and belowground plant parts, plant litter, soil organic materials and living cells, including human. Besides, the fungi can produce secondary metabolites and enzymes with wider industrial applications. However, the capacity of the *Trichoderma* spp. to act against other fungi is not only due to their suppression ability on pathogenic fungi, bacteria or nematodes but also due to their plant growth promotion attributes, such as solubilizing plant nutrients; improving plant stress tolerance ability, growth and vigour; and helping in bioremediation of heavy metals in the environment (Lorito et al. 2010; Mastouri et al. 2012; Shores et al. 2010; Hermosa et al. 2012).

3.2.1 Taxonomy of *Trichoderma* spp.

The name *Trichoderma* has a long history since 1794. It was first reported based on the samples collected from Germany and explained based on macroscopic features by Persoon (1794). He initially described the taxonomy of *Trichoderma* in his classification of fungi, but failed to illustrate *Trichoderma* species. Persoon had rather indistinctly explained four *Trichoderma* species and did not realize that he was reporting only the anamorphic state. However, later on, it was suggested that *Trichoderma* could have a relationship with *Hypocrea* species on its sexual state. Despite that, there was a difficulty to designate the species *Trichoderma/Hypocrea* morphologically. Hence, there was a necessity to develop a specific procedure to identify the species, and an attempt was made based on colony growth rate and microscopic features to describe it by Rifai (1969). Eventually, several *Trichoderma* species were revealed, and by 2013 there are more than 200 species phylogenetically defined based on *RPB2* sequence (Atanasova et al. 2013). The genus was subdivided into nine species by Rifai (1969). The categories proposed were based on conidiophore branching patterns and conidium morphology. Those were (1) *T. piluliferum*, (2) *T. polysporum*, (3) *T. hamatum*, (4) *T. koningii*, (5) *T. aureoviride*, (6) *T. harzianum*, (7) *T. longibrachiatum*, (8) *T. pseudokoningii* and (9) *T. viride*. As there was a problem on Rifai's key, several groups of researchers (Bissett 1984; Doi et al. 1987; Bissett 1991a, b; Gams and Bissett 1998; Samuels et al. 1998; Manczinger et al. 2012) revised the *Trichoderma* genus during the last few decades based on the morphological features. As revealed by Kamala et al. (2015), *Trichoderma* belongs to Ascomycota, subdivision Pezizomycotina, class Sordariomycetes, subclass Hypocreomycetidae, order Hypocreales and family Hypocreaceae.

3.2.2 Abundance of *Trichoderma* spp.

Trichoderma is most commonly found in all temperate and tropical soils and can be grown under laboratory conditions. They can colonize in plants including woody and herbaceous in nature where sexual teleomorph has been noticed. However,

several *Trichoderma* spp. are without their sexual stages. Naturally, vegetative structures persist as clonal, individual and heterokaryotic. *Trichoderma* spp. have rapid growth rate and are productive spore producers, strong antibiotic producers and opportunistic invaders even in high stressed environmental conditions, including space, nutrients and light (Herrera-Estrella and Chet 2003; Montero-Barrientos et al. 2011). The above characters make *Trichoderma* an overriding strain that can grow and develop in various substrates, such as forest, marsh, agricultural, salt and desert soils of all types of climatic conditions. Further, it can be found in lakes, plant biomass and seeds and in the adjacent regions of all living plant species (Montero-Barrientos et al. 2011). Among the different types of habitat, the most common ecological niche of the *Trichoderma* spp. is the rhizosphere, since the habitat can attract their prey (soil-borne fungi) and because of the availability of unique nutrients derived from plant roots (Druzhinina et al. 2011). As reported by Pięta et al. (2000), *Trichoderma* spp. are the most dominating fungi in the soils of cultivating cereals, especially rye, triticale and wheat in Poland. Further, it is the most abundant taxa among the fungal population in soils of *Triticum aestivum* L. (winter wheat) cultivated in Germany, and *T. atroviride* and *T. viride* were the most isolated species among them (Hagn et al. 2003). Wheat cultivation fields in China recorded highly diverse *Trichoderma* spp. (Liang et al. 2004). There were 11 species recorded in winter wheat fields in Hungary (Kredics et al. 2012). *Trichoderma* spp. reported in different types of crop fields in various geographical locations are shown in the Table 3.1.

3.2.3 Isolation and Identification of *Trichoderma* spp.

There are more possibilities to isolate *Trichoderma* spp. from all types of agricultural areas since they have various impacts on plants. Inducing systemic resistance, biologically controlling plant pathogens, increasing plant available nutrients, improving nutrient uptake, enhancing plant growth and ultimately improving the crop yield are the major positive impacts of *Trichoderma* (Harman 2006). As indicated by Harman et al. (2004a), *Trichoderma* members are the most frequently isolated soil fungi among others. Further, few of them are bounded to specific areas and others are ubiquitous in nature. Most of the research, which elaborate the isolation and identification of *Trichoderma* strains from various agricultural and horticultural crop fields in several agro-climatic zones, were undertaken in order to assess them for biological control capability against a variety of plant pathogens. *Trichoderma* spp. have the capability of showing a rapid growth in an adaptable environment leading to isolation of them using all available methods. There are several methods found to isolate the *Trichoderma* spp. using classical techniques. Some selected growth media are commonly used to identify *Trichoderma* visually using specific morphological structures. The most commonly used isolation method is diluting soil and culturing especially on potato dextrose agar (PDA) media (Askew and Laing 1993; Davet and Rouxel 2000). As indicated by Elad et al. (1981) and Papavizas and Lumsden (1982), *Trichoderma* Medium E and *Trichoderma* Selective

Table 3.1 *Trichoderma* spp. recorded in different crop field

Identified crop field	Country reported	Abundant <i>Trichoderma</i> species	Reference
Corn	Egypt	<i>Trichoderma harzianum</i>	Gherbawy et al. (2004)
	Venezuela	<i>T. asperellum</i> , <i>T. atroviride</i> , <i>T. erinaceum</i> , <i>T. harzianum</i> , <i>T. koningiopsis</i> , <i>T. pleurotum</i> , <i>T. reesei</i> , <i>T. spirale</i> and <i>T. virens</i>	Pavone and Domenico (2012)
Rice	Philippines	<i>T. viride</i> and <i>T. harzianum</i>	Cumagun et al. (2000); Nagamani and Mew (1987)
	Bangladesh	<i>T. harzianum</i>	Mostafa Kamal and Shahjahan (1995)
	Iran	<i>T. asperellum</i> , <i>T. atroviride</i> , <i>T. brevicompactum</i> , <i>T. hamatum</i> , <i>T. harzianum</i> and <i>T. virens</i>	Naeimi et al. (2011)
Potato	New Zealand	<i>T. asperellum</i> , <i>T. atroviride</i> , <i>T. hamatum</i> , <i>T. harzianum</i> , <i>T. koningii</i> and <i>T. tomentosum</i>	Bourguignon (2008)
	Germany	<i>Trichoderma</i> spp.	Meincke et al. (2010)
	Poland	<i>Trichoderma</i> spp.	Pięta et al. (2000)
Onion	New Zealand	<i>T. asperellum</i> , <i>T. atroviride</i> , <i>T. hamatum</i> , <i>T. harzianum</i> , <i>T. koningii</i> and <i>T. tomentosum</i>	Bourguignon (2008)
Coffee	Ethiopia	<i>T. harzianum</i> , <i>T. hamatum</i> , <i>T. asperelloides</i> , <i>T. spirale</i> , <i>T. atroviride</i> , <i>T. koningiopsis</i> , <i>T. gamsii</i> and <i>T. longibrachiatum</i>	Mulaw et al. (2010)
Cocoa	Ivory Coast	<i>T. asperellum</i> , <i>T. harzianum</i> , <i>T. virens</i> and <i>T. spirale</i>	Mpika et al. (2009)
Sugar beet	France	<i>T. gamsii</i> , <i>T. harzianum</i> , <i>T. tomentosum</i> and <i>T. velutinum</i>	Anees et al. (2010)
Oil seed rape	Germany	<i>Trichoderma</i> spp.	Berg et al. (2005)
Common bean	Brazil	<i>T. asperellum</i> , <i>T. erinaceum</i> , <i>T. harzianum</i> , <i>T. koningiopsis</i> and <i>T. tomentosum</i>	Cardoso Lopes et al. (2012)
Oil seed palm	Malaysia	<i>T. harzianum</i> , <i>T. virens</i> and <i>T. koningii</i>	Sariah et al. (2005)
Soy bean	Poland	<i>T. hamatum</i> , <i>T. harzianum</i> , <i>T. koningii</i> , <i>T. pseudokoningii</i> and <i>T. viride</i>	Pięta and Patkowska (2003)
Sorghum	Mexico	<i>T. atroviride</i> , <i>T. citrinoviride</i> , <i>T. harzianum</i> , <i>T. longibrachiatum</i> , <i>T. koningiopsis</i> and <i>T. reesei</i>	Larralde-Corona et al. (2008)
Radish	Japan	<i>T. hamatum</i> , <i>T. harzianum</i> , <i>T. koningii</i> and <i>T. viride</i>	Mghalu et al. (2007)
Tobacco	China	<i>T. harzianum</i> , <i>T. viride</i> and <i>T. hamatum</i>	Yu and Zhang (2004)
Cotton	USA	<i>Trichoderma</i> spp.	Baird and Carling (1998)

