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Review

Plant Defensive Responses Triggered by *Trichoderma* spp. as Tools to Face Stressful Conditions

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Abstract: The current agriculture is facing various challenges to produce enough food to satisfy the need of the human population consumption without having a negative impact on the environment, human health and ecosystems. The exploitation of bioinoculants has been a crucial alternative for green agriculture. Bioinoculants have two great benefits: to promote plant growth by making essential nutrients available to crops and, to increase the tolerance to biotic and abiotic stresses by inducing a long-lasting defense. Certain members of genus *Trichoderma* have been recognized as biocontrol agents, biofertilizers and stress alleviators for the plants. The use of *Trichoderma* spp. has also been extended to protect and stimulate growth of horticultural crops. Elucidating the plant signaling events triggered by *Trichoderma* is of high importance in order to understand the molecular basis involving plant protection against stresses. In this review, the signaling elements of the plants from *Trichoderma* perception through late defensive responses is discussed. Enhanced understanding how *Trichoderma* spp. activate defense will lead to improvement in the use of species of this genus to increase crop production with the consequent benefits for human health and care for the environment.

Keywords: priming of defense; G proteins; calcium signaling; mitogen-activated protein kinase; phytohormones; SA signaling; JA signaling; reactive oxygen species; antioxidant proteins; defense genes

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1. Introduction

Stress in plants can be defined as any external condition that limits the photosynthetic rate and reduces the energy conversion ability of a plant to biomass, affecting its growth, development or productivity [1,2]. Plant stress can be classified as abiotic or biotic. The abiotic stress refers to any environmental factor that negatively affects the plant growth and development. Abiotic stress (e.g., extreme temperatures, drought, salinity, radiation and toxic metals) causes serious losses of major crop plants around the world [3]. On the other hand, the presence of plant pathogenic living organisms, especially viruses, fungi, bacteria, nematodes, and herbivores are the causes of plants biotic stress [3].

Plants attempt to adapt and resist the stresses by adjusting their metabolism, signal transduction, gene expression, etc.; however, the plant survival under these stress conditions will depend on the intensity, frequency and exposure time [2].

Population growth as well as current climate change and the crop losses caused by emergence of plant pathogenic microorganisms are challenges that require immediate action to ensure food security and safety in coming years. It has been estimated that agricultural food production needs to increase by about 70% by 2050 to feed an expected world population of 9.1 billion of people [4].

Human food production must focus particularly on sustainable agriculture by the means of ecological practices that maximize food productivity and minimize negative consequences on the environment [5]. In recent years, bio-priming agents are receiving

large attention as a promising approach to mitigate the environmental and disease threats in agriculture [6–10].

Bio-priming has been recognized as a low-cost and eco-friendly technology that promotes growth and induces stress tolerance to achieve desired crop yield [11]. Bio-priming consists in the use of beneficial microorganisms [e.g., plant-growth-promoting bacteria (PGPB), fungi, etc.] or materials of biological origin (e.g., humus, chitosan, etc.). These materials can be used in the seeds or the whole plants to promote growth or to improve stress responses. Among these microorganism are included fungi, especially arbuscular mycorrhizal and *Trichoderma* spp. [12].

Trichoderma is mostly an asexual genus of filamentous fungi (the teleomorphic forms are *Hypocrea*) that usually are among the most common saprophytic microorganisms living in the rhizosphere [13]. *Trichoderma* genus contains 375 species that have been described by molecular phylogenetic analysis based on DNA sequencing data [14]. The drastic increase in the number of *Trichoderma* species has several explanations that are related to the technologies and applications used for identification [14].

Although *Trichoderma* was isolated for the first time in 1794 from soil and decomposing organic matter [15], it was not until the early 20th century that some *Trichoderma* species were found to have importance for biofuel industries and plant protection against pathogens by the use of mycoparasitism and/or antibiosis mechanisms [14,16,17]. In the years to follow, many strains of *Trichoderma* have been described as biocontrol agents [18]. Among *Trichoderma* species commercially available for agricultural use are *T. harzianum*, *T. virens*, *T. viride*, *T. asperellum* and *T. atroviride* [19].

The mechanism by which *Trichodema* spp. function as biocontrol agents is complex, and the mentioned biocontrol effect varies with the specie of *Trichoderma* and host plant involved in the interaction [18]. Clearly, environmental conditions (e.g., temperature, pH, salinity and nutrient availability) also influence the biocontrol mechanism [19].

Trichoderma spp. are considered as opportunistic and avirulent plant symbionts [20]. During interaction with host plants, *Trichoderma* spp. secrete several classes of chemical molecules (e.g., proteins, peptides, oligosaccharides and antibiotics) [10,21]. Some of these compounds may act as hormones that stimulate plant growth and development, or can also act as elicitors, activating defense responses in the host plant [22].

The activation of defense induced by *Trichoderma* spp. not only reduces plant diseases. It has also been proved that *Trichoderma* spp. application to the plant increases the tolerance to abiotic stress, such as drought [23–25], low temperatures [24,26], salinity [27,28], and can be used to reduce the presence of toxic metals [29,30]. This wide range of beneficial traits to their hosts is due to bio-priming, and is attributed to the induction of long plant basal resistance that improves the defensive capacity of the plants for subsequent stresses [31]. The application of bio-priming agents prepares the plant for a faster and more effectively response against future stresses [32].

Due to the ability of *Trichoderma* spp. to rapidly produce spores and antibiotic compounds, these fungi have been used for the massive production of commercial formulations that can be stored by months maintaining the beneficial effect for the crop [33]. The most widely used *Trichoderma* spp. products are formulated in a wettable powder or granules [19]. Ninety percent of various *Trichoderma* strains are applied to crops, within many horticulture species (e.g., Poaceae, Solanaceae and Cucurbitaceae) specially for the control of plant diseases due to the antagonistic characteristic against phytopathogens (see [34] for review).

The long-lasting dialogue established between plants and *Trichoderma* is one of the major gaps in the understanding of how this relationship works. In this review, we will focus on the plant signal elements underlying the priming function of *Trichoderma* spp. that may trigger plant adaptation to stress conditions.

