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## Plant Responses to *Trichoderma* spp. and their Tolerance to Abiotic Stresses: A review

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### Abstract

*Trichoderma* spp. is known to offer a beneficial relationship with the plants. They are used as inoculants for biocontrol, biofertilization and phytostimulation with their abilities to produce different bio-active compounds and elicitors which interact with roots of the host plant directly increasing plant growth potential and tolerance to various abiotic stresses. With their abilities of mycoparasitism and their antagonistic effect within the plant, they are able to induce defense-related genes and protect the host plant from microbial infection. They are also known to induce systemic resistance in the plant and also induce tolerance against abiotic stresses such as drought and salinity through increase root growth, nutritional uptake and inducing protection against oxidative stress. Recently, the genome of seven *Trichoderma* species has been sequenced and there is a great prospect in developing transgenic plant which may offer effective tolerance against changing climatic condition. In this review, we provide an updated overview of *Trichoderma* interaction and their tolerances against various abiotic stresses by different strains of *Trichoderma*.

**Keywords:** *Trichoderma*, biocontrol, abiotic stresses, phytostimulation, bio-active compounds, mycoparasitism

### Introduction

Bio-control fungi have emerged as a beneficial tool in modern agricultural system. They have the abilities to reduce the negative effects of plant pathogen and ameliorate abiotic stresses such as drought, salinity, extreme temperature and heavy metal stresses. Among the beneficial fungi *Trichoderma* spp. have gained much interest due to their high reproductive capacity, survived under unfavorable conditions, prolific producers of secondary metabolites and ability to resist against plant pathogenic fungi (Benitez *et al.*, 2004; Harman 2006; Contreras-Cornejo *et al.*, 2016) [11, 34]. In addition, they have been exploited in biotechnological applications and provide important endeavor in the field of agriculture such as their ability to ameliorate both biotic and abiotic stresses and enhance plant growth and yield (Lorito *et al.*, 2010; Hermosa *et al.*, 2013) [52].

Colonization with *Trichoderma* and plant root is the first process for successful interaction, exchanging of signals and production of elicitors leading to symbiotic association between them. Enzymes and antibiotics that are produced attack the fungal pathogens and successfully degrade the fungal hyphae and permit penetration into the host cell. Both the enzymes and antibiotics are antifungal and synergistic in their action (Shoresh, 2010) [93]. *Trichoderma* are known to resist a range of diseases such as *Alternaria alternata*, *Botrytis cinerea*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, *Pythium* spp. and *Fusarium* spp (Harman *et al.*, 2004; Druzhinia *et al.*, 2011) [37] including that of nematode (Sharon *et al.*, 2001) [92]. They also induce ISR (systemic induced resistance) to plant after successful colonization and leads to signal transduction of different hormones and ultimately promote growth (Shoresh *et al.*, 2010) [93].

Abiotic stresses such as salinity, drought, heavy metal accumulation, and extreme temperature affected crop production worldwide. However, recent studies reported that *Trichoderma* induces tolerance against abiotic stresses and improve growth (Yasmeen and Siddiqui, 2017) [9] such as in radish, cucumber, pepper, bottle gourd, periwinkle, bitter melon, chrysanthemum, lettuce and tomato (Donoso *et al.*, 2008; Bae *et al.*, 2009; Brotman *et al.*, 2013; Contreras-Cornejo *et al.*, 2016; Zeilinger *et al.*, 2016; Kashyap *et al.*, 2017) [8, 15, 9, 113, 47]. *Trichoderma* colonized plant produce certain compounds (Auxins, ethylene, gibberellins, plant enzymes, antioxidants) and phytoalexins and phenols that provide tolerance to abiotic stresses and enhance the branching capacity of the root system (Brotman *et al.*, 2013; Lopez-Bucio *et al.*, 2015) [15, 51]. This review focuses on the current knowledge of *Trichoderma*-plant interaction and their role in tolerance against abiotic stresses.

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### Colonization and interaction

Many *Trichoderma* strains were found to colonize plant roots of both monocot and dicots. (Harman and Shores, 2007). *Trichoderma*-root interactions involve recognition, attachment, penetration, colonization and nutrient transfer from the root (Mukherjee *et al.*, 2012) [65]. First, their hyphae coil around the roots, forming appressoria-like structures, and finally penetrate the root cortex (Yedid *et al.*, 1999) [110]. Attachment to the host plant root by appressoria like structures is mediated by two hydrophobin-like proteins, TasHyd1 from *T. asperelloides* and *gid 74* from *T. harzianum*. The gene *gid74* encodes a cysteine rich cell wall protein and the expansin-like protein swollenin TasHyd1 with a cellulose-binding domain which can recognize the cellulose and modify plant cell wall architecture by secreting cellulolytic and proteolytic enzymes (Viterbo and Chet, 2006; Brotman *et al.*, 2008; Samolski *et al.*, 2012) [108, 14, 84] which facilitate root colonization. This enables fungal –host recognition and adhesion during symbiotic associations (Viterbo and Chet, 2006) [108]. *T. harzianum* is reported to produce plant cell wall degrading enzymes like endopolygalacturonase which are involved in active root colonization (Moran-Diez *et al.*, 2009) [63]. Also *T. virens* was shown to produce auxins and other related compounds that may facilitate root colonization by enhancing root growth (Contreras *et al.*, 2009) [18].

Both symbiotic and non-symbiotic beneficial microbes are initially recognized as pathogenic and would trigger plant immunity through the perception of microbes –associated molecular patterns (MAMPs) by the plant mediated receptors (Jones and Dangl, 2006; Boller and Felix, 2009; Pieterse, 2012) [46, 13, 72]. However *Trichoderma* remodel or manipulate the plant immune response by reprogramming their transcriptome and proteome (Marra *et al.*, 2006; Alfano *et al.*, 2007; Segarra *et al.*, 2007; Shores and Harman, 2008) [55, 86, 94, 51]. Exchanges of molecular signals and deposition of fungal elicitors in root apoplast are the general mechanism involved in root colonization and interaction. For example, colonization by *T. harzianum* induces strong changes in shoot proteomes of maize seedlings even though T22 interacts with the roots (Shores and Harman, 2008; Contreras-Cornejo *et al.*, 2016) [94, 9]. Although well known for their ability to colonize the rhizosphere with limited root penetration, some *Trichoderma* species are known to reside in plants as typical endophytes, entering through trichomes by producing appressoria-like structures (Bae *et al.*, 2009) [8]. Hence, their interaction is mutually beneficial where *Trichoderma* can freely live in the soil and should consider good plant symbionts.