Medium are the most commonly used in isolation of *Trichoderma* species. Askew and Laing (1993) and McLean et al. (2005) developed a modified *Trichoderma* Selective Medium to detect *Trichoderma* colony forming unit on agar plates with the presence of extensive soil fungal populations. *Trichoderma viride* showed better growth and sporulation on PDA medium with fresh potato having the pH value of 5.5 (Pandey and Palni 1997). The same study suggested that the better pH value for the optimum growth of *T. harzianum* was between 5.5 and 7.0. Saha and Pan (1997) mentioned that *Trichoderma* Selective Medium was better than the *Trichoderma* Medium E for the quantitative isolation from the soil samples. There was optimum sporulation of *T. viride* and *T. harzianum* on gobar gas slurry followed by decomposed farmyard manure, dried cow dung, wheat bran and sorghum grain (Sangle et al. 2003). As demonstrated by Gupta et al. (2003), the best media for the mass production of *T. viride* are potato dextrose and Czapek's Dox. The growth rate of different *Trichoderma* spp. was studied by Kumar and Singh (2008) on different types of growth media, and better growth rates were observed as follows: *T. citrinoviride* on PDA and cellulose agar medium; *T. longibrachiatum*, *T. flavofuscum* and *T. harzianum* on PDA; *T. viride* on PDA, cellulose agar medium and special nutrient agar; *T. hamatum* in malt extract agar, PDA and special nutrient agar; *T. virens* in special nutrient agar, PDA and malt extract agar; and *T. koningii* in plate count agar and cellulose agar medium. Jayaswal et al. (2003) have suggested the fungal medium amended with sucrose, peptone and trehalose as a carbon source for the growth and sporulation of *T. viride*. Better growth of *T. viride* was observed after 3 days of inoculation at the temperature ranging from 25 to 30 °C, and a reduction in growth rate was observed beyond the above temperature range (Singh et al. 2008). Further, Kredics et al. (2003) reported that optimum growth and sporulation of *T. atroviride*, *T. harzianum* and *T. viride* were observed in media minimal and yeast extract agar at 25–30 °C with the pH ranging from 5 to 7.

3.3 Mode of Action of *Trichoderma* spp. against Plant Diseases

Bioagents of *Trichoderma* spp. are applied to plants to suppress plant pathogen population, and the BCAs of *Trichoderma* spp. protect the plants via a various range of biocontrol mechanisms or modes of action (Köhl et al. 2019). The host plant-*Trichoderma*-pathogen triangle, a complex network with many processes (Sood et al. 2020), plays a crucial part in plant disease control and plant growth promotion. The major interactions of *Trichoderma* spp. with pathogens are achieved through the direct contact of mycoparasitism, antibiosis and competition and the indirect mechanisms of *Trichoderma* with plants by induction of systemic disease resistance and plant growth promotion as shown in Fig. 3.1. The mode of actions related to the pathogen and host plant interactions with *Trichoderma* could be divided into two major areas: (1) *Trichoderma*-pathogen interactions and (2) *Trichoderma*-plant interactions, which are discussed below.

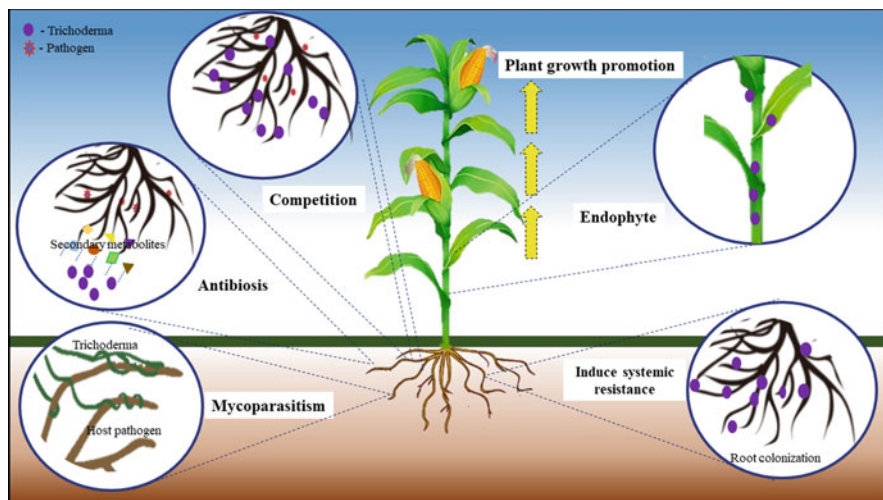


Fig. 3.1 The host plant-*Trichoderma*-pathogen interaction

3.3.1 *Trichoderma*-Pathogen Interaction

Amid the other biocontrol mechanisms employed by the *Trichoderma* spp., mycoparasitism (Karuppiyah et al. 2019), antibiosis (Juliatti et al. 2019) and competition (Ahluwalia et al. 2015) are direct mechanisms in which *Trichoderma* confront the pathogen to kill, hamper the growth and development or prevent the pathogen attack.

3.3.1.1 Mycoparasitism

Parasitism is one of the major modes of action involved in biocontrol activity by *Trichoderma* through the direct interaction with plant pathogens. *Trichoderma* spp. show mycoparasitism against other fungal pathogens in which chemotropism and recognition, attachment and twirling around host hyphae, discharge of extracellular enzymes, cell wall penetration with hypha and digestion of target fungal cell are the major steps (Zeilinger et al. 1999). Fungal cell walls are primarily composed of β -1,3-glucan and chitin. Mycoparasitic mechanism to degrade pathogenic fungal cell wall is carried out by the hydrolytic enzymes produced by *Trichoderma* spp., namely, chitinase, β -1,3-glucanase and lytic enzymes. The mycoparasitic potential of various *Trichoderma* spp. has been well reported by many researchers (Leiva et al. 2020; Pimentel et al. 2020; Ramírez-Cariño et al. 2020). In addition, the ability of any *Trichoderma* species to produce glucanase enzyme is considered as a key indicator of mycoparasitism (Mustafa et al. 2020). In a recent study, *T. asperellum* produced phytohormones and cell wall-degrading enzymes, chitinases and cellulases that are related to antagonistic and mycoparasitic effect upon *F. oxysporum* infection in *Stevia rebaudiana* plant (Díaz-Gutiérrez et al. 2021). *Trichoderma*-pathogen interaction is called as hyperparasitism when the plant pathogen is also a parasite

in nature. The hyperparasitic mechanism of *T. virens* against *Rhizoctonia solani* was explored with the help of electron microscopy. The mechanism includes the formation of knob-like structure, growth of *T. virens* hyphae inside host, twirling, lysing cell wall and swollen mycelial tips. Besides, it is also linked with the production of hydrolytic enzymes, viz. cellulose and chitinase, for the parasitism (Inayati et al. 2020).

