



AN OVERVIEW OF TRICHODERMAL INTERACTIONS WITH PATHOGENS AND PLANTS

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One of the most significant requirements of modern world agriculture is to achieve higher yields in an environment permissive manner. Among various plant growth promoting microorganisms, *Trichoderma* occupies a unique position. Genus *Trichoderma* represents a very large and diverse group of fungi which plays a crucial role in uplifting the plant productivity. This fungus has a distinct property to infect and colonize in the roots of various plants. Interaction of plant roots with *Trichoderma* induces various genetic and physical changes in the plants. *Trichoderma* employs various tactics like antibiosis, competition, iron chelation, Hyperparasitism/Mycoparasitism etc to inhibit the growth of pathogens residing in the neighborhood. Additionally they secrete various chemicals/ Proteins /hormones to uplift the growth of infected plants. Some of them resides as endophytes and promotes plant growth in many ways. Some *Trichoderma spp.* are known to induce systemic resistance against plant pathogens and tolerance against abiotic stress.

Keywords: Antibiosis; Competition; Endophytes; Induced systemic resistance; Iron Chelation; Mycoparasitism; plant growth promotion.

Introduction:

From the first decade of the last century, scientists knew the usefulness of filamentous fungi *Trichoderma* as a potential bio control agent against many plant pathogens¹. In this millennium *Trichoderma* has helped to sustain the agriculture yields and hence proved be a boon for human kind. This fungi is known to— enhance the soil fertility, improve the wellbeing of the crop plants, uplift the capability of the plants to degrade the toxic compounds, show antagonistic effect against pathogenic fungi and nematodes,

modify rhizosphere, enhance plant defense mechanism, impart tolerance against abiotic stress, solubilize plant nutrients, increase the reproductive capability and improve the plant defense mechanism^{2,3,4}. Symbiotic association of some species of *Trichoderma* with plant roots is known to result in induced systemic resistance (ISR) and systemic acquired resistance (SAR) in plants. Because of the above mentioned reasons many species of *Trichoderma* have been used as commercial bio-pesticide/ bio-fungicide. In fact, globally 60% of the bio-fungicides companies use *Trichoderma* as main bio- fungicide.

Some species of *Trichoderma* are also known to produce pigments (greenish-yellow, reddish and colourless), clinically important secondary metabolites and industrially important enzymes.

Trichoderma was first described long back in 1794⁵. This fungi is ubiquitous and is found predominantly in the agriculture and native soils throughout all climatic zones (nearly all tropical and temperate soils). They can grow as endophytes (in between living cells) or as saprophytes (in soil organic matter) or as human pathogens (in between mammalian tissues)^{6,7,8}. They can colonize in both herbaceous and woody plants. *Trichoderma* generally reproduces asexually with a few showing sexual telomorphs. In general they are found as clonal heterokaryotic individual. The extensive study of the genome of many species of *Trichoderma* like *T. virens*, *T. reesei*, *T. atroviride*, *T. harzianum* etc has revealed the presence of many genes that can produce a variety of expression patterns. Such differential pattern of gene expression allows this fungus to adapt to varied set of environmental conditions. The genomic study has revealed, to some extent, the changes that occur in the plant, pathogen and *Trichoderma* itself when they interact with each other⁹. This review deals with the recent phylogenetic position of the fungi *Trichoderma*. It also aims to give an insight on various Trichoderma interactions.

The systematics and phylogenetics of Trichoderma:

The name *Trichoderma* was introduced by Persoon⁵ and from then onwards the systematics and taxonomy of this fungus has developed. *Trichoderma* belongs to - Family: Hypocreaceae, Order: Hypocreales, Class: Sordariomycetes and Phylum: Ascomycetes. Up to very long i.e. 1969, only one species of this fungi namely *T. viride*