2. Defense Responses at Early Stages of Plant–*Trichoderma* Interaction

Little is known about the plant host mechanisms that connect the perception of *Trichoderma* root colonization to the downstream signaling pathways leading to activation of

defense and developmental responses [35]. It is assumed that plant defense triggered by *Trichoderma* spp. is initiated by the perception of microbial-associated molecular patterns (MAMPs) by pattern recognition receptors (PPRs), which are localized on the surface of plant cells [36]. This first phase defense induction is called MAMP-triggered immunity (MTI) [37]. MTI activated by *Trichoderma* spp. includes defense responses such as oxidative burst, callose deposition, Ca^{2+} and reactive oxygen species (ROS) signaling as well as the induction of phytoalexins and other secondary metabolites because, at that point, the plant does not recognize that it is a friendly attack [35,38,39].

2.1. Heterotrimeric G Proteins in Trichoderma Recognition

G proteins are membrane-associated, heterotrimeric, and composed of subunits α, β and γ. When GDP is bound, the subunit α associates with the βγ dimer to form an inactive heterotrimer that binds to a G-protein-coupled receptor (GPCR) [40]. When a GPCR detects an extracellular signal, α subunit decreases the GDP affinity and the leaving GDP is replaced with GTP. Once GTP is bound, the α subunit is activated and dissociated both from the GPCR and from βγ dimer [40]. Following activation, both the GTP-bound α subunit and the free βγ complex can bind to downstream effector molecules and mediate a variety of responses in the target cell, including adaptations to environmental and biotic stresses [41,42]. There is one report about the involvement of plant G-proteins after inoculation with *Trichoderma.* Pea roots inoculated only with *T. asperellum* showed a transcript accumulation of the Gα1 subunit of the heterotrimeric G protein [43]. This suggests G-proteins play an important role in the *Trichoderma* recognition by the plant and suggests that the Gα1 subunit (in its active form), could activate downstream signaling elements. Among the roles of Gα1 signaling, activation of plant plasma membrane Ca^{2+} channels and ROS accumulation have also been widely reported [44–46] (Figure 1).

2.2. Calcium Mediated Signalling in Trichoderma Bio-Priming

Calcium is a second messenger by which plants modulate signaling pathways to respond to a particular stress. The increase in intracellular calcium concentrations ($[Ca^{2+}]_i$) is one of the earliest signaling events when plants are challenged with biotic and abiotic stimulus [47,48]. Changes in $[Ca^{2+}]_i$ are commonly found during interaction between plants and beneficial microorganisms. This is the case for metabolites secreted by *T. atroviride* which increase $[Ca^{2+}]_i$ and defense responses in the first minutes after the treatment in soybean cells [49]. Also, the elicitor HYTOL1 (a hydrophobin abundantly secreted by *T. longibrachiatum* strain MK1 [50]) may be involved in adhesion of fungal hyphae to the root surface [51], inducing a transient increase of cytosolic Ca^{2+} in *Lotus japonicus* cells [52]. These results indicate that the induction of intracellular Ca^{2+} changes represents an early step during *Trichoderma*–plant interaction that primes defense mechanisms (Figure 1).

2.3. Early ROS Accumulation

One of the earliest responses during the plant defense strategy is a fast and transient production of intracellular ROS [53]. Plasma membrane NADPH oxidases, known as respiratory burst oxidase homologues (RBOHs), are one of the many sources of ROS that have been implicated in several essential processes in plants [54]. Growing lines of evidence from plants suggest the involvement of NADPH oxidase-generated oxidative burst in extracellular signaling to regulate a wide range of physiological functions in plants [55,56].

A networking between cytosolic concentrations of Ca^{2+} and RBOH-mediated ROS production has been shown in several studies [57–59]. Plant–*Trichoderma* systems have also demonstrated that these fungi or their metabolites can trigger transient increases in ROS and calcium levels in the first minutes of interaction, activating enhanced immune defense [49,60]. Additionally, tight connections of NADPH oxidases and mitogen-activated protein kinases (MAPKs) are recognized to regulate various biological processes, wherein NADPH oxidase-originated oxidative burst can act upstream to activate the MAPKs cascade [61]. It has

been demonstrated that association of *T. viride* Tv-1511 and peppermint plants produces the activation of a MAPK cascade via NADPH oxidase [61]. All these findings suggest that NADPH oxidase-dependent ROS production plays vital roles in the root colonization (Figure 1).