3.3.1.2 Antibiosis

In antibiosis process, organic, diffusible and low molecular weight compounds produced by the *Trichoderma* spp. interact and impede the growth of pathogenic microorganisms. The antibiosis mechanism is chiefly centred on the synthesis of secondary metabolites (SMs). About 186 SMs from the BCAs of *Trichoderma* spp. are structurally and biologically studied and reviewed by Reino et al. (2008). The SMs produced by *Trichoderma* spp. show bioactivity against plant pathogenic fungi and bacteria. The well-known biocontrol agent *T. harzianum* produces array of SMs, such as koniginins (Almassi et al., 1991); harzianopyridone (Dickinson et al., 1989; Vinale et al. 2006); harzianic acid (Vinale et al. 2009); cyclonerane sesquiterpenoids, including the known cyclonerodiol, together with its new derivatives, (10*E*)-12-acetoxy-10-cycloneren-3,7-diol and 12-acetoxycycloneran-3,7-diol (Fang et al., 2019); trichosordarin A (Liang et al., 2020) and trichodiene (Malmierca et al., 2015). Yan and Khan (2021) stated that SMs produced from *T. harzianum* registered antibacterial activity against *Ralstonia solanacearum* that causes bacterial wilt in tomato. Harzianic acid from *T. harzianum* strain disclosed antibiotic activity countering *Pythium irregular*, *R. solani* and *Sclerotinia scleotiorum* (Vinale et al. 2009). The ability of *Trichoderma* spp. in the production of antibiotic commonly depends on the species or isolates. The different kinds of antibiotics produced by *Trichoderma* spp. are listed below in Table 3.2.

Table 3.2 Antibiotic compounds produced by *Trichoderma* spp.

<i>Trichoderma</i> spp.	Antibiotic compounds
<i>Trichoderma viride</i>	Trichotoxin A Trichotoxin B Trichodecenins Trichorovins Trichocellins
<i>T. atroviride</i>	Atroviridins A–C Neoatroviridins A–D
<i>T. koningii</i>	Longibrachins Trichokonins
<i>T. longibrachiatum</i>	Tricholongins BI & BII
<i>T. harzianum</i>	Trichorzianins A & B Trichorzins HA & MA

Source: Sood et al. (2020)

3.3.1.3 Competition

Competition for the nutrient source and space is considered as one of the classical mechanisms of biocontrol by *Trichoderma* against plant pathogens (Elad et al. 1999). Exogenous nutrient requirement is vital among the plant pathogens for spore germination, multiplication and infection structure formation. However, the fast-growing ability of *Trichoderma* spp. creates them as a potential candidate for competition with plant pathogens for nutrients, biological niche, feeding place and infection spots in rhizosphere (Khan et al. 2020a, b). *Trichoderma* spp. strive for various sources of nutrients in the rhizosphere, which is rich in carbohydrates, amino acids, vitamins and ions, especially Fe, etc. The capability of *Trichoderma* spp. to absorb and mobilize nutrients is far better than the other rhizosphere-dwelling microorganisms that adds an advantage in management of plant pathogens. Delgado-Jarana et al. (2003) reported that the *glt1* gene in *T. harzianum* CECT 2413 codes for high-affinity glucose transporter, which expresses high affinity for glucose molecules at lower concentrations. These inherent attributes are excellent means for competition against plant pathogens. Besides, the reduction in the available nutrient sources and the competition for nutrients with *Trichoderma* spp. create a natural management of plant pathogens. Sarrocco et al. (2009) revealed that the competition for C source cellulose between *R. solani* and *Trichoderma* isolates was remarkable.

3.3.2 *Trichoderma*-Plant Interaction

Plants co-cultivated with various *Trichoderma* spp. aimed at plant disease management exhibit different benefits through *Trichoderma*-plant interactions, such as plant growth promotion and yield augmentation via positive regulation in plant physiological processes.

3.3.2.1 Plant Growth Promotion and Yield Improvement

Trichoderma spp. used as BCAs are not only able to control diseases in crops but also can promote plant growth and yield related attributes. A positive regulation in photosynthesis, respiration, nutrient absorption and assimilation and stomatal conductance via the interactions favours crop growth and development (Harman et al. 2004b; Bae et al. 2009; Mastouri et al. 2010; Brotman et al. 2012). Numerous research works support the claim that *Trichoderma* spp. could improve growth attributes, viz. seed germination (Kthiri et al. 2020), seedling growth (Vinale et al. 2013), shoot and root growth (Naseby et al. 2000), plant height (Izuogu and Abiri 2015), etc. Greenhouse and field trials with *Trichoderma* spp. also have shown improved yield in addition to biocontrol activity. Field experiments at two different locations in onion with *T. asperellum* BCC1 against the white rot-causing pathogen *Sclerotium cepivorum* showed an increase in onion bulb yield by 20.4% (Rivera-Mendez et al. 2020). The efficacy of *T. asperellum* and *T. harzianum* isolates against anthracnose disease-causing agent *Colletotrichum graminicola* in sorghum was evaluated in field conditions. The bioprimered plants with *T. asperellum* T3 isolate

registered up to 22.2% and 27.3% increment in yield in the tested consecutive years (Manzar et al. 2021). Further, the different *Trichoderma*-plant interactions that stimulate the plant growth and yield parameters are also mentioned in Tables 3.4 and 3.5.

3.3.2.2 Induction of Disease Resistance in Plants

The capability of *Trichoderma* spp. to induce plant defence response and systemic resistance against array of plant pathogens is crucial in addition to the various beneficial effects caused by the selected strains (Harman 2011). The *Trichoderma*-induced defence in plants may be included into two forms of systemic resistance, namely, induced systemic resistance (ISR) and systemic acquired resistance (SAR). The ISR in plants is not only initiated by pathogen infection, but also it is induced by root colonization and the interaction of *Trichoderma*. Further, the incorporation of the *Trichoderma* treatments could accelerate ISR to reduce the infection caused by pathogens (Mathys et al. 2012). Treatment with *Trichoderma* spp. has been reported to stimulate host plants to secure them against pathogenic infestation by eliciting a number of defence mechanisms via production of phytoalexins and phenolic compounds, accumulation of pathogenesis-related proteins and formation of the structural barriers. *T. reesi* isolate CSR-T-3-treated banana exhibited improved activity of plant defence-related enzymes, namely, β -1-3-glucanase, chitinase, peroxidase, polyphenol oxidase and phenylalanine ammonia lyase with more phenolic compounds (Damodaran et al. 2020).