was known¹⁰. Since then many species of genus *Trichoderma* like *T. harzianum* Rifai, *T. hamatum*, *T. viride*, *T. polysporum* and several others have been identified. In early nineties, 27 species and five sections of the genus *Trichoderma* were described by Bissett^{11,12,13}. Many workers tried to rearrange the genus *Trichoderma* on the basis of its morphology but most of the classification system encountered one or the other problem and lead to false identification of certain species, for instance – name *Trichoderma harzianum* was used for many different species¹⁴. More reliable classification came after the development of molecular biology techniques. Using advanced molecular biology tools, scientists identified few more species of the genus *Trichoderma*. Number of identified *Trichoderma* species moved to 47 in the year 2002¹⁴. Further advancement in molecular biology techniques (like oligonucleotide barcoding) along with the development of search tools like Tricho Blast added tremendously to our knowledge of species diversity of the genus *Trichoderma*^{15,16}. Many workers used phenotypic microarrays for identification¹⁷. Till now a total of 104 species have been listed by the International Sub-commission on *Trichoderma/Hypocrea*¹⁸. Some endophytic species have been reported by Chaverri and Samuels¹⁹. These species were analyzed on the basis of preference of their habitat and mode of nutrition. As a result various groups of endophytic *Trichoderma spp* were identified and their potential use in the development of innovative strategies of biological control was studied.

Trichoderma and its interactions:

Trichoderma is ubiquitous asexually reproducing fungi that can be frequently isolated from the soils of nearly all

environments. They are known to colonize in various plants ranging from herbaceous to woody. This genus is a fast growing strong opportunistic invader and is known to produce spores. Many of them can produce antibiotics and colonize in highly competitive environments²⁰. They can compete with a number of other microbes (both pathogenic and nonpathogenic) for nutrients and space²¹. The mechanism of competition and efforts of colonization by different species of *Trichoderma* in various ecological niche are diverse and well developed²².

Interactions with plant pathogens:

In the event of establishing itself in the niche, *Trichoderma* interacts with the pathogenic and nonpathogenic microbes in many ways. In the process it proves itself as a very strong contender against many plant pathogens. Among various processes Antibiosis, Hyper-Parasitism and Competition are the main strategies employed by this fungus.

Antibiosis: Antibiosis is one of the most common mechanisms used by many microorganisms to inhibit growth of other microbes present within the same niche. *Trichoderma* also produce and release a range of antibiotics which down-regulate the growth of pathogenic microbes present in the vicinity²³. Three classes of antibiotics viz peptaibols, volatile and water soluble have been isolated and characterized from *Trichoderma*. Examples of Peptaibols antibiotics are trichodecenins, trichotoxins A, trichotoxins B, trichorovins, tricholongins BI and BII, atroviridins A-C, neoatroviridins A-D and trichocellins. These compounds show antagonism against many pathogenic and non-pathogenic fungi, some Gram positive bacteria and few viruses. One or more of these are produced by various species of *Trichoderma* like *T.*

viride, *T. harzianum*, *T. longibrachiatum*, *T. koningii*, *T. atroviride* etc. Peptaibols antibiotics have a molecular weight of 500-2200 Da and are polypeptide in nature with a high concentration of non-proteinogenic amino acids²⁴. Alfa amino isobutyric acid is the most abundant non-proteinogenic amino acid found in Peptaibols antibiotics. Wiest et al²⁵, reported that the exogenous use of peptaibols stimulated the defense responsive genes in Tobacco plants. More over treated plants have reduced susceptibility towards Tobacco mosaic virus.

The typical smell of coconut in *T. viride* is suggestive of the presence of volatile compounds. 6-Pentyl- α -Pyrone (6 PAP) produced by *T. harzianum*, *T. viride* and *T. koningii* is a typical example of volatile antibiotic. 6 PAP so produced plays a key role in biological control of *Fusarium oxysporum*, *Botrytis cinerea* and *Rhizoctonia solani*. Other volatile compounds include salamethicins, tricholin, harzianic acid, massoilactone, gliovirin, glisoprenins and heptelidic acid. Viridin, Dermadin, Lignoren, Koningins, Trichoviridin and Koningic acid are examples of soluble antibacterial and antifungal compounds released by various species of *Trichoderma*²⁶. These compounds show antagonism against *Aspergillus niger*, *Penicillium expansum*, *Bacillus subtilis*, *Escherichia coli*, *Pseudomonas aeruginosa*, *Fusarium oxysporum* etc.

Monte²⁷ emphasized that many species of *Trichoderma* are especial in the sense that they can secrete lytic enzymes along with the antibiotics. Their combined action is more lethal. Lytic enzymes so produced have capacity to degrade the fungal cell walls and thus aids the penetration of antibiotics in the cell¹.