### Bio-active compounds involved in induction of plant responses and disease resistance

*Trichoderma* releases certain classes of compounds into the zone of interaction and induce resistance in plants. The first class is protein with enzymatic and other activity. Xylanases, cellulase and swollenin were secreted by *Trichoderma* species (Fuchs, 1989; Lotan and Fluhr, 1990; Anderson *et al.*, 1993; Martinez *et al.*, 2001) [29, 53, 6, 56]. These fungi produce plant growth promoting compounds which have the capacity to increase photosynthesis and biomass production and to elicit developmental programs via regulation of gene expression (Chacon *et al.*, 2007; Shores and Harman, 2008; Vargas *et al.*, 2009, 2011; Harman 2011; Studholme *et al.*, 2013; Martinez- Medina *et al.*, 2014; Pereira *et al.*, 2014; Rubio *et al.*, 2014) [94, 102, 11, 98, 57, 71, 81]. *Trichoderma virens* and *Trichoderma atroviride* produce auxins indole-3-acetic acid

(IAA), indole-3-ethanol (IET), indole-3-acetaldehyde (IALD) and indole-3-carboxaldehyde (ICALD). These compounds stimulate cell division, elongation and/or differentiation processes, ultimately increasing the growth and yield of the plant host (Contreras-Cornejo *et al.*, 2009, 2011) [17, 18]. This study correlates with the experiment on cherry root-stock where higher level of IAA was found in both leaves and roots (Sofa *et al.*, 2011) [96]. Phytostimulant properties of *Trichoderma* are also dependent on auxin accumulation in tomato (Chowdappa *et al.*, 2013; Martinez-Medina *et al.*, 2014) [57].

*Trichoderma* spp. produce secondary metabolites which include volatile and non-volatile substances, such as 6-n-pentyl-6H-pyran-2-one (6PP), gliotoxin, viridian, harzianopyridone, harzianone and peptaibols (Reino *et al.*, 2008; Vinale *et al.*, 2008) [78, 106, 107]. In *A. thaliana* seedling when exposed to volatile organic compound (VOC) emitted by *Trichoderma* increased root branching and biomass production and accelerated flowering (Ahung *et al.*, 2013; Contreras-Cornejo *et al.*, 2014). Recent studies revealed that *T. atroviride* produced 6-PP a volatile compound which promoted plant growth and regulated root architecture, inhibiting primary root growth and inducing lateral root formation (Garnica-Vergara *et al.*, 2015) [30]. *Sm1* which has a hydrophobin like properties found to be produced by strains of *T. virens*; it is known to induce terpenoid phytoalexin biosynthesis and peroxidase activity in cotton (Hanson and Howell, 2004; Djonovic *et al.*, 2006, 2007) [32, 24, 25]. Harzianic acid (HA), a nitrogen heterocyclic compound produced by *Trichoderma harzianum* has growth promoting effect (Vinale *et al.*, 2009) [104] which acts as antagonistic effect on fungal pathogens as reported in canola seedlings (Vinale *et al.*, 2009) [104]. Also they promote nutrients uptake and growth of plant by their ability to produce siderophores. This secondary metabolites binds essential metals ions such as iron (Vinale *et al.*, 2013) [105]. Siderophores produced by beneficially microorganism is considered crucial for plant iron uptakes, particularly in calcareous soil (Sharma *et al.*, 2003; Vinale *et al.*, 2013) [90, 105].

### *Trichoderma* induced resistance

Any foreign interaction or penetration in plant roots activates their immune system, however, *Trichoderma* spp. remodel the plant immune system and recognized as non-pathogenic (Zamioudis and Pieterse, 2012) [72]. Many recognized *Trichoderma* strains are able to elicit JA and ET synthesis which are involved in ISR (Induce systemic resistance) development (Contreras-Cornejo *et al.*, 2011; Salas-Marina *et al.*, 2011; Hermosa *et al.*, 2012; Nawrocka and Malolepsza, 2013) [17, 39]. Study done on maize with the use of specific inhibitors of JA and ET synthesis shows the signaling pathways transduce by these molecules in the protection against *C. graminicola* (Djonovic *et al.*, 2006) [24]. Similarly ISR induced resistance by *T. asperellum* or *T. harzianum* T39 against *B. cinerea* in *A. thaliana* was by also found (Karolev *et al.*, 2008; Segarra *et al.*, 2010; Velazquez-Robledo *et al.*, 2011; Nawrocka and Malolepsza, 2013) [87].

*Trichoderma* spp. plays a significant role in suppressing plant disease and growth of pathogens in both greenhouse and field condition (Harman *et al.*, 2004) [36, 37]. Given the fact that *Trichoderma* produces a range of elicitors which interact with plant receptors and recognition of *Trichoderma*, and induction of resistance in plants (Djonovic *et al.*, 2006; Sriram *et al.*, 2009; Shores *et al.*, 2010; Salas-Marina *et al.*, 2011; Mathys *et al.*, 2012) [24, 93, 83]. Moreover, different strain of

*Trichoderma* produces small secondary metabolites and shown to induce pathogenesis-related (PR) protein and reduces diseases symptoms systemically (Vinale *et al.*, 2008) [106, 107]. Mycoparasitism is considered a highly important in many system and has the potential to attack and lyses plant pathogenic fungi such as *Alternaria alternate*, *Botrytis cinerea*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, *Pythium spp.* and *Fusarium spp.* (Harman *et al.*, 2004; Druzhinia *et al.*, 2011) [36, 37]. This is clear that *Trichoderma* parasitizes the pathogen in its active and non-active resting spores by producing chitinases, glucanases, and proteases that help the flow of nutrient into the mycoparasite and degrade the host pathogen (Mukherjee *et al.*, 1995; Inch and Gilbert, 2011) [66, 41].

#### **Trichoderma conferring tolerance to abiotic stresses**

The major abiotic factors which include heat, drought, cold and salinity induces cellular damages in crop plants. However, fungal symbionts are found commonly in association with plant communities resisting naturally to different stress (Marasco *et al.*, 2012) [54]. *Trichoderma* strains are known to offer plant tolerance against abiotic stress such as drought and salinity (Mastouri *et al.*, 2010; Shores *et al.*, 2010) [58, 93] through increased root growth, nutritional uptake and inducing protection against oxidative stress.

Plants grown under *Trichoderma* treatment are much more resistant to water stress. Study done on tomato proves that T22 inoculated tomato seedlings in water deficit condition and in the presence of methy-viologen (MV) which is known to enhanced ROS production, reduced the oxidative inhibition of seed germination and improved seedling growth (Shores *et al.*, 2010; Mastouri *et al.*, 2012) [93, 59]. These might be due to the activation of antioxidant responses and increased activities of ascorbate and glutathione-recycling enzymes (Mastouri *et al.*, 2012) [59]. Drought causes increase in total amino acid content but when inoculated with *T. Hamatum* DIS2196 it mitigates the negative effects in cacao seedling and also delayed drought- induced changes which means it allows the plant to continue growth (Bae *et al.*, 2009) [8]. Moreover, maize plant treated with *T. hazianum* resists water deficit and enhanced deep rooting (Harman, 2000) [33]. Shores and Harman, (2008) [94] found that the maize plant inoculated with *Trichoderma* has high starch content in leaves. This could be beneficial in drought condition where prolonged stomatal conductance leads to carbon starvation. Shukla *et al.* (2012) [95] reported that *Trichoderma* application increase the root growth of rice regardless of the water deficit which causes delay in drought responses and also found to

decrease proline, MDA and hydrogen peroxide content and increased phenolic compound concentration.