Elicitors are low molecular weight compounds, which induce plant immune response by activating signal cascade (Zalak et al. 2020). These elicitors released by the *Trichoderma* may trigger the various types of signals transmitted in the host plant such as salicylic acid (SA), jasmonic acid (JA) or reaction species (ROS), inducing expression of defence-related proteins (Nawrocka and Małolepsza 2013). An elicitor, harzianolide, obtained from *T. harzianum* SQR-To37 upregulated the expression of the genes *PR1* and *GLU* involved in SA, and gene *PR1* induced jasmonate/ethylene signaling pathways and the pretreated plant with the elicitor with *S. sclerotiorum* caused higher systemic resistance by the reduction of lesion size (Cai et al. 2013). In the another study, 6-pentyl- α -pyrone (6PP), an elicitor isolated from *T. koningii* CTX1172, increased proline and pathogenesis-related enzymes superoxide dismutase, peroxidase and polyphenol oxidase, indicating the ISR in tobacco plants against tobacco mosaic virus. Besides, plants tested with 6PP exhibited the rapid expression of defence-related genes, such as *PR-a*, *PR-b* and *PR-10* (Taha et al. 2021). Treatment of *T. atroviride* TRS25 to protect *R. solani* pathogen in cucumber revealed the enhancement in defence-related enzymes guaiacol peroxidase, syringaldazine peroxidase, polyphenol oxidase, etc. In addition, the upregulation of *PR1* and *PR5* genes characterized the feature of SAR, and the formation of structural barrier-related compounds callose and lignin in plant cells protected vascular systems in cucumber (Nawrocka et al. 2018).

3.4 *Trichoderma* spp. to Control Various Plant Pathogens

There are a plethora of research available to prove the efficacy of various *Trichoderma* spp. against fungal, bacterial, nematode and viral pathogens. Different types of pathogens with their specific plant host and the efficacy are further discussed below.

3.4.1 *Trichoderma* spp. to Control Fungal Plant Pathogens

Plant pathogens, particularly soil-borne pathogens, cause severe losses in agriculture production, among them fungi are most injurious (Benítez et al. 2004). However, several species of *Trichoderma* have proven to be effective BCAs against plant pathogenic fungi (Table 3.3). *Fusarium oxysporum*, a widespread fungus, can cause significant losses on over 100 various plant species (Thatcher et al. 2016). It can induce wilt in different types of plants. Nevertheless, the use of *Trichoderma* to suppress the wilt pathogen is an effective technique in managing the disease (Zehra et al. 2017). Wells (1988) has observed the mycoparasitic mechanism of the *T. viride* on some selected fungal and oomycete pathogens, such as *Sclerotium rolfsii*, *Rhizopus*, *Pythium* and *Phytophthora*. Uptake of Fe is an essential factor for the viability of soil-borne fungi, so that certain *Trichoderma* spp. produce highly effective siderophores to chelate Fe and prevent the growth and development of another fungus (Chet and Inbar 1994).

Trichoderma-based biocontrol agents are mainly recognized by farmers as an eco-friendly approach in their fields (Malik et al. 2018). Few studies suggested that the integrated use of *Trichoderma* with fungicides could be used as a sustainable disease control strategy to minimize the usage of chemical fungicide applications. Hu et al. (2016) observed a significant reduction in *Sclerotinia sclerotiorum* causing oil seed rape disease when treated with a *Trichoderma* species with a chemical fungicide carbendazim. Wilson et al. (2008) revealed that the combined application of *T. harzianum* and flutolanil fungicide showed an effective decrease in the *Rhizoctonia solani* infection. It could be suggested that integrating a low toxic chemical fungicide with *Trichoderma* could strengthen the biocontrol ability against the fungal pathogens. Ji et al. (2021) have demonstrated that growth of *Alternaria alternata*, *Fusarium* spp. and *Cytospora mandshurica* was significantly inhibited with rates ranging from 34% to 58% by the *T. rossicum* and *T. harzianum*. Further, there was a reduction in plant pathogen populations while applying the mixture of *T. rossicum* and *T. harzianum* with soil irrigation. Chinnaswami et al. (2021) have revealed that *T. asperellum* (TAIK-1) showed the most effective control action against the soil-borne fungal pathogens in rice, *R. solani* and *Sclerotium oryzae*, and this method was suggested as a sustainable disease management strategy for a long-term basis in rice cultivation fields.

Treating wheat and black oat straw with *T. harzianum* caused a reduction in the prevalence of *Cochliobolus sativus*, *Fusarium graminearum* and other *Fusarium* spp. Further, it was mentioned that *T. harzianum* was more effective in colonizing

Table 3.3 *Trichoderma* spp. to Control Plant Pathogenic Fungi

<i>Trichoderma</i> species	Fungal pathogen	Disease	Host plant	References
<i>Trichoderma harzianum</i>	<i>Elsinoe fawcettii</i>	Citrus scab	Citrus	Singh et al. (2012)
	<i>Sclerotium ralfsii</i>	Collar rot	Tomato	Dutta and Das (2002)
		Stem rot	Groundnut	Biswas and Sen (2000); Rakholiya and Jadeja (2010)
	<i>Pythium aphanidermatum</i>	Damping-off	Tomato	Jayaraj et al. (2006)
	<i>Rhizoctonia solani</i>	Root rot	Chilli	Rini and Sulochana (2007)
		Root and collar rot	Cowpea	Pan and Das (2011)
		Root and stem rot	Soybean	Mishra et al. (2011)
		Stem canker and black scurf	Potato	Al-Askar et al. (2016)
		Sheath blight	Rice	Chaudhary et al. (2020)
	<i>Colletotrichum capsici</i>	Anthracnose	Chilli	Vasanthakumari and Shivanna (2013)
	<i>Alternaria alternata</i>	Leaf spot	Brinjal	Balai and Ahir (2011)
	<i>Rhizoctonia bataticola</i>	Dry root rot	Cotton	Gaur et al. (2005)
	<i>Aspergillus niger</i>	Crown rot	Groundnut	Kishore et al. (2001)
	<i>Ceratobasidium theobromae</i>	Vascular streak dieback	Cacao	Vanhove et al. (2016)
<i>T. viride</i>	<i>Fusarium oxysporum</i>	Bitter gourd wilt	Bitter gourd	Zhang et al. (2020a)
	<i>Cochliobolus heterostrophus</i>	Southern corn leaf blight	Maize	Wang et al. (2019a)
	<i>Rhizoctonia solani</i>	Root rot	Safed musli (<i>Chlorophytum borivilianum</i>)	Pokhar et al. (2013)
	<i>Elsinoe fawcettii</i>	Citrus scab	Citrus	Singh et al. (2012)
	<i>Sclerotium ralfsii</i>	Collar rot	Tomato and brinjal	Dutta and Das (2002); Jadon (2009)

(continued)

Table 3.3 (continued)

<i>Trichoderma</i> species	Fungal pathogen	Disease	Host plant	References
	<i>Alternaria alternata</i>	Leaf spot	Brinjal	Balai and Ahir (2011)
	<i>Aspergillus niger</i>	Crown rot	Groundnut	Kishore et al. (2001)
	<i>Pythium arrhenomanes</i> f. sp. adzuki and <i>Pythium arrhenomanes</i>	Root rot	Soybean	John et al. (2010)
	<i>Verticillium dahliae</i>	Wilt		Fan et al. (2020b)
	<i>Sclerotinia sclerotiorum</i>	Blossom Blight	Alfalfa	Li et al. (2005)
<i>T. atroviride</i>	<i>Rosellinia necatrix</i>	White root rot	Avocado	Ruano-Rosa et al. (2014)
	<i>Sclerotium ralfsii</i>	Collar rot	Tomato	Dutta and Das (2002)
<i>T. koningii</i>	<i>Sclerotium cepivorum</i>	Onion white rot	Onion	Rivera-Mendez et al. (2020)
<i>T. asperellum</i>	<i>Rhizoctonia solani</i>	Sheath Blight	Maize	Wu et al. (2017)
	<i>Rhizoctonia solani</i> and <i>Sclerotium oryzae</i>	Sheath Blight	Rice	Chinnaswami et al. (2021)
		Stem rot	Rice	Chinnaswami et al. (2021)
	<i>Alternaria alternata</i>		<i>Malus sieversii</i>	Ji et al. (2021)
<i>Trichoderma</i> spp.	<i>Pyrenophora tritici-repentis</i>	Tan spot	Wheat	Perelló et al. (2008)
	<i>Phaeomoniella chlamydospora</i> and <i>Phaeoacremonium minimum</i>	Black-foot and Petri diseases	Grapevine	del Pilar Martínez-Diz et al. (2021)

