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Secondary Metabolites as Effectors in *Trichoderma*–Plant Interactions

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SUMMARY

Plants are capable of perceiving microorganisms by coordinating processes to establish different forms of plant–microbe relationships. Plant colonization is governed in fungal and bacterial systems by secreted effector molecules, suppressing plant defense responses and modulating plant physiology to promote either virulence or compatibility. These secondary metabolites have been described as effector molecules that use different mechanisms to establish the interaction.

INTRODUCTION

Secondary metabolites (SM) are not essential for growth and development in fungi but play important functions in the sensing, signaling and counteracting processes for the organisms present in their environment. SMs comprise compounds of low molecular weight, diffusible in the culture medium or volatile, which are synthesized through a great variety of pathways. Antibiotic activity has been reported for SMs produced by *Trichoderma* species against various yeast, filamentous fungi and bacteria, causing growth inhibition or cell death. These SMs, acting synergistically with hydrolytic enzymes, are more likely to be implicated in the effectiveness of the strain producing them as a biological control agent (Reino *et al*., 2008). It includes lactones, phytohormones, terpenes, polyketides, trichothecenes, volatile organic compounds (VOC).

A) Lactones:

The best known SM for *Trichoderma* species is 6-pentyl-2H-pyran-2- one (6-PP), derived from linoleic acid. In plants, 6-PP interferes with the signaling pathway involving auxins and ET, promotes plant growth and regulates root architecture by inhibiting the growth of the primary root and inducing the formation of lateral shoots, by modulating the expression of genes encoding for auxin transporters. The modification related to the lateral shoots is mediated by the TIR1, AFB2, and AFB3 receptors and the ARF7 and ARF19 transcription factors, while the sensitization in the main root is mediated by EIN2.

B) Phytohormones:

Phytohormones are important growth regulators with relevant roles on metabolism and plant defense responses. Several root associated microbes are able to produce phytohormones that have an effect in plants. *T. virens* produces Indole-3-acetic acid (IAA) and indole-3-acetaldehyde (IAAId), which promotes plant growth and development in *A. thaliana* (Contreras-Cornejo *et al*., 2009).

C) Terpenes:

These are a highly diverse family of SMs at the structural and stereochemical level. Cytochrome p450 enzymes are involved in the reactions of synthesis and/or modification of terpenes. Recently 477 cytochrome P450s have been identified from seven *Trichoderma* species (Chadha *et al*., 2018). Cytochrome p450 activity is needed for the synthesis of SMs, which are related to the mycoparasitic capacity and/or its association with plants. The enzyme encoded by the G3 gene in *Trichoderma hamatum* is activated in response to *Sclerotinia* and *Sclerotium* species (Carpenter et al., 2008).

D) Polyketides:

These are one of the most abundant groups of SMs in nature, which includes macrolides, polyenes, and polyphenols. During the interaction of *T. virens* with maize plants, the expression of the defense-related genes *pal1* and *aos* (allene oxide synthase) is increased. This upregulation is related to SMs produced by *T. virens* through the activity of the PKS/NPRS encoded by the *Tex 13* gene. Strains affected in *Tex13* retained their ability to increase the expression of the gene *aos* in plant, but they could not upregulate the *pal1* gene (Mukherjee *et al*., 2012).

E) Trichothecenes:

Trichoderma brevicompactum produces trichodermin through a pathway involving the activity of p450 enzyme, encoded by Tri5 gene. The overexpressing strains of this gene had a negative effect in tomato plants, decreasing the root length and plant size (Malmierca *et al*., 2015). Harzianum A (HA), isolated from *T. arundinaceum,* did not show any effect over growth of tomato seedlings. However, mutant strains that do not produce HA were impaired to upregulate the expression of genes involved in plant defense at the same level. HA could be sensitizing the plant cell to induce those genes faster and at higher levels (Malmierca *et al*., 2012).

F) Volatile Organic Compounds (VOCs):

The VOCs group includes several small compounds with different chemical natures, playing relevant roles as essential signals in interactions among plant roots, microbes, and insects. Some strategies that could help to define their biological role are based on genetic manipulation in order to generate strains affected in key elements of the VOCs biosynthesis. Trichodiene (TD) is a VOC used as a substrate by the sesquiterpene synthase *Tri5* to produce the compound Harzianum A (HA) in *T. arundinaceum*. The heterologous expression of the gene *Tri5* in *T. harzianum* led to the production of TD. VOCs released by this *Tri5*- transformant and TD itself induced the expression of tomato defense genes related to SA (Malmierca *et al*., 2015) (Fig. 1).