Salinity affects most plant and alter water-relation in the tissue, disrupt ion balances and induces oxidative stress (Munns, 1993 and Shores *et al.*, 2010) [93, 67]. Study done in Indian mustard shows that higher concentration of NaCl (200mM) deteriorates growth, physio-biochemical attributes like plant height decreased by 33.7%, root length by 29.7% and plant dry weight by 34.5%. But when treated with *Trichoderma harzianum* it led to increase by 13.8, 11.8, and 16.7% in shoot, root length and plant DW respectively as compared to the plant treated with NaCl (200mM) alone (Ahmad *et al.*, 2015) [3]. Thus, application of *T. hazianum* mitigates the negative effect of NaCl stress. Same findings were shown in tomato (Mastouri *et al.*, 2012) [59]. Also salinity decreased the oil content in Indian mustard (Ahmad *et al.*, 2015) [3] which might be due to the limited supply of cytokinin from root to shoot that results in variation of cytokinin: ABA ratio in leaf (El-Keltawi and Croteau, 1987; Ahmad *et al.*, 2015) [28, 3]. However, *Trichoderma* treated plant restored the oil content in the leaves under NaCl stress (Ahmad *et al.*, 2015) [3]. In fact, beneficial microbes have been reported to limit the ABA accumulation during NaCl stress and enhanced the transportation from root to shoot (Aroca *et al.*, 2013; Alenazi *et al.*, 2015; Ahmad *et al.*, 2015) [38, 3].

Salt stress decreased the photosynthetic pigment. This might be due to the inhibition of synthesis of different enzymes such as  $\delta$ -aminolevulinic acid dehydratase and photochlorophyllide reductase which are involved in chlorophyll biosynthesis and to the impairment in supply of  $Mg^{2+}$ ,  $Fe^{2+}$ ,  $Zn^{2+}$  and  $Mn^{2+}$  that are required for synthesis of Chl (Padmaja *et al.*, 1990; Van Assche and Clijsters, 1990; Kupper *et al.*, 1996; Ahmad *et al.*, 2015) [70, 101, 49, 3]. Decrease in carotenoid content will lead to increased ROS production in NaCl stress which ultimately hampers plant growth by inducing oxidative damages to related DNA, RNA and protein (Mishra *et al.*, 2006; Ahmad *et al.*, 2010) [2, 4]. However, application of *T. hazianum* restored the chlorophyll and carotenoid content up to an appreciable level in saline condition (Ahmad *et al.*, 2015) [3] and this finding is correlated with Rawa *et al.* (2011) [77] in wheat and Zhang *et al.* (2013) [114] in cucumber. Hence, increasing the pigment concentration which might be due to phytohormone production in *Trichoderma* inoculated plant (Martinez-Medina *et al.*, 2014; Resende *et al.*, 2014) [57]. The increase in photosynthetic pigment may be due to the inhibition of Na uptake (Iqbal and Ashraf, 2013) [43].

**Table 1:** Effects of *Trichoderma* in plants subjected to various abiotic stresses

Sl.	Crops	<i>Trichoderma spp</i>	Stress subjected to	Effects	References
1.	Rice	<i>T.harzianum</i>	Salinity	Better photosynthetic performance, higher pigment concentration, high proline content	Yasmeen and Shaheed (2017) [9]
2.	Mustard	<i>T. harzianum</i>	Salinity	Mitigates the negative effect of salt stress and increase in oil content	Ahmad <i>et al.</i> (2015) [3]
3.	Arabidopsis	<i>T.virens/T.atroviride</i>	Salinity	Promotes plant growth, induction of lateral Roots and root hairs through auxin signaling	Conteras-Cornejo <i>et al</i> (2014)
4.	Maize	<i>T.harzianum</i>	Salinity	High water content and better photosynthetic performance	Yasmeen and Shaheed, (2017) [9]
5.	Tomato	<i>T.parareesei / T. reesei</i>	Salinity	Produces cellulase and xylanases, lateral root development and defense against <i>Botrytis cinerea</i>	Rubio <i>et al.</i> (2014) [81]
6.	Cacao	<i>T.hamatum</i> (DIS2196)	Drought	Delay drought-induced changes and continue growth	Bae <i>et al.</i> (2009) [8]
7.	Tomato	<i>T. harzianum</i>	Drought	Reduced oxidative inhibition and improved seedling growth	Mastouri <i>et al.</i> (2012) [59], Shores <i>et al.</i> (2010) [93]
8.	Rice	<i>T. harzianum</i>	Drought	Delays drought responses and increase phenolic	Shukla <i>et al.</i> (2012) [95]

				concentration	
9.	Maize	<i>T. harzianum</i>	Drought	Enhanced deep rooting and high starch content in leaves	Harman, (2000) [33]
10.	Arabidopsis	<i>T. harzianum</i>	Heat	Enhanced tolerance to heat and other abiotic stresses, producing heat-shock proteins	Montero-Barrientos <i>et al.</i> (2008,2010) [62, 61]
11.	Tomato	<i>T. harzianum</i> AK20G	Cold	Enhanced photosynthesis and growth rate, reduced lipid peroxidation rate and electrolyte leakage	Ghorbanpour <i>et al.</i> (2018) [31]
12.	Tobacco	<i>T. harzianum</i>	Heavy metal/salt	Enhanced tolerance to both stresses and resistance to <i>R. solani</i> and <i>P. syringae</i>	Dana <i>et al.</i> (2006) [21]
13.	Onion	<i>T. asperellum</i>	Heavy metal	Reduce Cu accumulation and translocation to leaves	Tellez-Vargas <i>et al.</i> (2017) [99]
14.	Mustard	<i>T. atroviride</i>	Heavy metal	Improves photoextraction efficiency and alleviate cellular toxicity of cadmium and nickel	Cao <i>et al.</i> (2008) [16]
15.	Sunflower	<i>T. logibrachiatum</i>	Heavy metal	Increase antioxidant enzymes in Pb <sup>2+</sup> oxidative stress	Devi <i>et al.</i> 2017 [23]

*Trichoderma* inoculated plant also found to increase potassium content in plants (Yedia *et al.*, 2001; Yildirim *et al.*, 2006) [111, 112]. Increasing potassium uptake ameliorates the negative effect of salinity (Shabala and Cuin, 2008) [88] and induces stomatal closure and salt stress-induced osmotic stress (Shoresh *et al.*, 2010) [93]. Salinity also reduces the calcium content in plants (Cramer, 2002; Neves-Piestun and Bernstein, 2005) [20, 69]. However, treatment with *Trichoderma* increased the calcium content under salt stress as compared to control (Yildirim *et al.*, 2006) [112].

Ahmad *et al.* (2015) [3] found that proline content in mustard plants is increased when treated with *Trichoderma* under salt stress. Proline is an important osmolyte which maintain the cell osmoregulation in NaCl stress (Ahmad *et al.*, 2010; Rasool *et al.*, 2013) [2, 4]. Similar findings were reported when *Trichoderma* inoculated *Arabidopsis* seedlings showed increased accumulation of proline as compared to control under salt stress (Contreras-Cornejo *et al.*, 2014). Proline has high antioxidative property that could scavenge ROS like hydrogen peroxide and protect the cell from oxidative damage (Ahmad *et al.*, 2010; Jogaiah *et al.*, 2013) [2, 4]. Moreover, accumulation of high proline enhanced the N fixation in plants (Hashem *et al.*, 2015).