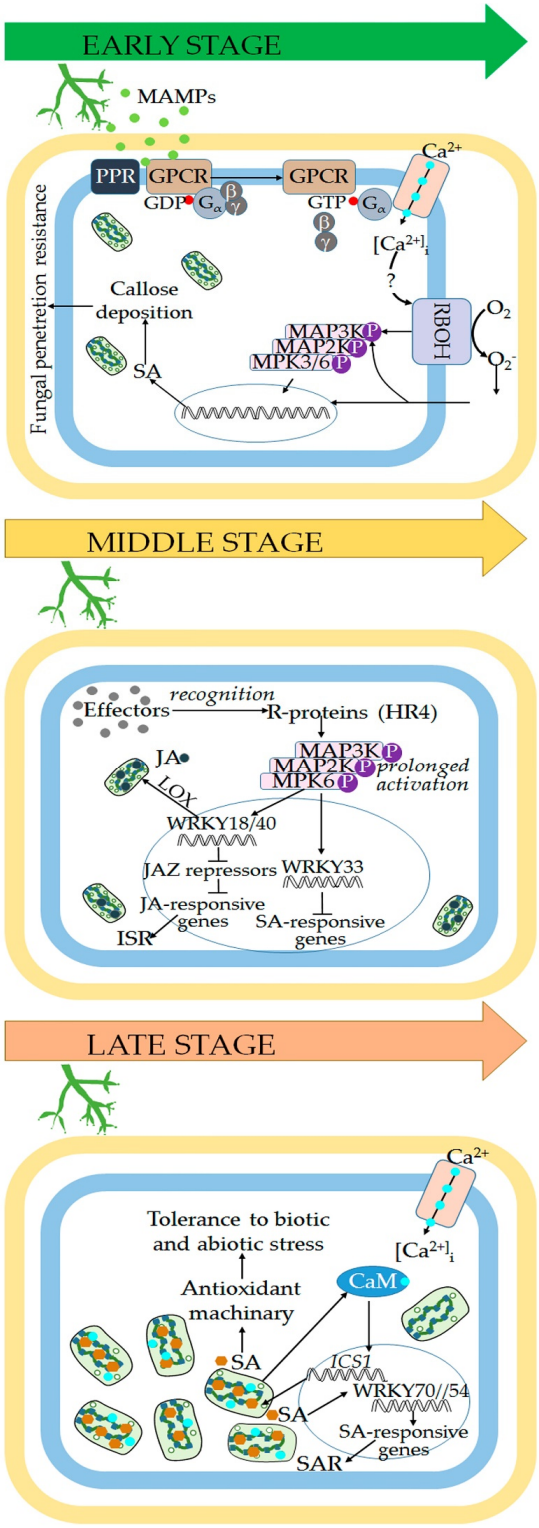

Figure 1. Mechanism of plant responses according to the time of interaction with *Trichoderma*. The model is divided into three stages. The earlier stage comprises the first hours of interaction, wherein the plant is avoiding fungal root colonization due to SA phytohormone and consequently the callose deposition. This first stage is initiated by the recognition of MAMPs secreted by *Trichoderma*, which

can trigger early defense responses mediated by Ca^{2+} and reactive oxygen species and by a rapid but transient activation of MAPK cascades through G heterotrimeric proteins. In the second stage, *Trichoderma* effectors are recognized by R-proteins to promote JA signaling by sustained MAPK activation, and to suppress SA signaling. Consequently, it is established a beneficial interaction. In the later stage, a second peak in the amount of SA is observed, which may induce antioxidative enzyme activities to reduce the oxidative damage to biomolecules and cells.

2.4. Salicylic Acid Restricts Trichoderma Invasion of Vascular System

The interactions between *Trichoderma* spp. and plant roots involve recognition, attachment, penetration, colonization and nutrient transfer [62]. It is well known that *Trichoderma* spp. grow on the outer layer of the roots of the plants [63,64].

During root colonization of *Trichoderma* spp., salicylic acid (SA) seems to be involved in preventing this fungus from entering the vascular system of the roots as well as in avoiding detrimental effects on plant growth and development of the host plants [65]. SA plays a key role in plant cell wall reinforcement (via callose synthesis) responsible for the limitation of *Trichoderma* colonization to the outer layers of roots [65]. Endogenous increase in SA levels has been reported in tomato plants inoculated with *T. virens* and *T. harzianum* T22 at 24 and 48 hpi, respectively [66,67]. The temporary induction of SA confirms a possible role in avoiding excessive *Trichoderma* penetration within the roots [65] and underlines the importance of SA in the first steps of the *Trichoderma*–plant interaction (Figure 1). It has also been shown that *T. atroviride* and *T. cremeum* induce changes in the composition of wheat seedlings roots [68]. These species promote lignin deposition and rearrangements of pectins after 14 days of incubation with *Trichoderma* spp., suggesting that modifications of wheat seedlings roots can be used as a tool against to pathogens [68].

3. Induction of Systemic Plant Defense by *Trichoderma* spp. Plays Key Role in the Crosstalk between Biotic and Abiotic Stress Responses

After MTI, *Trichoderma* spp. seem to activate a second layer of defense. In this stage, effectors secreted by fungi species prevent plant recognition and activate the plant systemic resistance to biotic and abiotic stress [36]. The second line of plant defense induction is called effector-triggered immunity (ETI), which is activated by plant resistance protein (R) and it is frequently associated with hypersensitive response (HR) [37]. Despite ETI and PTI involving a similar set of downstream defense responses, including calcium-mediated signaling, activation of MAPK cascades, production of ROS, transcriptional reprogramming, and biosynthesis of antimicrobial compounds [69–72], the responses during ETI have a longer duration and higher magnitude [73].

Induced resistance is the term used for the induced state of resistance in plants triggered by a biological or chemical inducer. This protects nonexposed plant parts from stresses [74]. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two types of induced resistance wherein plant defenses are preconditioned by prior infection or treatment that results in resistance against subsequent challenge by a pathogen or parasite [75]. Plants, in response to virulent, avirulent and nonpathogenic microbes, elicit SAR. For the activation of SAR, the molecule SA and the accumulation of PR proteins are required. In contrast, ISR is triggered by the infection of pathogens, response to insects, herbivores, or upon root colonization by beneficial microbes in the rhizosphere (such as *Pseudomonas* spp., *Bacillus* spp. and *Trichoderma* spp.). Typically ISR is regulated by jasmonic acid and ethylene (JA/ET) [75,76], in some particular cases, ISR can requiere SA accumulation [77].

The first evidence of TISR was published in 1997 by Bigirimana et al. [78], who demonstrated that soil treated with *T. harzianum* made the leaves of bean plants resistant to diseases that are caused by the fungal pathogens *Botrytis cinerea* and *Colletotrichum lindemuthianum*, even though *T. harzianum* was present only on the roots and not on the foliage. Similar results have been reported for a wide range of host plants with different

strains and species of *Trichoderma* and various classes of plant pathogen including fungi, bacteria, viruses and nematodes [39,78–80].

3.1. *Trichoderma* spp. *Induce a Prolonged Activation of Plant MAPK Cascades*

Mitogen-activated protein kinase (MAPK) cascades are well conserved signaling proteins in all eukaryotes [81]. Each cascade is minimally constituted of three proteins that are sequentially activated: a MAP kinase kinase kinase (MAPKKK or MAP3K), a MAP kinase kinase (MAPKK or MAP2K) and a MAP kinase (MAPK or MPK) [81,82].