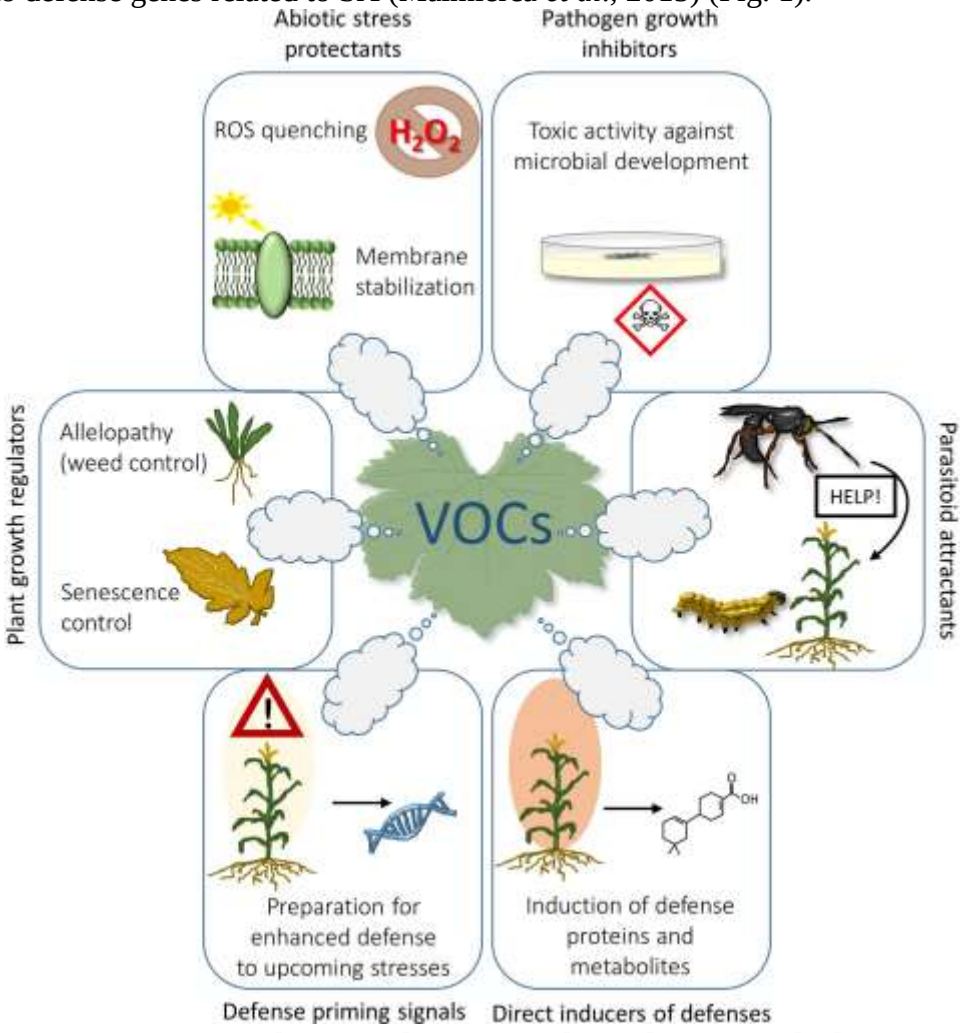

Fig. 1: VOCs Protect and Prime Plants to Withstand Biotic and Abiotic Stresses

CONCLUSION

Trichoderma spp. is widely recognized for secretion of antimicrobial secondary metabolites and their role in biocontrol of wide range of phytopathogens. In addition to antagonistic effect against phytopathogens, secondary metabolites from various *Trichoderma* spp. including *T. harzianum*, *T. virens*, and *T. atroviride* showed enhanced systemic and localized resistance in plants. Trichoderma metabolites are capable of acting on specific pathways of plants including resistance to biotic and abiotic stresses, nutrient uptake, and hormones synthesis, thus altering the plant metabolome and proteome.

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