Under severe stress condition plants are unable to scavenge the accumulation ROS and leads to damages of cellular components (Mittler, 2002) [60]. However, *Trichoderma* inoculated plants protect the plants by increasing the ROS scavenging abilities. Proteomics studies reveal that *Trichoderma* inoculated plants have increased levels of SOD, peroxidase, glutathione-reductase and glutathione-S-transferases (GST), and detoxifying enzymes in leaves (Shoresh, 2008) [94]. *Trichoderma* T22 inoculated seedlings also restored the vigor damaged by oxidative stress (Bjorkman, 1998) [12]. Recently, a study done on tomato inoculated with *Trichoderma harzianum* AK20G strain mitigate the negative effects of chilling stress resulting in reduced lipid peroxidation rate and electrolyte leakage overall increasing the leaf water content and proline accumulation (Ghorbanpour *et al.*, 2018) [31]. Similarly, *T. harzianum* inoculated *Arabidopsis* enhanced the tolerance to heat stress producing heat shock proteins (Montero-Barrientos *et al.*, 2008, 2010) [62, 61].

Plants are often subjected to heavy metal accumulation which imposed many deleterious effects on plant health such as inhibition of photosynthesis, lower nutrient uptake, reduction in cell division and germination percentage (Sharma and Dubey, 2005) [91]. Inoculation with *Trichoderma atroviride* F6 on soil contaminated with Cd and Ni significantly alleviate the cellular toxicity of mustard (Cao *et al.*, 2008) [16]. Devi *et al.* (2017) [23] reported that inoculation with *Trichoderma logibrachiatum* (WT2) on sunflower subjected to Pb<sup>2+</sup>

mitigate the oxidative stress induce to plant and found increased level of antioxidant enzymes. However, different strains of *Trichoderma* have a different range of growth promotion (Adam *et al.*, 2007) [1]. *Trichoderma harzianum* T22 inoculated plant have substantial increase in tree growth and less growth promotion in metal contaminated soils than in the uncontaminated soils (Adam *et al.*, 2007) [1]. However, *Trichoderma atroviride* F6 inoculated plant increase plant growth in the contaminated soils but doesn't effectively stimulate plant growth in uncontaminated soils which may be due the reduction in the damage caused by metal stress and ultimately increase plant growth (Devi *et al.*, 2017) [23]. Similar findings were found in onion where *Trichoderma asperellum* inoculated plant reduces the phytotoxic effect of copper (Tellez-Vargas *et al.*, 2017) [99].

#### Plant growth promotion by *Trichoderma* inoculants

Recently *Trichoderma* spp. were suggested as a plant growth promoting fungi (PGPR) due to their ability to produce siderophores, phosphates-solubilizing enzymes and phytohormones (Doni *et al.*, 2013, 2014). Promotion of plant growth is one of the beneficial traits of *Trichoderma* (Shukla *et al.*, 2012; Contreras-Cornejo *et al.*, 2016) [95, 19]. This can be realized through several mechanism involved like mycoparasitism, antibiosis, degradation of toxins, inactivation of pathogenic enzymatic pathways, resistance to pathogens, enhanced nutrient uptake leading to overall development (Harman 2006; Lorito *et al.*, 2010; Doni *et al.*, 2014) [34, 52]. Significant increase in plant height, leaf number, tiller number and root length in rice was reported by Doni *et al.* (2014) [27] which are possible because of the mechanism involved such as nutrient use efficiency and tolerance to abiotic and biotic stress. Production of phytohormones by *Trichoderma* treated plant is the key for enhanced plant growth (Chowdappa *et al.*, 2013). They are reported to produce cytokinin like molecules (eg. Zeatin) and gibberellins related molecules (GA3 or GA4) which could be beneficial for biological enhancements of crop fertility (Tucci *et al.*, 2011; Idowu *et al.*, 2016; Kashyap *et al.*, 2017) [100, 40, 47]. Higher photosynthetic rate was also observed in rice inoculated with *Trichoderma* (Doni *et al.*, 2014) [27]. Similarly, in maize plant *Trichoderma* increased growth, enhanced root biomass production and increased root hair development (Bjorkman *et al.*, 1998; Harman *et al.*, 2004) [12, 36, 37]. Rice plant treated with *Trichoderma* has better uptake of nutrient (Saba *et al.*, 2012; Doni *et al.*, 2014) [82, 27]. Rice plant treated with *T. harzianum* significantly increased the ability to tolerate drought and water deficit condition contributing to the better uptake of nutrient and plant growth (Shukla *et al.*, 2012; Doni *et al.*, 2014) [95, 27]. Study done on tomato seeds with *T. harzianum* proves that *Trichoderma* accelerates the seed germination, ameliorates water, osmotic,

salinity, chilling and heat stresses by inducing physiological protection against cellular damages. Mastouri *et al.* (2010) [58] also reported to increase foliar area, secondary root development and modulate root architecture (Chacon *et al.*, 2007). Furthermore, it has been reported that *Trichoderma* inoculated plants have increased growth in plants such as strawberries, tomatoes, soybeans, apples, cotton and gray mangroves (Porrás *et al.*, 2007; Morsy *et al.*, 2009; Shanmugaiah *et al.*, 2009; John *et al.*, 2010; Raman 2012; Saravanakumar *et al.*, 2013; Doni *et al.*, 2014) [73, 64, 89, 45, 75, 85, 27].

### Conclusion

Plant gene expression depends on the *Trichoderma* isolates colonizing the plants (Bailey *et al.*, 2006) [9]. They also respond differently depending upon the plant species or cultivars. Study done on maize show neutral or even negative responses due to significant varietal difference (Harman, 2006) [35]. Abiotic stress response in the plant is mainly controlled by ABA through defense signaling pathway including SA, JA and ET pathways (Robert-Seilaniantz *et al.*, 2011) [80]. However, recent studies highlighted the fact that plants respond differently to multiple stresses than to individual stresses (Atkinson and Urwin, 2012) [7]. Study done on grapevines exposed to heat and drought stress showed that, efficacy of T39-induced resistance was not affected by single stress but decreasing trends were observed when induced in both the stresses (Roatti *et al.*, 2013) [79]. This confirms that more information is needed on the effect of multiple abiotic factors, their resistance inducer and the signaling molecules involved by specific characterizations for each inducer and pathosystem. As the information seems to be very important because of changing climatic conditions, warmer and drier summers are predicted in several regions (IPCC 2007). So studies focusing on the abiotic stresses which affect crop responses to beneficial and pathogenic microorganism and analysis of their specific defense-related genes shall contribute to the biotechnological approach. Additionally, genes from *Trichoderma* could be isolated and transgenic plants generated with higher resistance against biotic and abiotic stresses. For example, genes from *T. atroviride* which codes for cell wall degrading enzymes have been isolated and inserted to rice which gave resistance to sheath blight caused by *R. solani* (Liu *et al.*, 2004) [50]. Recently, the genome of seven *Trichoderma* spp. has been sequenced (Srivastava *et al.*, 2014; Baroncelli *et al.*, 2016; Rai *et al.*, 2016) [97, 10, 74]. There is a great prospect in developing transgenic plants for greater health management and this will be biggest challenge in future.