Hyperparasitism: Another important

mechanism employed by *Trichoderma* which has established it as a biocontrol agent is Hyperparasitism or Mycoparasitism. This process involves direct attack of a fungal species on another fungus. In this mechanism a direct contact of *Trichoderma* and the pathogen is established. This process is accompanied in many stages *viz*; (1) pathogen recognition (after receiving signals from the host) (2) Chemotrophic growth of *Trichoderma* (3) Attack by secretion of extracellular enzymes (4) Gradual penetration of the hyphae into the pathogen cell (5) Lysis of the host and cell death^{22,28}.

Trichoderma synthesizes cell wall degrading lytic enzymes like Glucanase, Cellulase, Xylanase, Proteases and Chitinases which facilitate the hydrolysis of the fungal cell wall^{29,30}. Chitinases are the most important hydrolytic enzyme that plays key role in cell wall degradation.

Some *Trichoderma* species can produce siderophores. Some species of *Trichoderma* are also known to create acidic environments thereby establishing hostile conditions for the growth of pathogenic fungi³¹. Different *Trichoderma* strains may show varied responses. Gajera *et al.*³², has shown that the secretion of low levels of exochitinases by some *Trichoderma* strains can damage the cell wall of other fungi and hence play a significant role in inhibition of the growth of many pathogenic fungal strains. Some *Trichoderma* spp. Undergo morphological changes like coiling and formation of appressorium that contain high amount of osmotic solutes like glycerol. Coiling aids in penetration inside the host cells. Once attached to the pathogen, *Trichoderma* coils around the pathogen and forms appressoria. The appressorium formed releases its content. This results in production of peptides that cause

pathogenesis, facilitate entry of *Trichoderma* hyphae in the pathogen and digestion of pathogen cell wall¹. Many factors are known to affect this process including some 20 to 30 proteins and other metabolites³³. Few *Trichoderma* spp. have been reported to kill nematodes and hence they can be used as potential bio-nematicides. Gene-for-Gene experiments are being done for further understanding³³.

Competition: Within a niche, *Trichoderma* acts as a very dominant competitor and does not permit intense growth of fungal and bacterial neighbors. Hence, competition proves to be a powerful weapon for the eradication of the pathogens. This eradication is primarily done by starvation and scarcity of the growth limiting nutrients. Hence, strategy of competition proves most significant when effective biological control of fungal and bacterial pathogens is needed.

Trichoderma effectively competes with other microbial pathogens for carbon and iron. Under starvation conditions, like other fungi, it also produces siderophores. Siderophores are iron chelating substances which are used to mobilize and take up iron from the surrounding environment. The siderophores produced by *Trichoderma* are highly efficient and chelates iron more effectively as compared to other fungi in the neighborhood³⁴. Hence iron becomes limiting factor and this is how *Trichoderma* can effectively control the growth of fungal pathogens.

Similarly, *Trichoderma* competes effectively for carbon source and can limit the growth of other fungi. The extraordinary utilization of nutrients by *Trichoderma* can be attributed to the fact that it has unique capability to synthesize ATP from a variety of nutrients. *Fusarium oxysporum*, *Pythium*, *Ceratocystis paradoxa*, *Botryotinia cinerea*, *Rhizoctonia*, *Phytophthora* and many more

pathogens are by *Trichoderma*. Use of *Trichoderma* in many pre and post-harvest damage.

Trichoderma-plant interactions:

The colonization of *Trichoderma* in the rhizosphere provides multifaceted benefit. A facultative symbiotic relation develops between the plants and the *Trichoderma* where the fungal partner obtains nutrient like sugars, vitamins etc from the plant partner and in turn the presence of *Trichoderma* help to improve the overall growth of the plant partner³⁵. *Trichoderma* has a unique property where on the one hand it can attack and limit pathogens present in the soil while on the other hand it promotes the plant defense.

Moreover, *Trichoderma* are also known to produce chemicals capable of enhancing seed germination like gibberellin and zeaxanthin. Some species of *Trichoderma* are capable of producing acids like coumaric acid, gluconic acid and citric acid. These acids help to release phosphorous and other microelements from the soil and the organic matter. Thus this fungus ensures availability of nutrients to the plants³⁵.