MAPKs are intracellular proteins that can be activated by various stimuli [81]. MAPKs cascades transduce extracellular signals to cellular responses, including the biosynthesis of phytohormones, ROS generation, changes in gene expression, among others [83]. Activation of MAPK cascades is one of the earliest signaling events after plant sensing of PAMPs/MAMPs [84–87]; however sustained activation of MAPK confers a robust innate immunity [73,88]. *Arabidopsis thaliana* MPK3 and MPK6, as well as their orthologs in other species, such as tobacco SA-induced protein kinase (SIPK) and wounding-induced protein kinase (WIPK), are involved in plant responses to biotic and abiotic stresses [84,86,87,89,90]. Some studies have found the activation of MPKs associated with plant defense during plant–*Trichoderma* interactions [35,91–95]. For instance, xylanase, an elicitor from the cell walls of *T. virens* (TvX), induces the slow and prolonged activation of SIPK in tobacco [91]. Similarly, inoculation with *T. atroviride* (a specie known to promote root growth by producing auxine-like compounds [94]) in *Arabidopsis* roots induces the MPK6 activation [95]. Since the modulation of MPK6 is also responsive to auxin-like compounds, it has been suggested that *T. atroviride* alters root-system architecture modulating MPK6 and auxin action [95]. In addition, the activation of an analog of *Arabidopsis* MPK6 in peppermint by *T. viridae* is related with the modulation of essential oil metabolism at the transcriptional level and for enzymatic activation [61]. Interestingly enough, menthol, which is the main terpenoid of peppermint oil, exhibits potential abilities as plant defense potentiator in agriculture and horticulture [92].

Besides activating MPKs through posttranslational modifications, bio-priming with *Trichoderma* spp. induce expression of plant *MPK* genes. For example, the inoculation of cucumber (*Cucumis sativus*) roots with *T. asperellum* leads to a long-term expression of a *Trichoderma*-induced MPK (*TIPK*) gene, which is an ortholog of *WIPK* and *MPK3* [93], while the elicitor HYTOL1 also up-regulates the early and transient expression of *MPK3* in *L. japonicus* [52]. After inoculation in *Arabidopsis*, *T. hamatum* induces the expression of *MPK3* after 48 h [96] and *T. asperelloides* of *MPK11* at 24 h [35]. It is noteworthy that this last MPK is also responsive to PAMPs/MAMPs [97,98].

It is known that sustained activation of MPK3/6 elicits a massive reprogramming of the defense metabolome, with an accumulation of camalexin and indole glucosinolate derivatives [99]. The activation of both MPKs is also accompanied by many defense-related phytohormones such as SA, JA, and ET [99], suggesting that extended MPK activation could be involved in the modulation of the robustness of the immune signaling during plant–*Trichoderma* interactions (Figure 1).

3.2. *Hormone Signalling Pathways Involved in Systemic Resistance induced by Trichoderma* spp.

Plant hormones play a crucial role in the immune signaling networks in response to pathogens and beneficial microbes [100]. Among the most relevant hormones related to the modulation of defense responses are SA, JA, ET and abscisic acid (ABA), however auxin, gibberellic acid (GA), cytokinin (CK), brassinosteroids and peptide hormones could also be implicated in plant defense signaling pathways [101].

Several studies have shown that *Trichoderma* species induce the production of phytohormones in the host plants such as JA, SA and ET. Since *Trichoderma* spp. can also produce small amounts of phytohormones such as auxins, GA, SA and ABA [102–105], it makes difficult to discern the origin of hormones detected in some plant–*Trichoderma* spp.

interactions. The role of specific hormones during plant–*Trichoderma* interaction seems to be dependent on the experimental condition and organisms involved [66,96,106].

3.2.1. Salicylic Acid

SA plays a key role in plant defense against biotrophic pathogens [107]. The accumulated evidence shows that partial suppression of SA-dependent responses in plants is necessary for the occurrence of the symbiotic association between beneficial microbes and plants [108–112], including *Trichoderma* spp. [35,113,114]. In this regard, evidence shows a down-regulation of *PR-1,* a useful marker for the SAR response, in the first hours of various plant–*Trichoderma* spp. interactions [52,115].

SAR is a long lasting defense modulated by SA. Recently, it has been found that systemic resistance in maize plants primed with *T. atroviride* at seedling stage is detected until two months later with an increase of SA levels, suggesting SA is a key component of a regulatory network controlling the immunity of silks during systemic resistance [116]. Similarly, *Arabidopsis* seedlings exposed to *T. asperellum* Ism T5 volatile for 9 days, stimulate SA accumulation [117]. In recent years, experimental studies have found that application of exogenous SA induces biotic and abiotic stress [118–122], possibly by modulating antioxidative enzyme activities, thereby potentially reducing the damaging levels of ROS [120,123,124]. It is thus possible that alleviation of biotic or abiotic stress observed in plant–*Trichoderma* systems would involve SA in later stages of the interactions (Figure 1).

3.2.2. Jasmonic Acid

JA is synthesized from the α-linolenic acid of chloroplast membranes by the octadecanoid pathway. JA is a phytohormone involved in diverse physiological processes including plant growth and development [125], and also actively participates in the mediation of plant responses and defenses against herbivore attack, pathogen infection and abiotic stresses, including ozone, ultraviolet radiation, high temperatures, and freezing [125–128].

Multiple reports have confirmed that *Trichoderma* spp. can increase the levels of JA in host plants. For instance, during the interaction between tomato plants with *T. virens*, an increase in endogenous JA levels at 24 hpi has been observed [67]. Similarly to the content of SA, JA significantly increase in *T. longibrachiatum* H9-inoculated cucumber plants at 96 hpi [114], and in A*rabidopsis* co-cultivated with both *T. virens* and *T. atroviride* 8 days after interaction [129], implying that SA and JA play important roles in regulating the plant response and enhancing plant defense in plants (Figure 1).

3.3. Induction of Plant Defense Gene Expression in Response to Trichoderma spp.

Reprogramming of a cell in response to the perception of an external stimulus involves complex changes in gene expression. The expression of genes appears to be regulated by intracellular signal transduction pathways. For instance, the interaction of plants with a variety of microorganisms results in changes in the level of SA, JA and ET, which are positive regulators of transcription factors (WRKYs), defense genes (PRs), and receptors (*R* genes) [130].