### References

- Adams P, De-Leij FAAM, Lynch JM. *Trichoderma harzianum* Rifai 1295-22 mediates growth promotion of crack willow (*Salix fragilis*) saplings in both clean and metal-contaminated soil. *Microbial. Ecol.* 2007; 54:306-313.
- Ahmad P, Jaleel CA, Sharma S. Antioxidant defense system, lipid peroxidation, proline-metabolizing enzymes, and biochemical activities in two *Morus alba* genotypes subjected to NaCl stress. *Russian J Plant Physiol.* 2010a; 57:509-517.
- Ahmad P, Abeer H, Elsayed FAA, Alqarawi AA, Riffat J, Dilfuza E *et al.* Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L.) through antioxidative defense system. *Frontiers in Plant Science.* 2015; 6:868.
- Ahmad P, Jaleel CA, Salem MA, Nabi G, Sharma S. Roles of enzymatic and non-enzymatic antioxidants in plants during abiotic stress. *Critical Reviews in Biotechnology.* 2010b; 30:161-175.
- Alfano G, Ivey MLL, Cakir C, Bos JIB, Miller SA. Systemic modulation of gene expression in tomato by *Trichoderma hamatum* 382. *Phytopathology.* 2007; 97:429-37.
- Anderson RD, Bailey BA, Taylor R, Sharon A, Avni A. Fungal xylanase elicits ethylene biosynthesis and other defense responses in tobacco. In *Cellular and Molecular Aspects of the Plant Hormone Ethylene.* ed. JC Pech, A Latch'e, C Balague, Dordrecht, Neth.: Kluwer 1993, 197-204.
- Atkinson NJ, Urwin PE. The interaction of plant biotic and abiotic stresses: From genes to the field. *J. Exp. Bot.* 2012; 63:3523-3543.
- Bae H, Sicher RC, Kim MS, Kim SH, Strem MD. The beneficial endophyte *Trichoderma hamatum* isolate DIS 219b promotes growth and delays the onset of the drought response in *Theobroma cacao*. *J. Exp. Bot.* 2009; 60:3279-95.
- Bailey B, Bae H, Strem M, Roberts D, Thomas S. Fungal and plant gene expression during the colonization of cacao seedlings by endophytic isolates of four *Trichoderma* species. *Planta.* 2006; 224:1449-64.
- Baroncelli R, Zapparata A, Piaggese G, Sarrocco S, Vannacci G. Draft whole-genome sequence of *Trichoderma gamsii* T6085, a promising biocontrol agent of *Fusarium* head blight on wheat. *Genome Announc.* 2016; 4(1):e01747-15. doi:10.1128/genomeA.01747-15
- Benítez T, Rincón AM, Limón MC, Codón, AC. Biocontrol mechanisms of *Trichoderma* strains. *Int. Microbiol.* 2004; 7:249-260
- Bjorkman T, Blanchard LM, Harman GE. Growth enhancement of shrunken-2 sweet corn with *Trichoderma harzianum* 1295-22: effect of environmental stress. *J. Am. Soc. Hortic. Sci.* 1998; 123:35-40.
- Boller T, Felix G. A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern recognition receptors. *Annu Rev Plant Biol.* 2009; 60:379-406
- Brotman Y, Briff E, Viterbo A, Chet I. Role of Swollenin, an expansin-like protein from *Trichoderma*, in plant root colonization. *Plant Physiol.* 2008; 147:779-89.
- Brotman Y, Landau U, Cuadros-Inostroza A. *Trichoderma* plant root colonization: escaping early plant defense responses and activation of the antioxidant machinery for saline stress tolerance. *PLoS Pathog.* 2013; 9:e1003221.
- Cao L, Jiang M, Zeng Z, Du A, Tan H, Liu Y. *Trichoderma atroviride* F6 improves phytoextraction efficiency of mustard (*Brassica juncea* (L.) Coss. var. *foliosa* Bailey) in Cd, Ni contaminated soils. *Chemosphere.* 2008; 71(9):1769-1773. <https://doi.org/10.1016/j.chemosphere.2008.01.066>
- Contreras-Cornejo HA, Mac'ias-Rodr'iguez L, Beltra'n-Pen' a E. *Trichoderma*-induced plant immunity likely involves both hormonal and camalexin dependent mechanisms in *Arabidopsis thaliana* and confers resistance against necrotrophic fungi *Botrytis cinerea*. *Plant Signal Behav.* 2011; 6:1554-63.