the substrate and in diminishing the occurrence of pathogens in wheat than in black oat (Fernandez 1992). Harish et al. (2007) demonstrated that use of *Trichoderma* is an efficient method for controlling brown spot disease in rice. Under greenhouse condition, rice plants treated with a spore suspension of *T. harzianum* showed a significant reduction in the intensity of the brown spot disease condition (Abdel-Fataah et al. 2007). Khalili et al. (2012) evaluated the efficacy of *Trichoderma* spp. in management of brown spot under glasshouse condition using seed treatment and foliar spray methods. The results revealed that two strains of *T. harzianum* significantly suppressed the disease incidence and a strain of *T. atroviride* increased the seedling growth. As Chaudhary et al. (2020) reported, *T. harzianum* has the potential to use against rice sheath blight disease and to enhance the growth of rice plant. In future, there are more possibilities to use the formulations of *Trichoderma*-based

products to enhance plant growth and to manage fungal diseases in rice cultivation and may be used in organic-based rice cultivation.

3.4.2 *Trichoderma* spp. to Combat against Bacterial Plant Diseases

Next to fungi and viruses, bacterial plant pathogens affect crop production, and the diseases caused by phyto bacteria place a chief barrier in agriculture that causes significant losses worldwide (Sundin et al. 2016). About 150 species of bacterial pathogens cause detrimental effects in plants, and the most important bacterial species belong to *Agrobacterium*, *Dickeya*, *Erwinia*, *Ralstonia*, *Pectobacterium*, *Pseudomonas*, *Xanthomonas* and *Xylella* (Mansfield et al. 2012). Most of the bacterial plant diseases are ephemeral. Even though a multitude of bacterial species can incite deleterious diseases, only few cause entire crop failure (Carolee et al. 2016). Use of resistant varieties, crop rotation practices, field sanitization and using synthetic chemicals are used to control bacterial diseases in plants (Agrios 2005). However, bacterial disease management faces difficulties, mainly due to the rapid spread of the pathogen, limited chemicals and resistant bacterial strains to the chemicals (Thind 2015). Current control measures chiefly rely on using bactericides containing copper as a primary source or antibiotics, which are not environmentally safe. However, the desired management of bacterial diseases via alternative, sustainable and eco-friendly strategies is still awaited. Biocontrol of these pathogens using antagonistic microorganisms is a promising possible and alternative arena. Interestingly, various *Trichoderma* spp. have been evaluated against most widespread diseases caused by *Xanthomonas* spp., *Erwinia* spp. and *Pseudomonas* spp. in crops. Besides, in vitro, pot and field applications of several *Trichoderma* spp. on different crops have been proven successful in biocontrol, growth and yield promoting activities against bacterial plant pathogens as shown in Table 3.4.

Pepper bacterial spot caused by *Xanthomonas euvesicatoria* (Kyeon et al. 2016) is a major threat that causes severe losses in fresh pepper berries. The antagonists' suppression of *X. euvesicatoria* was determined using diffusion disk method, and the BCAs used in the study were *Lactobacillus*, *Pseudomonas*, *Saccharomyces* and *Trichoderma*. Results revealed that biocontrol of *X. euvesicatoria* was possible with the broth samples of *Lactobacillus* MK3 and *Trichoderma reesei* QM 9414 and the supernatant samples of *Pseudomonas aeruginosa* I128 (Pajčin et al. 2020). In a pot experiment, pine bark mix compost fortified with *T. hamatum* 382 against bacterial leaf spot pathogens *Xanthomonas campestris* pv. *vesicatoria* and *X. campestris* pv. *armoraciae* in lettuce, radish and tomato registered less disease severity than those of commercial peat mix or vermiculite treated pots (Aldahmani et al. 2005).

Further, secondary metabolites from *Trichoderma* spp., namely, gliotoxin, gliovirin, peptaibols, polyketides, pyrones and terpenes, show anti-microbial potentials against various plant pathogens, including bacteria (Monte 2001; Vizcaino et al. 2005; Vinale et al. 2008). An antimicrobial peptaibol, Trichokonins, extracted from *T. pseudokoningii* SMF2 was tested on *Pectobacterium carotovorum*

Table 3.4 *Trichoderma* spp. to control various plant pathogenic bacteria

Bacterial pathogen	Disease	Host plant	<i>Trichoderma</i> species	Remarks	References
<i>Agrobacterium vitis</i>	Crown gall disease	Grapevine (<i>Vitis vinifera</i> cv. <i>corvina</i> and cv. <i>corvinone</i>)	<i>Trichoderma asperellum</i> , <i>T. harzianum</i> and <i>T. harzianum</i>	<i>In planta</i> trials conducted for 2 years reduced disease symptom incidence (75%) and gall size (53.5%) in <i>T. asperellum</i> -added assays	Ferrigo et al. (2017)
<i>Xanthomonas euvesicatoria</i>	Bacterial spot	Tomato	<i>Trichoderma</i> spp.	<i>Trichoderma</i> isolates registered 24.1 to 95.9% protection against <i>X. euvesicatoria</i> and reduced the severity of the diseases	Fontenelle et al. (2011)
<i>Xanthomonas perforans</i>	Bacterial spot	Tomato	<i>T. asperellum</i>	Foliar or growth medium application of tested agent reduced the disease severity by 25.6–56%	Chien and Huang (2020)
<i>Streptomyces</i> spp.	Common scab	Potato	<i>T. harzianum</i>	Soil application of the microbial product consisted of <i>T. harzianum</i> decreased disease index and improved yield	Wang et al. (2019b)
<i>Ralstonia solanacearum</i>	Bacterial wilt	Chilli	<i>T. asperellum</i>	Inhibition of the bacterial wilt development by 12.5–50%	Irawati et al. (2020)
<i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i>	Canker	Tomato	<i>T. harzianum</i>	The commercial formulate of <i>T. harzianum</i> reduced the disease incidence of the canker under greenhouse set-up	Utkhede and Koch (2004)
<i>Pseudomonas syringae</i> pv. <i>tachrymans</i>	Angular leaf spot	Cucumber	<i>T. asperellum</i>	About 80% of reduction in disease symptoms and systematic haltering in bacterial cell proliferation	Yedidia et al. (2003)
<i>Ralstonia</i> spp.	Ralstonia wilt	Tomato	<i>Trichoderma</i> spp.	<i>Trichoderma</i> spp. controlled 92% of the infection in the field	Yendyo and Pandey (2017)
<i>Ralstonia solanacearum</i>	Ralstonia wilt	Tomato	<i>Trichoderma</i> spp.	Reduction of pathogen density and disease incidence and increase in tomato yield	Kariuki et al. (2020)
<i>Xanthomonas axonopodis</i> pv. <i>malvacearum</i>	Blight	Cotton	<i>T. hamatum</i>	<i>T. hamatum</i> was effective in reducing colony growth of the pathogen	Jagtap et al. (2012)

(continued)

Table 3.4 (continued)