To link particular pathways with actual defense responses, some molecular tools, such as qPCR, allow the use of the expression of several marker genes as indicators of the activation of specific pathways [9]. Expression studies on defense/stress-related genes suggested that *Trichoderma*-induced systemic resistance (TISR) might involve both SA- and JA-related pathways.

Comparing plants treated with *Trichoderma* spp. with mock-treated controls, hundreds of genes that are differentially expressed during ISR-prime have been identified [35,66,96] (Tables 1–3). The products of the genes are related to defense responses, signal transduction, systemic acquired resistance, antioxidant systems, programmed cell death, etc. [96]. It is difficult to establish a specific time point when early defense responses end, but it has been proposed that 48 hpi would indicate the moment of transition when the plant reprograms

its transcriptional machinery mainly towards redox and defense processes, fully accepting that *Trichoderma* is not an enemy [38,66].

3.3.1. WRKY Transcription Factors

WRKY is a family of transcription factors found exclusively in plants [131]. They bind W-box and/or other *cis*-elements located in the promoter of their target genes [131]. Most *WRKY* genes are responsive to pathogens, elicitors, and defense-related phytohormones such as SA or JA, implying a major role for the *WRKY* gene family in plant immunity [132], but also, the WRKY transcription factors play an important role in the alleviation of abiotic stresses [131,133].

The WRKY proteins regulate the gene expression directly or indirectly by modulating the downstream target genes, by activating or repressing the other genes (encoding transcription factors) or by self-regulating their own expression [131].

Molecular studies have revealed that *Arabidopsis* plants under interaction with *T. atroviride* induces the expression of *WRKY8*, *WRKY33*, *WRKY38*, *WRKY42* and *WRKY60*, all of which are considered as positive regulators in JA pathway, while *WRKY70* and *WRKY54*, regulated by the SA pathway, could be activated at later stages of the interaction, when the fungus is fully established in the plant roots [134]. Similarly, the treatment of *L. japonicus* with hydrophobin HYTOL from *T. longibrachiatum*, or the inoculation of the common bean (*Phaseolus vulgaris* L.) with *T. velutinum*, lead to the expression of *WRKY33*, but not *PR-1* [52,115], suggesting that expression of *WRKY33* induced by *Trichoderma* spp. negatively regulates the SA pathway to evade the plant immunity and to establish a prolonged mutualistic association (Table 1).

On the other hand, the expression of *WRKY18*, *WRKY40* and *WRKY60* transcription factors genes in *Arabidopsis* inoculated with *T. asperelloides* is observed as early as 9 h. The three WRKY show redundant function in negatively regulating PTI in *Arabidopsis* [135]. In response to *T. asperelloides*, these transcription factors negatively regulate the induction of transcript levels of SA marker genes *FMO1*, *PAD3* and *CYP71A13,* but positively regulate the expression of *LOX2* and *AOS* related to the JA pathway through inhibition of expression of the jasmonate ZIM domain (JAZ) repressors (Figure 1). Because FMO1 negatively regulates root colonization, *WRKY18* and *WRKY40* could negatively regulate *FMO1* to allow a moderate level of colonization [35].

3.3.2. PR Proteins

Pathogenesis-related proteins (PRs) are a structurally diverse group of plant proteins that are induced by various types of pathogens. They are widely distributed in host plants in trace amounts, but are produced in much higher concentration following pathogen attack or stress conditions [136]. PR proteins impede pathogen invasion but also helps in growth and metabolism of the host plants. The PR proteins are grouped according to their properties and functions, and include β-1,3-glucanases, endochitinases, proteinases, proteinase inhibitors, peroxidases, RNases, inhibitors of pathogen hydrolases, and others [137]. Chitinases and β-1,3-glucanases are the major hydrolytic enzymes abundant in plants after fungal pathogen infection [138]. An earlier report showed that cucumber roots induced the activity of peroxidase, β-1,3-glucanase and chitinase, which are apparently of plant origin, 72 h post-inoculation with *T. harzianum* [13], suggesting that *Trichoderma* association could reduce disease through activation of both enzymes by hydrolyzing the main constituents of the structural barrier of pathogenic cell wall fungi.

Likewise, induction of *PR* gene expression is also essential for the development of induced resistance and can require the molecules SA or JA/ET. In *Arabidopsis PR-1* that inhibits fungal growth, *PR2* also called β-1,3-glucanase and *PR-5* are considered to be markers for SAR, while *PR-3* (chitinase), *PR-4* (chitinase) and *PR-12* (plant defensin) are used as markers for JA pathway. Transcriptomic analyses have shown the expression of *PR* genes in response to *Trichoderma* spp. (Table 2). The rhizosphere colonization by *Trichoderma* spp. can support the transcription of some defense-related genes for a relatively

long period [139,140]. This effect is particularly strong for those inducible by SA (Table 2), suggesting that the long-term response to *Trichoderma* in plants may involve SA signaling.

Table 1. Expression of *WRKY* genes up-regulated by *Trichoderma* species.

Signaling Pathways Related	Gene	Host Plant (Full Name in the Legend)	*Trichoderma* Specie or Elicitor	Time after Inoculation	Reference
JA/abiotic stress	*WRKY33*	*A. thaliana*	*T. atroviride*	96–144 h	[134]
			T. asperelloides T203	9–24 h	[35]
		L. japonicus	Hydrophobin HYTOL from *T. longibrachiatum*	2 h	[52]
		P. vulgaris	*T. velutinum* T028	45 days	[115]
		S. lycopersicum	*T. erinaceum*	24–48 h	[141]
JA/ET	*WRKY8*	*A. thaliana*	*T. atroviride*	24–48 h	[134]
			T. asperelloides T203	24–48 h	[35]
	WRKY38	*A. thaliana*	*T. atroviride*	96 h	[134]
	WRKY42			96–144 h	
	WRKY60			72–144 h	
	WRKY41	*A. thaliana*	*T. asperelloides* T203	9–24 h	[35]
	WRKY53			24 h	
	WRKY55			24 h	
	WRKY18			9–24 h	
	WRKY60			9–24 h	
	WRKY40			9–48 h	
	WRKY1	*V. vinifera*	*T. harzianum* T39	4 days	[142]
	WRKY-C10 (*WRKY transcription factor 6*)	*V. vinifera*	*T. harzianum* T39	4 days	[142]
Negatively regulated by JA/ET. Represses plant basal defense mechanisms	*WRKY48*	*A. thaliana*	*T. asperelloides* T203	9–24 h	[35]
SA	*WRKY30*	*A. thaliana*	*T. asperelloides* T203	9 h	[35]
	WRKY54			9 h	
	WRKY15			9–24 h	
	WRKY46			9–24 h	
	WRKY70			48 h	
	WRKY54	*A. thaliana*	*T. atroviride*	144 h	[134]
	WRKY70 *			144 h	
Involved in plant defense	*WRKY37*	*S. lycopersicum*	*T. erinaceum*	24–48 h	[141]