18. Contreras-Cornejo HA, Macías-Rodríguez L, Cortés-Penagos C, López-Bucio J. *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in *Arabidopsis*. *Plant Physiol.* 2009; 149:1579-1592.
19. Contreras-Cornejo HA, Macías-Rodríguez L, Del-Val E, Larsen J. Ecological functions of *Trichoderma* spp. and their secondary metabolites in the rhizosphere: interactions with plants. *FEMS Microbiol Ecol.* 2016; 92:fiw036
20. Cramer GR. Sodium-calcium interactions under salinity stress. In *Salinity: Environment—Plants—Molecules*. ed. A L'auçhli, U L' uttge, *Amsterdam: Springer*, 2002, 205-28.
21. Dana MM, Pintor-Toro JA, Cubero B. Transgenic tobacco plants overexpressing chitinases of fungal origin show enhanced resistance to biotic and abiotic stress agents. *Plant Physiol.* 2006; 142:722-730.
22. DeSouza JT, Bailey BA, Pomella AWW, Erbe EF, Murphy CA. Colonization of cacao seedlings by *Trichoderma stromaticum*, a mycoparasite of the witches' broom pathogen, and its influence on plant growth and resistance. *Biol. Control.* 2008; 46:36-45.
23. Devi S, Sreenivasulu Y, Rao K. Protective role of *Trichoderma logibrachiatum* (WT2) on Lead induced oxidative stress in *Helianthus annuus* L. *Indian Journal of Experimental Biology.* 2017; 55:235-241. Retrieved from [http://nopr.niscair.res.in/bitstream/123456789/41180/1/IJEB\\_55%284%29\\_235-241.pdf](http://nopr.niscair.res.in/bitstream/123456789/41180/1/IJEB_55%284%29_235-241.pdf)
24. Djonovic S, Pozo MJ, Dangott LJ, Howell CR, Kenerley CM. *Sm1*, a proteinaceous elicitor secreted by the biocontrol fungus *Trichoderma virens* induces plant defense responses and systemic resistance. *Molec. Plant-Microbe Interact.* 2006; 8:838-53.
25. Djonovic S, Vargas WA, Kolomiets MV, Horneski M, Wiest A, Kenerley CM. A proteinaceous elicitor *Sm1* from the beneficial fungus *Trichoderma virens* is required for induced systemic resistance in maize. *Plant Physiol.* 2007; 145:875-89.
26. Doni F, Al-Shorgani NKN, Tibin EMM, Abuelhassan NN, Anizan I, Che-Radziah CMZ *et al.* Microbial involvement in growth of paddy. *Curr Res J Biol Sci.* 2013; 5(6):285-290.
27. Doni F, Isahak A, Zain CRCM, Ariffin SM, Mohamad WNW, Yusoff WMW. Formulation of *Trichoderma* sp. *SL2* inoculants using different carriers for soil treatment in rice seedling growth. *Springer plus.* 2014; 3:532. doi: 10.1186/2193-1801-3-532
28. El-keltawi NE, Croteau R. Salinity depression of growth and essential oil formation in spearmint and marjoram and its reversal by foliar applied cytokinin. *Phytochemical.* 1987; 26:1333-1334. doi:10.1016/S0031-9422(00)81806-3
29. Fuchs Y, Saxena A, Gamble HR, Anderson JD. Ethylene biosynthesis-inducing protein from cellulysin is an endoxylanase. *Plant Physiol.* 1989; 89:138-43.
30. Garnica-Vergara A, Barrera-Ortiz S, Muñoz-Parra E. The volatile 6-pentyl-2H-pyran-2-one from *Trichoderma atroviride* regulates *Arabidopsis thaliana* root morphogenesis via auxin signaling and *ETHYLENE INSENSITIVE 2* functioning. *New Phytol.* 2015; 209:1496-1512.
31. Ghorbanpour A, Salimi A, Ghanbary MAT, Pirdashti H, Dehestani A. The effect of *Trichoderma harzianum* in mitigating low temperature stress in tomato (*Solanum lycopersicum* L.) plants. *Scientia Horticulturae.* 2018; 230:134-141.
32. Hanson LE, Howell CR. Elicitors of plant defense responses from biocontrol strains of *Trichoderma viren*. *Phytopathology.* 2004; 94(2):171-176.
33. Harman GE. Myths and dogmas of biocontrol. Changes in perceptions derived from research on *Trichoderma harzianum* T-22. *Plant Dis.* 2000; 84:377-393.
34. Harman GE. Overview of mechanisms and uses of *Trichoderma* spp. *Phytopathology.* 2006; 96:190-194.
35. Harman GE. Multifunctional fungal plant symbionts: new tools to enhance plant growth and productivity. *New Phytol.* 2011; 189:647-649.
36. Harman GE, Howell CR, Viterbo A, Chet I, Lorito M. *Trichoderma* species—opportunistic, a virulent plant symbionts. *Nat Rev Microbiol.* 2004; 2:43-56
37. Harman GE, Petzoldt R, Comis A, Chen J. Interactions between *Trichoderma harzianum* strain T22 and maize inbred line Mo17 and effects of this interaction on diseases caused by *Pythium ultimum* and *Colletotrichum graminicola*. *Phytopathology.* 2004; 94:147-53.
38. Alenazi M, Egamberdieva D, Ahmad P. Arbuscular mycorrhizal fungi mitigates NaCl induced adverse effects on *Solanum lycopersicum* L. *Pak. J Bot.* 2015; 47(1):327-340.
39. Hermosa R, Viterbo A, Chet I, Monte E. Plant beneficial effects of *Trichoderma* and of its genes. *Microbiology.* 2012; 158:17-25.
40. Idowu OO, Oni AC, Salami AO. The interactive effects of three *Trichoderma* species and damping-off causative pathogen *Pythium aphanidermatum* on emergence indices, infection incidence and growth performance of sweet pepper. *Int J Recent Sci Res.* 2016; 7:10339-10347.
41. Inch S, Gilbert J. Scanning electron microscopy observations of the interaction between *Trichoderma harzianum* and perithecia of *Gibberella zeae*. *Mycologia.* 2011; 103:1-9
42. IPCC. Climate Change 2007: Synthesis Report, A Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R. K. and Reisinger, A. (eds.)], IPCC, Geneva, Switzerland, 2007.
43. Iqbal M, Ashraf M. Alleviation of salinity-induced perturbations in ionic and hormonal concentrations in spring wheat through seed preconditioning in synthetic auxins. *Acta Physiol. Plant.* 2013; 35:1093-1112. doi: 10.1007/s11738-012-1147-z
44. Jogaiah S, Govind SR, Tran LS. Systems biology-based approaches toward understanding drought tolerance in food crops. *Crit. Rev. Biotechnol.* 2013; 33:23-39. doi:10.3109/07388551.2012.659174
45. John RP, Tyagi RD, Prévost D, Brar SK, Pouleur S, Surampalli RY. Mycoparasitic *Trichoderma viride* as a biocontrol agent against *Fusarium oxysporum* f. sp. adzuki and *Pythium arrhenomanes* and as a growth promoter of soybean. *Crop Prot.* 2010; 29:1452-1459.
46. Jones JD, Dangl JL. The plant immune system. *Nature.* 2006; 444:323-29.
47. Kashyap PL, Kumar S, Srivastava AK. Nanodiagnostics for plant pathogens. *Environ Chem Lett.* 2017; 15:7-13.
48. Korolev N, Rav-David D, Elad Y. The role of phytohormones in basal resistance and *Trichoderma*