Bacterial pathogen	Disease	Host plant	<i>Trichoderma</i> species	Remarks	References
<i>Pseudomonas syringae</i> pv. <i>actinidiae</i>	Canker	Kiwifruit	<i>Trichoderma</i> spp.	Early inoculation of <i>Trichoderma</i> during kiwi plant growth and development improved plant health, survival and control of <i>P. syringae</i> pv. <i>actinidiae</i>	Hill et al. (2015)
<i>Erwinia carotovora</i>	Soft rot	Okra	<i>T. asperellum</i>	Greenhouse experiments showed that reduction in the negative effects of the pathogen in the okra seedlings	Idowu et al. (2016)
<i>Erwinia carotovora</i> subsp. <i>carotovora</i>	Potato tuber soft rot	Potato	<i>T. viride</i> and <i>T. harzianum</i>	Tubers applied with <i>T. viride</i> and <i>T. harzianum</i> manifested minimal disease incidence 20.3% and 16.5%, respectively. Growth restriction in <i>E. carotovora</i> was allied with increment in plant height and fresh and dry weights of plants emerged from the treated tubers	Sulaiman et al. (2020)

subsp. *carotovorum* inciting soft rot disease in Chinese cabbage. Application rate of 0.3 mg L^{-1} of Trichokonins induced resistance via upregulation of the expression of salicylic acid-responsive pathogenesis-related protein gene acidic *PR-1a* in tested plants conferring the activation of salicylic acid in plant defence signaling (Li et al. 2014).

Ralstonia solanacearum is a soil-borne gram-negative bacterial pathogen causing vascular wilt, brown rot and moko diseases in various crops. The bacterial wilt caused by *Ralstonia* spp. in eggplant, tobacco, tomato and potato has already been tested against BCAs, viz. *T. asperellum* (Srinivas 2013; Mohamed et al. 2020), *T. harzianum* (Barua and Bora 2008; Maketon et al. 2008) and *T. virens* (Mathew et al. 2007). However, recent findings give more insights into the biocontrol ability of *T. asperellum*. Field applications of *T. asperellum* isolates T4 and T8 postponed wilt development, decreased disease incident caused by *R. solanacearum* and enhanced plant growth and yield of tomato plants (Konappa et al. 2018). Besides, the investigation revealed an increment in the activities of defence responses by the accumulation of peroxidase (POX), phenylalanine ammonium lyase (PAL), polyphenol oxidase (PPO), β -1,3 glucanase and total phenolic compounds (TPC) in *T. asperellum* isolates-treated tomato crops infected with *R. solanacearum*, indicating the trigger of defence mechanism by *T. asperellum* isolates against the infection. In another study, seed treatment with *Pseudomonas fluorescens* Pf3 plus *T. longibrachiatum* UNS11 exhibited about 61% pathogen suppression and protection against *R. solanacearum* under field conditions. The defence-related enzymes, namely, POX, PAL and PPO, were highly expressed in the tomato plants, and the induced resistance was possible to deliver growth and yield promotion in the tested plants (Konappa et al. 2020). In another study, Mohamed et al. (2020) investigated the effects of BCAs *Enterobacter cloacae* PS14 and *T. asperellum* T34 in greenhouse and field conditions to control potato wilt causal agent *R. solanacearum*. The tested *T. asperellum* T34 has reduced wilt severity by 42.2% and augmented tuber yield of potato by 40.96% in field conditions. Further, the suppression of pathogen was confirmed by POX, PPO, lipoxigenase, TPC and salicylic acid, which are concomitant with the induction of systemic resistance of potato plants. However, the potential effect of *Trichoderma* spp. is always not effective against certain bacterial pathogens. A recent finding by Morán-Diez et al. (2020) showed that *T. parareesei* T6, *T. asperellum* T25 and *T. harzianum* T34 were not adequately controlled pathogenic *Pseudomonas syringae* pv. *tomato* DC3000 strain in tomato plants. Nevertheless, minor protection of 9.4% was given by *T. asperellum* T25 against the pathogen.

3.4.3 Controlling Plant Parasitic Nematodes Using *Trichoderma* spp.

Plant parasitic nematodes (PPN) are microscopic roundworms that cause significant economic losses to vegetables, fruits and cereal crops worldwide if management fails (Sivasubramaniam et al. 2020). The parasitic nematodes often limit crop production, and yield losses are estimated about 8.8–14.6% per annum (Nicol et al. 2011), which

accounts for \$157 billion globally (Singh et al. 2015). Given the substantial economic losses caused by the nematodes in agriculture, many approaches have been developed to control the damages. Among them, chemical nematicides are the most common and short-term management strategy (Hajihassani et al. 2019; Medina-Canales et al. 2019) and still an effective way to control nematodes when the nematode load is too high (Chen et al. 2020). Nevertheless, ban and restriction are made on the various synthetic chemicals for managing PPN, and arbitrary usage causes significant environmental hazards and side effects on human health and non-target organisms (Ansari et al. 2020; Sikandar et al. 2020). These drawbacks have created a necessity for effective, alternative and sustainable control measures in nematode management (Sikder and Vestergard 2020). On the other hand, an array of biocontrol approaches, natural compounds, soil amendments and new evolving methods are successfully practised and included in the environmentally safe nematode management (Atolani and Fabiyi 2020; Forghani and Hajihassani 2020). Among the various BCAs, the nematophagous *Trichoderma* spp. are also becoming a scientific significance as they can be utilized against PPN.

Trichoderma spp. show several mechanisms or mode of actions against PPN, viz. direct parasitism, antibiosis, competition, induction of host plant resistance by defence responses, enzyme hydrolysis and production of toxic compounds (Ibrahim et al. 2020; Poveda et al. 2020), and the mechanisms are investigated and documented (Howell 2003; Vinale et al. 2009). The parasitism potential of *Trichoderma* spp. against eggs; juveniles, i.e. chiefly the second stage (J2); and adults of PPN has been well identified. Zhang et al. (2017) found that egg parasitism of *T. longibrachiatum* T6 includes germination and formation of a large number of hyphae on the surface of the *Heterodera avenae* eggs, completely covering it by dense mycelia and lysis of the egg contents. Besides, the gene expression analysis revealed the egg parasitism by *T. harzianum* upregulated the transcriptional activities of *chi18-5* (*chit42*) and *chi18-12* (*chit33*) genes encoding chitinolytic enzyme system (Szabó et al. 2012). On the contrary, the J2 parasitism comprises the production of a large number of hyphae and penetration of hyphae via cuticle and causes the deformation of the juvenile J2. In another investigation, the scanning electron microscopy has shown that parasitism of *T. asperellum* and *T. atroviride* on *Meloidogyne javanica* involves the development of coil and appressorium-like structures that support during attachment (Sharon et al. 2007). Antibiosis mechanism in *Trichoderma* spp. is mainly due to production of small and low molecular weight diffusible compounds or antibiotics. Dermadin, trichoviridin, trichodermin and sesquiterpene heptalic acid are classic examples of antibiotics secreted by *T. viride* that possess a potential activity in the suppression of PPN (Abd-Elgawad and Askary 2020). Further, efficacy of different *Trichoderma* spp. in controlling root-knot nematodes, cyst nematodes, root-lesion nematodes and dagger nematodes is well documented by numerous studies as shown in Table 3.5.