WRKY70 is an Arabidopsis gene that is upregulated by two different strains of Trichoderma: *T. asperelloides* and *T. atroviride*. *Arabidopsis thaliana*, *Lotus japonicus*, *Phaseolus vulgaris*, *Solanum lycopersicum*, *Vitis vinifera*.

Table 2. Induction of *Pathogenesis Related (PR)* genes expression by *Trichoderma* species.

Marker for	Gene	Protein Function	Host Plant (Full Name in the Legend)	*Trichoderma* Specie	Time after Inoculation	References
JA/ET	*PR-3*	Chitinase Class 1. Hydrolytic enzymes that disrupt mycelial cell wall Antifungal properties	*A. thaliana*	*T. asperelloides* T203	24 h	[35]
			O. sativa	*T. harzianum*; *T.erinaceum*; *T. atriviride*; *T. hebeiensis*; *T. parareesei*; *T. longibrachiatum*; *T. resei*	NR *	[8]
			S. lycopersicum	*T. erinaceum*	24–48 h	[141]
	Acidic endochitinase 3 (Chit3)	Chitinases	*V. vinifera*	*T. harzianum* T39	4 days	[142]
	PR-4	Basic Chitinases	*A. thaliana*	*T. asperelloides* T203	24–48 h	[35]
	PR-P2	It is a pathogenesis related 4 (*PR4*) gene	*S. lycopersicum*	*T. atroviride*; *T. harzianum*	2 months	[139]
	PDF1	Plant defensin. Membrane permeabilizing functions.	*A. thaliana*	*T. asperelloides* T203	24 h	[35]
	PDF1.2				24 h	[35]
	PDF1.2c				24 h	[35]
	PDF1.2		*S. lycopersicum* cv. Oogata-fukuju	*T. virens*	4–24 h	[67]
	Defensin		*O. sativa*	*T. harzianum*; *T.erinaceum*; *T. atriviride*; *T. hebeiensis*; *T. parareesei*; *T. longibrachiatum*; *T. resei*	NR *	[8]
SA	*PR-1*	Antimicrobial function and defense signal amplification.	*A. thaliana*	*T. virens*; *T. atroviride*;	6–8 days	[129]
				T. hamatum T382	48–72 h	[96]
			S. lycopersicum	*T. atroviride*; *T. harzianum*	2 months	[139]
			S. lycopersicum cv. Oogata-fukuju	*T. virens*	4–24 h	[67]
	PR-2	Beta-1,3-endoglucanase. Hydrolytic enzymes that disrupt mycelial cell wall	*A. thaliana*	*T. hamatum* T382	48–72 h	[96]
			S. lycopersicum	*T. erinaceum*	24–48 h	[141]
	β-1,4-glucanase	Hydrolytic enzyme that disrupts mycelial cell wall	*C. sativus*	*T. asperellum*	48 h	[143]
	PR-5	Osmotins. Membrane permeabilizing proteins.	*A. thaliana*	*T. hamatum* T382	48–72 h	[96]
				T. asperelloides T203	24 h	[35]
			S. lycopersicum	*T. hamatum*	5 weeks	[140]
	OSM2	*Trichoderma*-induced osmotin 2	*V. vinifera*	*T. harzianum* T39	4 days	[142]

* NR = Not reported. *Arabidopsis thaliana*, *Oryza sativa*, *Solanum lycopersicum*, *Vitis vinifera*, *Cucumis sativus*.

3.3.3. Other Defense Gene Markers

The expression of *PR* genes can be transitory, but strongly potentiates the expression of defense-related proteins when plants are affected with biotic stress. Proteins encoded by resistance genes (*R*) are found among them. The R proteins recognize effectors from beneficial and pathogenic microorganisms to activate a stronger defense. The *HR4* gene that codifies an R protein is induced 96 h after of the *Arabidopsis–T. atroviride* interaction, suggesting the fungus is activating the recognition system and promoting a beneficial interaction establishment in the plant [130], however, little is known about *R* genes in beneficial interactions.

Additionally, there is evidence of a link between the accumulation of the phytohormones and changes in the expression of marker genes, which have been identified by analysing their expression patterns after exogenous application of single or combined phytohormone solutions [144]. The evidence has demonstrated that *Trichoderma* spp. can simultaneously or separately induce ISR and SAR associated with the biosytnthesis of SA, JA and ET according with the induction of the expression of specific resistance marker genes, which are summarized in Table 3.

Table 3. Expression of gene markers positively regulated by *Trichoderma* species.