- induced systemic resistance to *Botrytis cinerea* in *Arabidopsis thaliana*. *BioControl*. 2008; 53:667-83.
49. Küpper H, Küpper F, Spiller M. Environmental relevance of heavy metal substituted chlorophylls using the example of water plants. *J Exp. Bot.* 1996; 47:259-266. doi:10.1093/jxb/47.2.259 L. Wilzeck. *Soil Biol Biochem* 35:887-894.
  50. Liu M, Sun ZX, Zhu J, Xu T, Harman GE, Lorito M. Enhancing rice resistance to fungal pathogens by transformation with cell wall degrading enzyme genes from *Trichoderma atroviride*. *J Zhejiang Univ Sci.* 2004; 5:133-136.
  51. López-Bucio J, Pelagio-Flores R, Herrera-Estrella A. *Trichoderma* as biostimulant: exploiting the multilevel properties of a plant beneficial fungus. *Sci Hortic.* 2015; 196:109-123
  52. Lorito M, Woo SL, Harman GE, Monte E. Translational research on *Trichoderma*: From 'omics to the field. *Ann Rev Phytopathol.* 2010; 48:395-417.
  53. Lotan T, Fluhr R. Xylanase, a novel elicitor of pathogenesis-related proteins in tobacco, uses a non ethylene pathway for induction. *Plant Physiol.* 1990; 93:811-17
  54. Marasco R, Rolli E, Ettoumi B, Vigani G, Mapelli F, Borin S, Abou-Hadid AF *et al.* A drought resistance-promoting microbiome is selected by root system under desert farming. *PLoS One.* 2012; 7:e48479.
  55. Marra R, Ambosino P, Carbone V, Vinale F, Woo SL. Study of the three-way interaction between *Trichoderma atroviride*, plant and fungal pathogens using a proteome approach. *Curr. Genet.* 2006; 50:307-21.
  56. Martinez C, Blanc F, Le-Claire E, Besnard O, Nicole M, Baccou JC. Salicylic acid and ethylene pathways are differentially activated in melon cotyledons by active or heat-denatured cellulase from *Trichoderma longibrachiatum*. *Plant Physiol.* 2001; 127:334-344.
  57. Martínez-Medina A, Alguacil MDM, Pascual JA, Wees SCMV. Phytohormone profiles induced by *Trichoderma* isolates correspond with their biocontrol and plant growth-promoting activity on melon plants. *J Chem Ecol.* 2014; 40:804-815.
  58. Mastouri F, Bjorkman T, Harman GE. Seed treatment with *Trichoderma harzianum* alleviates biotic, abiotic, and physiological stresses in germinating seeds and seedlings. *Phytopathology.* 2010; 100:1213-1221.
  59. Mastouri F, Bjorkman T, Harman GE. *Trichoderma harzianum* enhances antioxidant defense of tomato seedlings and resistance to water deficit. *Mol Plant Microbe Interact.* 2012; 25:1264-1271.
  60. Mittler R. Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.* 2002; 7:405-10.
  61. Montero-Barrientos M, Hermosa R, Cardoza, RE, Gutierrez S, Nicolás C, Monte E. Transgenic expression of the *Trichoderma harzianum* HSP70 gene increases *Arabidopsis* resistance to heat and other abiotic stresses. *J Plant Physiol.* 2010; 167:659-665.
  62. Montero-Barrientos M, Hermosa R, Nicolas C, Cardoza RE, Gutierrez S. Overexpression of a *Trichoderma* HSP70 gene increases fungal resistance to heat and other abiotic stresses. *Fungal Genet Biol.* 2008; 45:1506-1513.
  63. Morán-Diez E, Hermosa R, Ambosino P, Cardoza RE, Gutiérrez S, Lorito M, Monte E. The ThPG1 endopolygalacturonase is required for the *Trichoderma harzianum*-plant beneficial interaction. *Mol Plant Microbe Interact.* 2009; 22:1021-1031.
  64. Morsy EM, Abdel-Kawi KA, Khalil MNA. Efficiency of *Trichoderma viride* and *Bacillus subtilis* as biocontrol agents against *Fusarium solani* on tomato plants. *Egypt J Phytopathol.* 2009; 37(1):47-57.
  65. Mukherjee M, Mukherjee PK, Horwitz BA, Zachow C, Berg G, Zeilinger S. *Trichoderma*-plant-pathogen interactions: Advances in genetics of biological control. *Indian J Microbiol.* 2012; 52:522-529.
  66. Mukherjee PK, Mukhopadhyay A, Sarmah D, Shrestha S. Comparative antagonistic properties of *Gliocladium virens* and *Trichoderma harzianum* on *Sclerotium rolfsii* and *Rhizoctonia solani*: its relevance to understanding the mechanisms of biocontrol. *J. Phytopathol.* 1995; 143:275-79
  67. Munns R. Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant Cell Environ.* 1993; 16:15-24.
  68. Nawrocka J, Małolepsza U. Diversity in plant systemic resistance induced by *Trichoderma*. *Biol Control.* 2013; 67:149-156.
  69. Neves-Piestun BG, Bernstein N. Salinity-induced changes in the nutritional status of expanding cells may impact leaf growth inhibition in maize. *Funct. Plant Biol.* 2005; 32:141-52.
  70. Padmaja K, Prasad DDK, Prasad ARK. Inhibition of chlorophyll synthesis in *Phaseolus vulgaris* seedlings by cadmium acetate. *Photosynthetica.* 1990; 24:399-405.
  71. Pereira JL, Queiroz RML, Charneau S, Felix CR, Ricart CA, Lopes-da Silva F *et al.* Analysis of *Phaseolus vulgaris* response to its association with *Trichoderma harzianum* (ALL-42) in the presence or absence of the phytopathogenic fungi *Rhizoctonia solani* and *Fusarium solani*. *PLoS One.* 2014; 9:e98234.
  72. Pieterse CMJ, Van-der-Does D, Zamioudis C, Leon-Reyes A, Van-Wees SCM. Hormonal modulation of plant immunity. *Annu. Rev. Cell Dev. Biol.* 2012; 28:489-521.
  73. Porrás M, Barrau C, Romero F. Effects of soil solarization and *Trichoderma* on strawberry production. *Crop Prot.* 2007; 26:782-787.
  74. Rai S, Kashyap PL, Kumar S. Identification, characterization and phylogenetic analysis of antifungal *Trichoderma* from tomato rhizosphere. *Springer Plus.* 2016; 5:1939. doi:10.1186/s40064-016-3657-4.
  75. Raman J. Response of *Azotobacter*, *Pseudomonas* and *Trichoderma* on Growth of Apple Seedling. *International Conference on Biological and Life Sciences IPCBEE*, IACSIT Press, Singapore, 2012
  76. Rasool S, Ahmad A, Siddiqi TO, Ahmad P. Changes in growth, lipid peroxidation and some key antioxidant enzymes in chickpea genotypes under salt stress. *Acta Physiol. Plant.* 2013; 35:1039-1050. doi:10.1007/s11738-012-1142-4
  77. Rawat L, Singh Y, Shukla N, Kumar J. Alleviation of the adverse effects of salinity stress in wheat (*Triticum aestivum* L.) by seed biopriming with salinity tolerant isolates of *Trichoderma harzianum*. *Plant Soil.* 2011; 347:387-400. doi: 10.1007/s11104-011-0858-z
  78. Reino JL, Guerrero RF, Hernández-Gal'an R. Secondary metabolites from species of the biocontrol agent *Trichoderma*. *Phytochem Rev.* 2008; 7:89-123.
  79. Roatti B, Perazzolli M, Gessler C, Pertot I. Abiotic stresses affect *Trichoderma harzianum* T39-induced resistance to downy mildew in grapevine. *Phytopathology.* 2013; 103:1227-1234.