PPN control using *Trichoderma* spp. has also caused the production of defence components after the inoculation. Zhang et al. (2017) reported that wheat plants inoculated with *T. longibrachiatum* under the *Heterodera avenae* infection induced resistance enzymes and defence-related chemicals, such as chitinase and β -1,3-

Table 3.5 *Trichoderma* spp. used as biocontrol agents against plant parasitic nematodes infesting various crops

Nematodes	Host plant	<i>Trichoderma</i> spp.	Remarks	References
<i>Meloidogyne incognita</i>		<i>Trichoderma viride</i>	Secondary metabolites from <i>T. viride</i> showed juvenile (J2) mortality and inhibition of egg hatching	Khan et al. (2020a, b)
<i>M. incognita</i>	Tomato	<i>T. citrinoviride</i>	<i>T. citrinoviride</i> inhibited egg hatching, reduced root gall and egg mass and enhanced the shoot and root length of tomato	Fan et al. (2020a)
<i>M. javanica</i>	Tomato	<i>T. harzianum</i> and <i>T. viride</i>	<i>Trichoderma</i> spp. suppressed the nematode reproduction, reduced the galling and increased plant growth	Al-Hazmi and TariqJaveed (2016)
<i>M. graminicola</i>	Rice	<i>T. viride</i>	Reduction in root galls	Amarasinghe and Hemachandra (2020)
<i>M. incognita</i>	Tomato and carrot	<i>T. asperellum</i> and <i>T. brevicompactum</i>	About 86% and 80% of suppression in egg production was observed with <i>T. brevicompactum</i> and <i>T. asperellum</i> , respectively, and <i>T. asperellum</i> enhanced tomato yields by over 30%. In carrot plots, about 94% suppression in J2 densities by <i>T. asperellum</i> was observed	Affokpon et al. (2011)
<i>Globodera rostochiensis</i>	Potato	<i>Trichoderma</i> spp.	Inhibited multiplication of nematodes	Trifonova (2010)
<i>Pratylenchus brachyurus</i>	Soybean and maize	<i>Trichoderma</i> spp.	About 44% of reduction in total nematode population	Pacheco et al. (2020)
<i>Heterodera avenae</i>	Wheat	<i>T. longibrachiatum</i>	Parasitized on egg, J2 and deformation of nematodes. The cysts and juveniles in soil were reduced by 89.8 and 92.7%; the juveniles and females in roots were reduced by 88.3 and 91.3%	Zhang et al. (2017)
<i>H. avenae</i>	Wheat	<i>T. longibrachiatum</i>	Exhibited strong lethal and juvenile parasitism on J2	Zhang et al. (2014)
<i>M. javanica</i>	Tomato	<i>T. harzianum</i>	Inhibition in egg hatching	Naserinasab et al. (2011)

(continued)

Table 3.5 (continued)

Nematodes	Host plant	<i>Trichoderma</i> spp.	Remarks	References
<i>M. javanica</i>	Tomato	<i>T. harzianum</i>	<i>T. harzianum</i> affected the nematode penetration into the roots rather than nematode development inside the roots	Sharon et al. (2001)
<i>M. incognita</i>	Chilli	<i>T. harzianum</i>	Reduction of root galls and nematode population	Izuogu et al. (2019)
<i>M. incognita</i>	Eggplant	<i>T. harzianum</i>	Decreased root galls and egg masses and improved yield	Osman et al. (2018)
<i>M. javanica</i> and <i>Rotylenchulus reniformis</i>	Eggplant	<i>T. harzianum</i> , <i>T. viride</i> , <i>T. koningii</i> , <i>T. reesei</i> and <i>T. hamatum</i>	All <i>Trichoderma</i> spp. caused significant reduction in females and egg masses. One-week duration of exposure to tested species inhibited the nematode movements due to the toxic metabolites	Bokhari (2009)
<i>M. incognita</i>	Soybean	<i>T. harzianum</i>	Reduced nematode population and gall formation and improved plant height and yield	Izuogu and Abiri (2015)
<i>M. incognita</i>	Cowpea	<i>T. harzianum</i>	Significantly reduced gall index and nematode population in root and soil	Olabiya et al. (2016)
<i>M. incognita</i>	Pea	<i>T. harzianum</i> , <i>T. viride</i> and <i>T. virens</i>	Numbers of galls, egg masses and J2 per root were reduced, and the tested <i>Trichoderma</i> spp. increased plant growth by 46.1%	El-Nagdi et al. (2019)
<i>M. javanica</i>	Green gram	<i>T. harzianum</i> , <i>T. hamatum</i> , <i>T. viride</i> , <i>T. koningii</i> , <i>T. pseudokoningii</i> , <i>T. atroviride</i> and <i>T. asperellum</i>	Maximum decline was noticed in reproductive factor with 81% and 78% in <i>T. viride</i> and <i>T. harzianum</i> , respectively	Mukhtar et al. (2021)
<i>M. javanica</i>	Okra and mungbean	<i>T. viride</i> , <i>T. harzianum</i> and <i>T. hamatum</i>	Soil drench application of conidial suspensions reduced root knot formation, nematode population and egg hatching	Siddiqui et al. (2001)
<i>Radopholus similis</i> , <i>Pratylenchus coffeae</i> and <i>Helicotylenchus multicinctus</i>	Banana cv. Robusta	<i>T. viride</i>	Soil application of <i>T. viride</i> reduced nematode populations	Shanthi and Rajendran (2006)
<i>M. javanica</i>	Pineapple	<i>T. asperellum</i> and <i>T. atroviride</i>	<i>T. asperellum</i> reduced galls and egg mass and increased root fresh weight	Kiriga et al. (2018)

glucanase and flavonoids and lignin, respectively, and the compounds can contribute for reprogrammed metabolic cascade associated with plant defence and signaling. Commercial formulates of *T. asperellum* and *T. harzianum* were used as BCAs against avirulent *M. incognita* in tomato and cucumber. The tested formulates provoked systemic resistance in tomato carrying *Mi-1.2* resistance gene but not in cucumber (Pocurull et al. 2020). In another study, Leonetti et al. (2017) found that *T. harzianum* colonization primed roots for systemic acquired resistance against *M. incognita* in tomato plants. Gene expression analysis showed that the augmentation in transcription of *ACO* gene encodes for an enzyme required for catalyzing the final stage of ethylene biosynthesis.

3.4.4 *Trichoderma* spp. to Control Plant Viral and Viroid Related Plant Diseases

Plant viruses are widespread and one of the crucial types of pathogens capable of causing severe damage to plants that has harmful effects on agriculture production sustainability. Generally, few viruses depend on vectors, such as fungi, nematodes, plant parasitic insects and seeds. The introduction of IPM strategies with the use of chemical and biological control methods has significantly reduced the rate of virus spread by enhancing host resistance and plant growth. Ultimately, it raises the plant tolerance to virus infection. Virus ability to significantly hinder plant physiological processes is closely related to a range of symptoms. There is a lack of information about *Trichoderma* spp. effects on the induction of plant defence mechanisms against viruses (Luo et al. 2010; Elsharkawy et al. 2013). Furthermore, there is a lack of studies on physiological changes in the plant under treatment with *Trichoderma* spp. in the plant-virus pathological system. There is no effective chemical treatment method to control plant viruses. A study by Vitti et al. (2015) has suggested using of *T. harzianum* as a new method to control plant viruses that stimulates the induction of defence responses of tomato against cucumber mosaic virus (CMV). Inhibition of RNA-dependent RNA polymerase gene and the association of ROS as secondary messengers were the action of *T. harzianum* in the modulation of viral symptoms and the defence response against the CMV (Vitti et al. 2015). The possible application of the bioagent *T. harzianum* against the CMV could be vital not only for developing an understanding of the interaction between plant, pathogen and biological control agent complex but also for developing realistic approaches to manage viral diseases.

Luo et al. (2010) have indicated that antimicrobial peptides (trichokonin) produced by *T. pseudokoningii* showed induced systemic resistance defence response against tobacco mosaic virus infection in tobacco. The phenolic compound production and reactive oxygen species are increased in tobacco when treated with trichokonin. It was reported that *T. asperellum* had the ability to induce resistance against CMV in *Arabidopsis* by increasing the expression levels of salicylic acid and jasmonic acid inducing genes in leaves of the plant and pretreatment of root with *T. asperellum* led to defence responses against CMV (Elsharkawy et al. 2013).