Marker for	Gene	Protein Function	Host Plant (Full Name in the Legend)	*Trichoderma* Specie	Time after Inoculation	Reference
JA/ET	*Lox1*	Lipoxygenase enzyme involved in JA synthesis	*C. sativus*	*T. asperellum*	24 h	[61]
			A. thaliana	*T. harzanium*	72 h	[65]
			A. thaliana	*T. asperelloides* T203	24 h	[35]
			S. lycopersicum	*T. parareesei*	6 days	[145]
	Lox2		*A. thaliana*	*T. virens*, *T. atroviride*	8 days	[129]
	Lox3		*A. thaliana*	*T. asperelloides* T203	24 h	[35]
	Lox4		*A. thaliana*	*T. asperelloides* T203	24 h	[35]
	LoxA		*S. lycopersicum*.	*T. atroviride*, *T. harzianum*	2 months	[139]
	HPL	Hydroperoxide lyase	*C. sativus*	*T. asperellum*	24–48 h	[146]
	hGS	Homoglutathione synthetase related with oxidative stress	*P. vulgaris*	*T. velutinum* T028	45 days	[115]
ET	*CTR1*	Ethylene signal-associated serine/threonine protein kinase	*C. sativus*	*T. asperellum*	24 h	[143]
	ETR1					
	EIN2	Key component in ethylene signaling	*A. thaliana*	*T. asperelloides* T203	48 h	[35]
	EIN4					
	ERF-A2	Ethylene-responsive transcription factor	*S. lycopersicum*	*T. parareesei*, *T. asperellum*, *T. harzianum*	4 weeks	[147]
	CH5b	Endochitinase precursor related to ethylene signaling	*P. vulgaris*	*T. velutinum* T028	45 days	[115]
SA	*PAL1*	Phenylalanine and histidene ammonia-lyase. Enzyme involved in the production of antimicrobial compounds	*C. sativus*	*T. asperellum*	24 h	[143,146]
			A. thaliana	*T. asperelloides* T203	9–24 h	[35]
			O. sativa	*T. harzianum*, *T.erinaceum*, *T. atriviride*, *T. hebeiensis*, *T. parareesei*, *T. longibrachiatum*, *T. resei*	NR *	[8]
	PAL2		*A. thaliana*	*T. asperelloides* T203	24 h	[35]
	ICS1	Isochorismate synthase is involved in SA biosynthesis	*A. thaliana*	*T. harzanium*	72 h	[65]
	Cals	Callose synthase, involved in callose biosynthesis	*A. thaliana*	*T. harzanium*	72 h	[65]

* NR = Not reported. *Cucumis sativus*, *Arabidopsis thaliana*, *Solanum lycopersicum*, *Phaseolus vulgaris*, *Oryza sativa*.

3.4. Induction of Antioxidant Enzyme Activity Is Modulated by Trichoderma spp.

As noted before, one of the common responses under stress conditions is the generation of ROS. Overproduction of ROS could result in damage to macromolecules such as lipids,

proteins and DNA, via oxidation, and in severe cases, leads to cell death. So it is crucial to overcome these effects either by enhancing the intrinsic antioxidant defense or by repairing the damage [148].

Stress-induced ROS accumulation can be counteracted by plant antioxidative defense that consist of enzymatic or nonenzymatic systems. Superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), peroxidases (POD) and glutathione peroxidase (GPX) are the main enzymatic scavengers of superoxide (O_2^-) and hydrogen peroxide (H_2O_2) [149], while glutathione (GSH) and ascorbic acid (ASA) are the major non-enzymatic antioxidants that, among other vital functions, maintain cellular redox homeostasis [150]. Keeping ASA and GSH in reduced form is critical for redox homeostasis and cellular vitality [151]. The activity of the enzymes that regenerate these molecules is correlated with resistance to abiotic stresses. These enzymes include glutathione reductase (GR) (which regenerates oxidized GSH), monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR), which regenerate ASA from monodehydroascorbate (MDHA) and dehydroascorbate (DHA) [149].

Recent literature has revealed that *Trichoderma* spp. reduce the negative effects of plants stressed with biotic and abiotic stimuli through the modulation of the ROS by inducing antioxidant enzymes [24,152,153]. For instance, in the presence of *T. harzianum* T22, the ratios of reduced to oxidized forms of the molecules for ascorbate and glutathione, and the activity of SOD, APX, MDHAR, DHAR and GR in tomato seedlings are higher than non-inoculated plants. This indicates that *T. harzianum* T22 enhances systems of ROS scavenging and redox maintenance [151]. Also, *T. erinaceum* bioprimed tomato plants increase the activities of SOD and CAT compared to a control, and T. hamatum enhances the activity of enzymes CAT, POD, APX, GR and SOD in Ocharenus baccatus [154]. Similarly, the inoculation of maize and rice seeds as well as wheat seedlings with *T. harzianum* or its metabolites extracts increases SOD and CAT antioxidant enzymes activity [155,156]. This demonstrates that the pre-treatment of biocontrol Trichoderma results in increased activities of the antioxidant enzymatic pool [141].

Trichoderma strains also increase the activity of antioxidative defense through enhanced expression of genes encoding the component enzymes [148]. Transcriptional reprogramming of the oxidative stress response may also influence *Trichoderma* spp. bio-priming to overcome oxidative damage in stressed plants. Some examples of overexpression of antioxidant-related genes induced by *Trichoderma* spp. are summarized in Table 4.

Table 4. Induction of expression of plant antioxidant genes by Trichoderma species.

Gene	Host Plant (Full Name in the Legend)	*Trichoderma* Specie or Elicitor	Time after Inoculation	Reference
CAT	*C. sativus*	*T. asperelloides* T203	24 h	[35]
CAT	*O. sativa*	*T. harzianum*; *T.erinaceum*; *T. atriviride*; *T. hebeiensis*; *T. parareesei*; *T. longibrachiatum*; *T. resei*	* NR	[8]
CAT	*T. aestivum* cv.'Yongliang 4	*T. longibrachiatum T6*	* NR	[157]
GPX	*S. lycopersicum*	*T. erinaceum*	24–48 h	[141]
POD	*T. aestivum* cv.'Yongliang 4	*T. longibrachiatum T6*	* NR	[157]
POD	*O. sativa*	*T. harzianum*; *T.erinaceum*; *T. atriviride*; *T. hebeiensis*; *T. parareesei*; *T. longibrachiatum*; *T. resei*	* NR	[8]
SOD	*O. sativa*	*T. harzianum*; *T.erinaceum*; *T. atriviride*; *T. hebeiensis*; *T. parareesei*; *T. longibrachiatum*; *T. resei*	* NR	[8]
SOD	*S. lycopersicum*	*T. erinaceum*	24–48 h	[141]
SOD	*T. aestivum* cv.'Yongliang 4	*T. longibrachiatum T6*	* NR	[157]
SOD (Mn)	*C. sativus*	*T. asperelloides* T203	24 h	[35]
SOD (Cu)	*C. sativus*	*T. asperelloides* T203	24 h	[35]

* NR = Not reported. *Cucumis sativus*, *Oryza sativa*, *Triticum aestivum*, *Solanum lycopersicum*.