Interaction of *Trichoderma* with plants starts with colonization (both internally and externally) in roots. The initial course of fungus-root association is not much understood as compared to the later part where fungal attachment, penetration and internal colonization takes place. Many species of *Trichoderma* are known to generate signals in the form of chemicals, proteins and hormones which promote colonization of the fungus in the roots. Some of the species produce hydrophobic like proteins. They are cysteine rich proteins that assist in attachment. Qid74 of *T. harzianum* and TasHyd1 from *T.* of such proteins^{36,37}. Both

these proteins play an important role in fungal attachment to the roots and lateral growth of roots together with the formation and elongation of root hairs. As a result of the above said modifications, uptake of nutrient and their translocation in various parts of shoot takes place. This results in an overall increase in the plant biomass. *Trichoderma* is also known to secrete Auxins. Auxins promote the growth of the roots and enhance its surface area. The increased surface area of the root aids in fungal colonization³⁸. Some *Trichoderma* species can produce a cellulose binding extracellular protein which facilitates their penetration in the root. They can also synthesize endopolygalacturonase which aids in their penetration inside the root. After penetration, fungi start to grow intercellularly within the epidermal layer and the outer cortex. Interaction of some species of *Trichoderma* with plant roots also results in – boosting of photosynthesis, activation of various metabolic processes, induction of defense and stress related pathways to boost the plant immunity and induction of cell wall metabolism to strengthen cell barriers.

Here it is to note that *Trichoderma* are generally resistant to the compounds like terpenoids, flavonoids, phytoalexins, and phenols which are secreted by the plant partners in response to the fungal infection. Plant partner generally secretes these compounds to inhibit root colonization by the fungus.

Many workers^{1,39,40-42} have reported that *Trichoderma* can also stimulate systemic resistance in plants i.e. presence of *Trichoderma* provides resistance to the plants against the bacterial, fungal and viral diseases. *T. asperellum*, *T. virens*, *T. atroviride* and *T. harzianum* are representatives that have been studied

extensively for induced systemic resistance.

Many metabolites like Chitinases, Xylanases, low molecular weight compounds (released from the fungal cell wall or infected plants) etc play a critical role in inducing this resistance. Fungal infection in plants results in an increase in the concentration of enzymes and metabolites like chitinases, phytoalexins, glucanases and phenylalanine ammonia lyase (PAL) which are responsible for induced systemic resistance (ISR)⁴³. Rubio *et al*⁴⁴, reported induction of 40 genes (related to stress management and metabolism of RNA, DNA and proteins) in tomato plants infected with *Trichoderma hamatum* 382. Similarly about 200 differentially expressed proteins were identified in Maize plants infected with *Trichoderma harzianum* T226.

Immediately after infection, the infected plants undergo a prompt ion flux followed by an oxidative burst. Callose deposition and polyphenol synthesis follows the oxidative burst. These events stimulate the jasmonate/ ethylene (JA/ET) and salicylate (SA) signaling. All such events enable the plants to acquire resistance against a variety of pathogens⁴². This resistance resembles the action of plant growth stimulating bacteria and is termed as JA/ET-mediated induced systemic resistance (ISR). When present in higher concentrations, *Trichoderma* can elicit salicylate mediated acquired resistance. Many chemicals released by *Trichoderma* like xylanase, trichovirin II etc can also stimulate immune responses in plants. Sm1/EPL1 a small hydrophobin like protein belonging to cerato-platanin (CP) family is the best characterized elicitor^{16,45}.

Some comparatively new species of *Trichoderma* like *T. evansii*, *T. martiale*, *T. amazonicum* etc have been reported to live

as endophytes⁴⁶. They can induce transcriptomic changes in plants. Their presence induces expression of many genes which in one way or other protect the plants from abiotic stress. The changes are also seen in gene expression pattern of the shoot. Such changes alter the plant physiology, helps in better uptake of fertilizers and enhanced photosynthetic efficiency¹⁹. They may colonize in the surface of glandular trichomes and form appressoria-like structures⁶.

Conclusion:

Trichoderma spp. provides a great tool for the betterment of agriculture yields. They help the plants to resist abiotic stress, uptake nutrients and develop systemic resistance. Thus they help the plants in many ways so as to improve the productivity. They have a great gene pool. Through extensive study, this pool can be utilized for various biotechnological applications. Hence, further detailed study of this fungal genus can be of great help for the mankind in an environmentally acceptable manner.

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