Ability of *T. harzianum* against CMV in tomato was explained by Vitti et al. (2015), which induced the defence responses against this virus.

Plant viroids are known as plant pathogens since 1971, which cause damages to agricultural production ranging from slight to severe. Control of plant viroids is complex since it is having a short stretch of circular, non-protein coding single-stranded RNA with autonomic replication. Few methods can be practised to control viroids, including inducing resistance, controlling vectors, and following cultural control methods. Application of *Trichoderma*-based control strategies can indirectly have effects on the control of plant viroids by control of the vectors and promotion of plant growth. The effective methods to control the plant viroids are same as the plant viruses, including controlling the vectors, following cultural control methods and inducing resistance. Based on the previous references, there is a lack of studies on using *Trichoderma* as a biocontrol agent against plant viroids. *Trichoderma* has the potential to act against this plant pathogen and related diseases by indirectly affecting the pathogen. However, it can be recommended to use *Trichoderma* against plant viroids in future since it can be involved in inducing resistance, controlling vectors, enhancing plant growth and encouraging defence and tolerance mechanisms in plants (Al-Ani 2018).

3.5 Advantages and Limitations of *Trichoderma* spp. as Biocontrol Agent

3.5.1 Advantages

3.5.1.1 A Suitable Alternative to Replace Synthetic Chemicals

Microbial pesticides produced from *Trichoderma* spp. to manage various plant diseases are now promising options to replace synthetic chemicals used to control most plant diseases nowadays. *Trichoderma* spp.-based biopesticides are natural in their origin that are highly recommended for organic crop production. Plant disease management approaches have used direct protection using synthetic chemicals as a prime principle (Ul-Haq et al. 2020). However, the *Trichoderma* spp.-based commercial formulations could be used to substitute for an alternative to copper, sulphur or antibiotic-based fungicides, bactericides and nematicides.

3.5.1.2 Versatile in Nature

Trichoderma spp. are effective BCAs for managing countless soil- and airborne diseases in plant protection and a potential versatile option in agriculture production where it combines several advantages in one product (Al-Ani 2018). The ability to involve in inter- and cross-kingdom interactions is the prime reason for the versatility of *Trichoderma*'s connections (Alfiky and Weisskopf 2021). Various species of *Trichoderma* have shown several benefits, apart from controlling plant pathogens. Many studies have proven positive plant growth promotion and yield enhancement, independent of chemical fertilization and induction of systemic resistance against plant pathogens, which are very significant in greenhouse and field conditions.

Besides, the most widely used *Trichoderma* spp. for the biocontrol of plant diseases are also known to reduce the stresses by abiotic factors, such as drought, salt and osmotic, temperature and cold stress (Rubio et al. 2017; Ghorbanpour et al. 2018; Ma et al. 2020).

3.5.1.3 Cost-Effective

Application of synthetic chemicals against plant pathogens can help manage specific diseases; in contrast, continuous and haphazard usage can increase overall input cost in crop production. Using *Trichoderma* spp. in control plant diseases is relatively low cost (Sood et al. 2020). Masso et al. (2016) used *Trichoderma* as a bioinoculant to control potato blight and stated that input cost and crop productivity of *Trichoderma* are economical compared to synthetic inputs. The yield enhancement due to *Trichoderma* boosts up productivity, thus increasing the total revenue.

3.5.1.4 Eco-Friendly and Minimized Safety Concerns

Trichoderma-based products do not leave any residues in the environment as synthetic chemicals do. They are not lethal to pollinators; therefore, they are eco-friendly (Sood et al. 2020). Biological functions performed by *Trichoderma* spp. are also suitable for the agriculture industry to implement eco-friendly agricultural practices (Zin and Badaluddin 2020). Besides, the minimal or free from toxicity of *Trichoderma* spp.-based biopesticides marks its advantages not only for the farmer or worker who is applying it in the field but also for the consumers who consume the products and ensure the minimal risks associated with it. Further, the eco-friendly nature of the BCAs of *Trichoderma* spp. makes them a useful tool for IPM strategies that are sustainable means in agriculture.

3.5.1.5 Easy to Commercialization

Another benefit of *Trichoderma* spp. is that they can be simply manipulated and used; in the meantime, many strains can be cultured and tested because they have a good shelf life that helps commercialize them quickly (Harman 2011).

3.5.2 Limitations

3.5.2.1 Slower Effect

Microbicidal activities of *Trichoderma* spp. related to biocontrol in disease management are slow compared to existing synthetic chemicals (Mukherjee et al. 2012). The spores of *Trichoderma* spp. are quiescent in soil. Due to this reason, the fungal species of *Trichoderma* require some time to colonize and proceed with their mode of actions, primarily via mycoparasitic action to control plant pathogens. This is where the direct and robust antibiosis mechanism by *Trichoderma* is essential to speed up the control process (Pertot et al. 2016).

3.5.2.2 Effect on Other Soil Microbiota

In common, BCAs do not affect non-target organisms when the application is made. The impact of *Trichoderma* spp. on soil microbial communities is comprehensively reviewed by Jangir et al. (2019). They stated that various modes of actions shown by *Trichoderma* spp. might cause temporary or long-term effect on the inhabitant soil microbes and pose a risk to beneficial non-target soil microbiotas. The volatile and non-volatile compounds, toxins and antibiotics secreted by *Trichoderma* spp. might affect beneficial microorganism, too (Jangir et al. 2019). Application of *Trichoderma* spp. has increased (Pang et al. 2017) and decreased (Naseby et al. 2000) bacterial and fungal diversities in soil. In a recent study, soil inoculation of *T. asperellum* controlled the Fusarium wilt pathogen *F. oxysporum* f. sp. *niveum* that affects watermelon production. The bioagent *T. asperellum* not only controlled the pathogenic fungi but also enhanced bacterial communities of *Pseudomonas*, *Sphingomonas*, *Actinomadura* and *Rhodanobacter* and reduced fungal diversity in the soil (Zhang et al. 2020b).

3.5.2.3 Uncertainty in Field Performance

In terms of efficacy, *Trichoderma* spp. may exhibit deviations in field performance concerning various environmental conditions of abiotic factors, i.e. soil type, soil temperature, soil pH, soil moisture content and presence of heavy metals (Mukhopadhyay and Kumar 2020), and biotic factors, i.e. soil microbiome diversity and activity, crop diversity and cultivars (Behzad et al. 2008). The broad utilization of commercialized biopesticides or bio-fertilizers of *Trichoderma* spp. has been hampered due to erratic efficacy under field circumstances (Alfiky and Weisskopf 2021). Therefore, the potential of *Trichoderma* in disease control should be evaluated in both lab and field conditions. Field trials should be carried out in various soil types with different microbiotas and climatic conditions before recommendation and commercialization.

3.6 Conclusion

Numerous strains and isolates of *Trichoderma* have been tested to control an array of diseases in various crop systems. Biological control approaches using *Trichoderma* spp. have shown positive results in laboratory, greenhouse and field conditions against fungi, bacteria, nematode and virus plant pathogens that cause a severe threat to agriculture. Understanding plant-*Trichoderma*-pathogen interaction plays a crucial role in *Trichoderma*-induced disease management. The role of *Trichoderma* in the studied areas revealed its specificity in biocontrol activity and interactions as they differ with the different *Trichoderma* spp., types of crop plants and type of pathogens. In addition to the biocontrol, *Trichoderma* spp. as BCAs have provided various advantages, such as yield augmentation, alternative to synthetic chemicals, versatility, cost-effective and eco-friendly. Therefore, *Trichoderma* spp. are potential BCAs in plant disease management to overcome various threats caused by current management practices.

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