80. Robert-Seilaniantz A, Grant M, Jones JDG. Hormone crosstalk in plant disease and defense: More than just jasmonate-salicylate antagonism. *Annu. Rev. Phytopathol.* 2011; 49:317-343.
81. Rubio MB, Quijada NM, Pérez E, Domínguez S, Monte E, Hermosa R. Identifying beneficial qualities of *Trichoderma parareesei* for Plants. *Appl. Environ. Microbiol.* 2014; 80:1864-1873. doi:10.1128/AEM.03375-13
82. Saba HDV, Manisha M, Prashant KS, Farham H, Tauseff A. *Trichoderma* – a promising plant growth stimulator and Biocontrol agent. *Mycosphere.* 2012; doi:10.5943/mycosphere/3/4/14
83. Salas-Marina MA, Silva-Flores MA, Uresti-Rivera EE, Castro-Longoria E, Herrera-Estrella A, Casas-Flores S. Colonization of Arabidopsis roots by *Trichoderma atroviride* promotes growth and enhances systemic disease resistance through jasmonic acid/ethylene and salicylic acid pathways. *Eur. J. Plant Pathol.* 2011; 131:15-26.
84. Samolski I, Rincón A, Pinzón LM. The *qid74* gene from *Trichoderma harzianum* has a role in root architecture and plant biofertilization. *Microbiology.* 2012; 158:129-38.
85. Saravanakumar K, Arasu VS, Kathiresan K. Effect of *Trichoderma* on soil phosphate solubilisation and growth improvement of *Avicennia marina*. *Aquat Bot.* 2013; 104:101-105
86. Segarra G, Casanova E, Bellido D. Proteome, salicylic acid, and jasmonic acid changes in cucumber plants inoculated with *Trichoderma asperellum* strain T34. *Proteomics.* 2007; 7:3943-52.
87. Segarra G, Casanova E, Aviles M, Trillas I. *Trichoderma asperellum* strain T34 controls *fusarium* wilt disease in tomato plants in soilless culture through competition for iron. *Microb. Ecol.* 2010; 59:141-149.
88. Shabala S, Cuin TA. Potassium transport and plant salt tolerance. *Physiol. Plant.* 2008; 133:651-69.
89. Shanmugaiah V, Balasubramanian N, Gomathinayagam S, Manoharan PT, Rajendran A. Effect of single application of *Trichoderma viride* and *Pseudomonas fluorescens* on growth cotton plants. *African J Agri Res.* 2009; 4(11):1220-1225.
90. Sharma A, Johri BN, Sharma AK, Glick BR. Plant growth-promoting bacterium *Pseudomonas* sp. strain GRP 3 influences iron acquisition in mung bean (*Vigna radiata* L. Wilzeck). *Soil Biology and Biochemistry.* 2003; 35(7):887-894.
91. Sharma P, Dubey RS. Lead toxicity in plants. *Braz J Plant Physiol.* 2005; 17-35.
92. Sharon E, Bar-Eyal M, Chet I, Herrera-Estrella A, Kleifeld O, Spiegel Y. Biological control of the root-knot nematode *Meloidogyne javanica* by *Trichoderma harzianum*. *Phytopathology.* 2001; 91:687-93.
93. Shores M, Harman GE, Mastouri F. Induced systemic resistance and plant responses to fungal biocontrol agents. *Annu Rev Phytopathol.* 2010; 48:21-43.
94. Shores M, Harman GE. The molecular basis of shoot responses of maize seedlings to *Trichoderma harzianum* T22 inoculation of the root: a proteomic approach. *Plant Physiol.* 2008; 147:2147-2163. doi:10.1104/pp.108.123810
95. Shukla N, Awasthi RP, Rawat L. Biochemical and physiological responses of rice (*Oryza sativa* L.) as influenced by *Trichoderma harzianum* under drought stress. *Plant Physiol Biochem.* 2012; 54:78-88.
96. Sofo A, Scopa A, Manfra M. *Trichoderma harzianum* strain T-22 induces changes in phytohormone levels in cherry rootstocks (*Prunus cerasus* X *P. canescens*). *Plant Growth Regul.* 2011; 65:421-5.
97. Srivastava M, Shahid M, Pandey S, Singh A, Kumar V. *Trichoderma* genome to genomics: a review. *J Data Min Genom Proteom.* 2014; 5:162
98. Studholme DJ, Harris B, Cocq KL, Winsbury R. Investigating the beneficial traits of *Trichoderma hamatum* GD12 for sustainable agriculture-insights from genomics. *Front Plant Sci.* 2013; 4:258
99. Téllez-Vargas J, Rodríguez-Monroy M, López-Meyer M, Montes-Belmont R, Sepúlveda-Jiménez G. *Trichoderma asperellum* ameliorates phytotoxic effects of copper in onion (*Allium cepa* L.). *Environmental and Experimental Botany.* 2017; 136:85-93. <https://doi.org/10.1016/j.envexpbot.2017.01.009>
100. Tucci M, Ruocco M, Masi LD, Palma MD, Lorito M. The beneficial effect of *Trichoderma* spp. on tomato is modulated by the plant genotype. *Mol Plant Pathol.* 2011; 12:341-354.
101. Van-Assche F, Clijsters H. Effects of metals on enzyme activity in plants. *Plant Cell Environ.* 1990; 13:195-206. doi:10.1111/j.1365-3040.1990.tb01304.x
102. Vargas WA, Mandawe JC, Kenerley CM. Plant-derived sucrose is a key element in the symbiotic association between *Trichoderma virens* and maize plants. *Plant Physiol.* 2009; 151:792-808.
103. Velázquez-Robledo R, Contreras-Cornejo H, Macías-Rodríguez LI. Role of the 4-phosphopantetheinyl transferase of *Trichoderma virens* in secondary metabolism, and induction of plant defense responses. *Mol Plant Microbe Interact.* 2011; 24:1459-71.
104. Vinale F, Flematti G, Sivasithamparam K. Harzianic acid, an antifungal and plant growth promoting metabolite from *Trichoderma harzianum*. *J Nat Prod.* 2009; 72:2032-5.
105. Vinale F, Nigro M, Sivasithamparam K. Harzianic acid: a novel siderophore from *Trichoderma harzianum*. *FEMS Microbiol Lett.* 2013; 347:123-9.
106. Vinale F, Sivasithamparam K, Ghisalberti EL, Marra R, Barbetti MJ, Li H *et al.* A novel role for *Trichoderma* secondary metabolites in the interactions with plants. *Physiol. Mol. Plant Pathol.* 2008a; 72:80-86.
107. Vinale F, Sivasithamparam K, Ghisalberti EL, Marra R, Woo SL, Lorito M. *Trichoderma* – plant – pathogen interactions. *Soil Biol. Biochem.* 2008b; 40:1-10.
108. Viterbo A, Chet I. TasHyd1, a new hydrophobin gene from the biocontrol agent *Trichoderma asperellum*, is involved in plant root colonization. *Mol. Plant Pathol.* 2006; 7:249-258.
109. Yasmeeen R, Siddiqui ZS. Physiological responses of crop plants against *Trichoderma harzianum* in saline environment. *Acta Botanica Croatica.* 2017; 76(2):154-162. <https://doi.org/10.1515/botcro-2016-0054>
110. Yedidia I, Benhamou N, Chet I. Induction of defense responses in cucumber plants (*Cucumis sativus* L.) by the biocontrol agent *Trichoderma harzianum*. *Appl. Environ. Microbiol.* 1999; 65:1061-70.
111. Yedidia I, Srivastva AK, Kapulnik Y, Chet I. Effect of *Trichoderma harzianum* on microelement concentrations and increased growth of cucumber plants. *Plant Soil.* 2001; 235:235-42

112. Yildirim E, Taylor AG, Spittler TD. Ameliorative effects of biological treatments on growth of squash plants under salt stress. *Sci. Hortic.* 2006; 111:1-6
113. Zeilinger S, Gruber S, Bansal R, Mukherjee PK. Secondary metabolism in *Trichoderma*-Chemistry meets genomics. *Fungal Biol Rev.* 2016; 30:74-90
114. Zhang F, Yuan J, Yang X, Cui Y, Chen L, Ran W *et al.* Putative *Trichoderma harzianum* mutant promotes cucumber growth by enhanced production of indole acetic acid and plant colonization. *Plant Soil.* 2013; 368:433-444. doi: 10.1007/s11104-012-1519-6