SA has been widely recognized as a promoter of antioxidant defense, including CAT, SOD, and APX, as well as non-enzymatic antioxidants, to alleviate oxidative stress in plants [124,158–160], so the late increase of endogenous SA observed in bioprimed plants with *Trichoderma* spp., might be responsible for the antioxidant enzymatic mechanism pathway improving the performance of plants under stress conditions (Figure 1). Thus, growing evidence suggests that application of strains of *Trichoderma* spp. may be an ecological strategy to help plants to recover from biotic and abiotic stress-induced oxidative damage to continue the metabolic and physiological activities in a better way.

3.5. Effects of Trichoderma on Chloroplasts

Chloroplasts are key organelles of the higher plants in which photosynthesis takes place. The chloroplasts are also the major production site of defense molecules including hormones (such as SA, JA, ABA) and secondary messengers like Ca^{2+} and ROS [161].

The effect of Trichoderma interaction on chloroplast has been poorly explored. Recently, it was observed that T. asperellum and *T. harzianum* consortium at 10^8 CFU/mL concentration increased the number and size of chloroplasts in spongy parenchyma of Passiflora caerulea after 60 days [162]. These chloroplasts also showed a reduction of starch grains, which could be related to starch degradation and the translocation of monosaccharides from chloroplasts to the rest of the cell and/or to the phloem [162] (Figure 1).

Additionally, it has been proved that some Trichoderma strains enhance photosynthetic capacity compared to uninoculated controls (see [163] for review) by increasing the photosynthetic pigment content or the expression of genes regulating the biosynthesis of chlorophyll, proteins of the light-harvesting complex, or components of the Calvin cycle [164]. Chloroplasts are considered as sensors and regulators of plant responses to biotic and abiotic stresses [165]. When plants are exposed to stress, they usually lose their photosynthetic capability by an overproduction of ROS formed during excitation of chlorophyll in photosynthesis, causing an oxidative stress in chloroplasts [166]. However, it has been shown that plants inoculated with certain strains of Trichoderma and then challenged by a stress overcome the reduction of photosynthetic capability [26,39,148,167]. This might be due to the protection against ROS levels described previously, but also to the increase in the content of carotenoids detected in the interaction of some plants with *Trichoderma* spp. [164,168–171], since carotenoid pigments act as antioxidants that quench singlet oxygen and trap peroxyl radicals [172].

Since chloroplasts produce ROS during cellular stress and ROS act as promoters of programmed cell death (PCD), *Trichoderma* spp. may be preventing cell death in plants subsequently exposed to stress. Moscatiello et al. [52] demonstrated that despite the fact that HYTOL induced the expression of defense genes, it did not affect cell viability and ultrastructure of L. japonicus cells after treatment. However, other studies have reported some markers of PCD (e.g., caspase 3-like caspase protease activity and by chromatin condensation) in soybean and tobacco cells treated with metabolite mixtures from T. atroviride or xylanase, respectively [49,173].

4. Conclusions and Future Perspectives

The negative consequences of climate change on living organisms and the environment are already forcing us to search for alternative ways of reducing these catastrophic events. Eco-friendly practices for food production have been highlighted to achieve sustainability. In horticultural crops, plant biostimulants have been proposed as agronomic tools to mitigate environmental/abiotic stress effects. However, since our knowledge about the mechanism involved during plant–biostimulant interaction is currently limited, more research is needed to understand exactly what is taking place during interactions. The elucidation of the mechanisms of action will allow us to develop new methods that involve beneficial microorganisms with better performance for the solution of agricultural problems.

Trichoderma spp. induce multiple beneficial effects on plants by reducing the severity of diseases, but also by alleviating abiotic stress-induced damage in plants. These promising results are opening the door for sustainable agriculture to exploit the potential of Trichoderma in a safe way for crop plants, agroecosystems, and humans.

Further research into the molecular bases of dialogue in plant–Trichoderma interactions should predict the impact of certain species of this genus on crops or cultivars performance to ensure their effective use.

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Abbreviations

Abscisic acid (ABA); allene oxide synthase (AOS); ascorbate peroxidase (APX); catalase (CAT); cytochrome P450 family 71 polypeptide (CYP71A13); dehydroascorbate reductase (DHAR); ethylene (ET); effector-triggered immunity (ETI); flavin monoxygenase 1 (FMO1); gibberellic acid (GA); guanosine diphosphate (GDP); G-protein-coupled receptor (GPCR); glutathione peroxidase (GPX); glutathione reductase (GR); glutathione (GSH); heterotrimeric G-protein α (Gα1); hypersensitive response (HR); hydrophobin secreted by T. longibrachiatum strain MK1 (HYTOL1); induced systemic resistance (ISR); jasmonic acid (JA); jasmonate ZIM domain (JAZ); lipoxygenase 2(LOX2); microbe-associated molecular patterns (MAMPs); mitogen-activated protein kinases (MAPKs); monodehydroascorbate reductase (MDHAR); MAMP-triggered immunity (MTI); nicotinamide adenine dinucleotide phosphate (NADPH); phytoalexin deficient3 (PAD3); pathogen-associated molecular patterns (PAMPs); programmed cell death (PCD); plant-growth-promoting bacteria (PGPB); peroxidases (POD); pattern recognition receptors (PPRs); pathogenesis-related protein (PR); pattern-triggered immunity (PTI); resistance proteins (R); respiratory burst oxidase homologues (RBOHs); reactive oxygen species (ROS); salicylic acid (SA); systemic acquired resistance (SAR); tobacco SA-induced protein kinase (SIPK); superoxide dismutase (SOD); Trichoderma-induced MPK (TIPK); Trichoderma-induced systemic resistance (TISR); wounding-induced protein kinase (WIPK); transcription factors with the domain WRKYs (WRKY).

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